

Molecules and Morphology in South American Stipeae (Poaceae)

Mary E. Barkworth,¹ Mirta O. Arriaga,² James F. Smith,³ Surrey W. L. Jacobs,⁴ Jesús Valdés-Reyna,⁵ and B. Shaun Bushman⁶

¹Intermountain Herbarium, Department of Biology, 5305 Old Main Hill, Utah State University, Logan, Utah 84322-5305 U.S.A.

²Herbario, Museo Argentino de Ciencias Naturales “Bernadino Rivadavia”, Av. Angel Gallardo 470, 1405 Buenos Aires, Argentina

³Department of Biology, 1910 University Drive, Boise State University, Boise, Idaho 83725 U.S.A.

⁴National Herbarium of New South Wales, Royal Botanic Gardens, Mrs Macquaries Road, Sydney, New South Wales, Australia 2000

⁵Departamento de Botánica, Universidad Autónoma Agraria “Antonio Narro”, Buenavista, 25315 Saltillo, Coahuila, Mexico

⁶U.S.D.A. Forage and Range Research Laboratory, 6300 Old Main Hill, Logan, Utah 84322-6300 U.S.A.

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Abstract—We conducted phylogenetic analyses of molecular data (ITS, *trnH-psbA*, *trnC-trnL*, and *trnK-rps16*) for 71 species of stipoid grasses. Of these species, 30 are native to South America, seven are native to Mexico and/or the southwestern United States, 15 to other parts of North America, 12 to Eurasia and/or the Mediterranean region, and seven to Australia. The outgroup was *Glyceria declinata*, a member of the Meliceae, a tribe that is in the same clade as and possibly sister to, the Stipeae. The purpose of the study was to evaluate alternative generic treatments of the South American Stipeae, all of which are based on morphological and anatomical information. Questions of particular interest were the merits of recognizing *Amelichloa* and of including *Stipa* subgg. *Pappostipa* and *Ptilostipa* in *Jarava*. Trees obtained from separate analyses of the ITS and cpDNA data were poorly resolved. The majority rule consensus tree obtained from the combined data provided strong support for the monophyly of only two currently recognized genera, *Piptochaetium* and *Hesperostipa*. There was strong support for a lineage comprising *Amelichloa*, *Jarava* s. str., most North American species of *Achnatherum*, and most samples of *Nassella*. *Amelichloa* was included within a poorly resolved *Nassella* clade that was sister to the *Jarava* clade. *Austrostipa*, with the exception of one sample, was monophyletic and sister to the poorly supported *Achnatherum-Amelichloa-Nassella-Jarava* clade. *Stipa* subgg. *Pappostipa* formed a separate strongly supported clade if the North American samples of *S. speciosa* were excluded from consideration. None of the trees support including *S.* subgg. *Pappostipa* in *Jarava*. For *S.* subgg. *Ptilostipa* we obtained no ITS data and cpDNA data for only one species. The cpDNA data placed the species in a clade with two *Nassella* species.

Keywords—ITS, cpDNA, Grasses, Phylogeny, Poaceae, South America, Stipeae.

The Stipeae (Poaceae) include over 580 species (Barkworth, unpubl. data), most of which are characterized by having spikelets with glumes that reach or exceed the base of the lemma awns, a single floret per spikelet, and lemmas that are indurate to coriaceous and have a single, clearly demarcated terminal awn. Until 1955, the number of genera recognized was approximately 20, the largest and most widespread genus being *Stipa*, which was considered to be present on all continents except Antarctica. Nowadays, the number of genera recognized is only slightly larger, 23, but some of the generic boundaries have been substantially changed, primarily on the basis of morphological information. One consequence of these changes is that the primarily South American genus *Nassella*, with about 116 species, is now the second largest genus in the tribe. *Stipa*, which is now considered to be confined to Eurasia and Africa, is the largest genus, having around 140 species.

Approximately 225 species of Stipeae grow in South America (Soreng et al. 2003). Until 1950, they were usually placed in five genera: *Stipa*, *Piptochaetium*, *Nassella*, *Ortachne*, and *Aciachne*. Within the South American species of *Stipa*, five major groups were recognized: subgg. *Jarava*, *Pappostipa*, *Ptilostipa*, and *Stephanostipa* plus the informal group Obtusae (Parodi 1946). In the last three decades, *Nassella* has been expanded to include *Stipa* subgg. *Stephanostipa* (Barkworth 1990; Barkworth and Torres 2001), the Obtusae have been recognized as a genus, *Anatherostipa* (Peñailillo 1996; Torres 1997), and *Jarava* has been expanded to include *Stipa* subgg. *Pappostipa* and *Ptilostipa* plus some South American species of *Stipa* with panicles concealed in their basal leaf sheaths (Peñailillo 2002). Arriaga and Barkworth (2006) transferred

the species of *Jarava* with concealed panicles to a new genus, *Amelichloa*. Thus, when we initiated this study, seven genera were recognized as native to South America: *Piptochaetium*, *Nassella*, *Ortachne*, *Aciachne*, *Jarava* (including *Stipa* subgg. *Pappostipa* and *Ptilostipa*), *Anatherostipa*, and *Amelichloa*. Each of these was originally circumscribed morphologically (Table 1); some have also been supported by anatomical data (Parodi 1946; Parodi and Freier 1945; Thomasson 1978, 1979; Barkworth 1981, 1982, 1990; Arriaga 1983; Barkworth and Everett 1987; Barkworth and Torres 2001; Arriaga and Barkworth 2006).

There are few published phylogenetic studies of the Stipeae. Jacobs et al. (2000, 2007) used the ITS region to examine relationships among a wide range of stipoid species. Their 2007 study included 11 genera and 96 species, among which were several American species, but none of *Aciachne*, *Amelichloa*, *Ortachne*, or *Stipa* subgg. *Ptilostipa*. They found *Piptochaetium* to be sister to North American species of *Piptatherum* but their results did not support the monophyly of *Nassella* or *Jarava*, nor the transfer of *Stipa* subgg. *Pappostipa* to *Jarava*. They noted that, because of low number of non-Australian species sampled, their conclusions with respect to such species had to be regarded as tentative.

Cialdella et al. (2007) examined the relationships among 53 primarily South American species using both morphological and cpDNA data. Their cpDNA data revealed two clades. One clade, having Bremer Support = 7, showed *Stipa* (*Pappostipa*) *vaginata* [= *Jarava vaginata* (Phil.) Peñailillo] as sister to an unresolved clade comprising *Piptochaetium* and *Aciachne* + *Anatherostipa*. The other clade, which had Bremer Support of 8, included *Jarava* s. str. and *Stipa* subgg. *Ptilostipa* in a poorly

TABLE 1. Distinctive morphological features of the South American supraspecific taxa examined and the changes that have occurred in their treatment. Numbers following the names indicate the approximate number of species in the taxon.

Taxon (species)	Distinctive morphological characteristics and, where applicable, alternative treatments currently in use
<i>Aciachne</i> (3)	Cushion plants; leaves stiff, sharply pointed; glumes shorter than floret, glumes and lemmas indurate; awn not or weakly demarcated; paleas as long as lemmas, glabrous, veined, tips pinched.
<i>Anatherostipa</i> (12)	Cespitose plants; prophyllum 2–5 cm, 2-awned; fundamental cells of lemma epidermis with thick, sinuous walls; paleas subequal to lemmas, veined, often with hairs. <i>Changes in treatment</i> : Originally described as the informal group "Obtusae" (Parodi 1946); formally recognized as a genus by Peñailillo (1996).
<i>Ortachne</i> (3)	Glumes shorter than floret; awn poorly demarcated; leaves filiform, not stiff; paleas subequal to lemmas, veined, sometimes with hairs.
<i>Amelichloa</i> (5)	Leaves sharply pointed; caryopses with "ribs"; paleas subequal to lemmas, hairy, veined. <i>Changes in treatment</i> : Has been included in both <i>Achnatherum</i> and <i>Jarava</i> (Barkworth 1993; Jacobs et al. 1995; Peñailillo 2002; Soreng and Valdés-Reyna 2003).
<i>Jarava</i> s.str. (25)	Florets 2.5–6 mm, often with 2–3 mm long, strongly divergent hairs near the tip; calluses 0.2–0.3 mm; awns glabrous or shortly strigose; paleas 1/2–2/3 the length of the lemmas, usually glabrous, veins absent or 1/2–2/3 the length of palea and inconspicuous. <i>Changes in treatment</i> : Peñailillo (2002) included <i>Stipa</i> subgg. <i>Pappostipa</i> and <i>Ptilostipa</i> and <i>Amelichloa</i> in <i>Jarava</i> .
<i>Stipa</i> subg. <i>Pappostipa</i> (23)	Basal branching of culms intravaginal; not branched above the base; florets 5–18 mm, lemmas without divergent hairs distally; calluses 0.5–3 mm long; awns long-hairy on the first segment only; paleas usually about as long as the lemma, veins reaching almost to the tip. <i>Changes in treatment</i> : Included in <i>Jarava</i> by Peñailillo (2002); raised to generic status by Romaschenko et al. (2008; note added in proof).
<i>Stipa</i> subg. <i>Ptilostipa</i> (5)	Basal branching of culms often extravaginal, upper nodes often with branches; florets 3–12 mm, lemmas without divergent hairs distally; calluses 0.4–2 mm long; awns long-hairy throughout or the basal portion glabrous; paleas usually almost as long as the lemma, hairy, veins reaching almost to the tip, conspicuous. <i>Changes in treatment</i> : Included in <i>Jarava</i> by Peñailillo (2002).
<i>Nassella</i> (116)	Lemma margins strongly overlapping at maturity; awns not pilose; paleas less than half as long as lemmas, glabrous, without veins. <i>Changes in treatment</i> : Expanded to include <i>Stipa</i> subg. <i>Stephanostipa</i> (Barkworth 1990; Barkworth and Torres 2001).
<i>Piptochaetium</i> (36)	Lemmas indurate, golden-brown, surface striate; paleas sulcate, longer than lemmas, glabrous, veined, sides truncate, tip "pinched". <i>Changes in treatment</i> : Expanded in 1944 to include <i>Stipa</i> subg. <i>Podopogon</i> (Parodi 1944).

resolved clade that included all the species of *Nassella* plus the only species of *Piptatherum* in the study, *P. miliaceum*. None of the branches had jackknife support >50%. Combining morphological and molecular data enabled Cialdella et al. to recover most genera, but not *Jarava* s. lat.

Two phylogenetic studies that have been presented as posters have abstracts available on the Web. In each case, the authors kindly made a copy of their poster available to Barkworth. Hames et al. (2006), using both ITS and cpDNA information, found each of *Piptochaetium*, *Aciachne* + *Anatherostipa*, *Piptochaetium* + *Aciachne* + *Anatherostipa*, and *Nassella* + *Jarava* s. str. + *Stipa* subg. *Ptilostipa* to be monophyletic with bootstrap support >70%. The only species of *Stipa* subg. *Pappostipa* in their study was excluded from the *Nassella* + *Jarava* + *Ptilostipa* clade. Romaschenko et al. (2007) examined the ITS region of 150 species and 23 genera. They found *Stipa* subg. *Pappostipa* to be monophyletic (bootstrap support 75%) but not closely related to *Jarava* s. str.

Our primary goal in this study was to evaluate alternative generic treatments for the South American Stipeae, with particular emphasis on *Amelichloa* and *Jarava* s. lat., by conducting phylogenetic analyses of nuclear and chloroplast sequences for representative taxa. In selecting species for this study, we focused on American species, particularly South American species, because it is probable that the closest relatives of *Amelichloa* are American. We included some Eurasian and Australian taxa so that the results of our study could more easily be compared to the other studies. We examined the ITS region because it is the nuclear region examined in other molecular studies of the tribe (Jacobs et al. 2000, 2007; Hames et al. 2006; Romaschenko et al. 2007) and grasses in general (Hodkinson et al. 2007). We added three chloroplast DNA regions to provide additional insight into the maternal phylogeny. This is important because the lowest known chromosome number in the Stipeae is $2n = 10$ (Curto and Hendersson 1988); most frequent numbers are in the range 22–44 (Barkworth, unpubl. data). These numbers suggest that

many, and possibly all, the species are polyploid, in which case reticulation may have played an important role in their evolution as postulated by Johnson for *Oryzopsis* and *Piptatherum* (Johnson 1945a).

MATERIALS AND METHODS

Most of the plant material used was obtained from herbarium specimens that had been collected in the wild. Material of *Celtica gigantea*, *Ampelodesmos mauritanicus*, and *Austrostipa ramossissima* came from plants obtained from Digging Dog Nursery, California, and grown in Logan, Utah; the samples of *Piptochaetium avenacioides* and *P. avenaceum* were collected into silica gel for this study.

The 253 specimens sampled represented 16 species-groups and 119 species. Most of the species-groups are known as genera, *Stipa* subgg. *Pappostipa* and *Ptilostipa* being exceptions. For convenience, we refer to these two subgenera as *Pappostipa* and *Ptilostipa*, respectively, except when giving a binomial. We ignored the infrageneric groupings of the European species of *Stipa* sampled because so few were included in the study. *Glyceria declinata*, a member of the Meliceae, was used as the outgroup, the Meliceae being in the same clade as, and possibly sister to, the Stipeae (Grass Phylogeny Working Group 2001; Salamin et al. 2002).

Most of the South American samples were taken from specimens identified by Dr. Amelia Torres (LP), the North American specimens and the living plant material by Barkworth, the Mexican specimens by Valdés-Reyna, the Australian specimens by Jacobs, the European specimens by Dr. Francisco Vazquez (HSS), and *Ptilagrostis pelliitii* by Acad. N.N. Tsvelev (LE). Voucher and distribution information is presented in the appendix for those accessions that yielded sequences that could be used in this study. Distribution information for the Eurasian taxa was obtained from GRIN (2007+).

DNA Extraction, PCR Amplification, Purification, and Sequencing—DNA was extracted from herbarium tissue using the Qiagen DNeasy 96 plant kit (Valencia, California) according to the manufacturer's instructions. Three chloroplast intergenic regions (*trnH-psbA*, *trnC-trnL*, *trnK-rps16*) and one nuclear internal transcribed spacer (ITS1 = ITS5a/2c) region were analyzed (Kress et al. 2005; Taberlet et al. 1991; White et al. 1990). Only ITS1 was used in the analyses because few of the samples could be adequately sequenced for the second region. Amplification of DNA used a Bio-Xact High-Fidelity polymerase (Bioline, Randolph, Massachusetts). Conditions for PCR were 94°C for 90 sec; followed by 35 cycles of 94°C for 30 sec, 55°C for 30 sec, and 72°C for 60 sec; with a final extension at 72°C for 7 minutes. The PCR products were purified prior to sequencing with ExelaPure 96-well plates (Edge Biosystems, Gaithers-

burg, Maryland). Sequencing reactions used BigDye v3.1 (Applied Biosystems, Foster City, California), and dye terminator removal was done with Performa v3 96-well plates (Edge Biosystems, Gaithersburg, Maryland). The sequences have been submitted to Genbank (see Appendix).

Sequence Alignment and Analyses—The sequences for both the ITS and cpDNA data were aligned using Sequencher software (Gene Codes, Ann Arbor, Michigan). Insertions or deletions (indels) were coded using the “simple” method proposed by Simmons and Ochoterena (2000). For analysis, the three cpDNA regions were combined into one contiguous sequence. For both data sets, identical sequences were combined and phylogenetic analyses conducted on the unique sequences. A combined cpDNA - ITS dataset was created from samples that yielded both cpDNA and ITS sequences for which there was no evident discrepancy between their positions on the two trees. The resulting data set included 103 individuals. Samples that were excluded from the combined data set because of discrepancies between their locations on the two trees were *Achnatherum stillmanii*, *Austrostipa stipoides*, *Jarava plumosa* 5, *Nassella trichotoma* 2, and *Stipa (Pappostipa) speciosa* 1, 2, 4, 5, 7, 9, 10, 11. The ITS and cpDNA data were analyzed separately and together.

The data were analyzed using PAUP* 4.0b10 (Swofford 2002) for maximum parsimony (MP) and bootstrap (BS) support (Felsenstein 1985). Prior to combining ITS and cpDNA sequences an ILD test (Farris et al. 1994) was run, implemented as the partition homogeneity test (PHT) of PAUP*. As this test is often sensitive to low signal in some of the partitions (Reeves et al. 2001; Yoder et al. 2001), separate maximum parsimony bootstrap analyses were run for each of the partitions (cpDNA and ITS) to search for areas of hard incongruence (Seelanan et al. 1997). Indels were treated as missing data. For the MP analyses, the data were analyzed using the search option of Olmstead and Palmer (1994) where five searches are performed using 1,000 replicates with nearest neighbor interchange and MulTrees Off saving all shortest trees. The results of each of these searches were then used as the starting trees for a search using tree-bisection reconnection (TBR) and MulTrees on. The shortest trees from all searches were combined and a strict consensus was created. Bootstrap replicates were performed with 100 searches with 10 random replicates using full heuristic search with TBR and MulTrees on.

Modeltest version 3.7 (Posada and Crandall 1998) was used to determine the model that best fit the data for Bayesian inference (BI). Both the likelihood ratio test (LRT) and Akaike information content criteria (AIC) models were examined separately. Modeltest was run separately for the ITS and cpDNA data sets and for the combined dataset. Results of these tests were used as priors in BI with a complex (different model for each partition; cpDNA and ITS) or simple model for the combined data as well as for ITS and cpDNA separately. The analyses shown were run using only complete data sets. Bayesian inference employed MRBAYES 3.0B4 (Huelsenbeck and Ronquist 2001). Analyses were run using two million generations, saving trees every 100 generations with a burn-in of 25,000 generations. Analyses were repeated for each model used with the order of taxa scrambled between the two runs. Modeltest selected the K81uf + I + G (I = 0.6050, G = 0.9848) model for the cpDNA alone, TrN + I + G (I = 0.3462, G = 0.6785) and TIM + I + G (I = 0.3482, G = 0.6794) models for ITS alone, based on hLRT and AIC, respectively, and GTR + I + G (I = 0.6190, G = 0.6665) for the combined data (both hLRT and AIC). The separate BI runs for each of the data sets using either different models (ITS alone) or randomized taxon order (all three data sets) produced nearly congruent majority-rule consensus trees that differed primarily in having slightly different posterior probabilities. Nevertheless, some parts of the tree were not well-supported and differed between runs. The weak branches that differed between runs, as well as differences between ITS and cpDNA when run separately, are indicated on the trees.

The matrices and trees are available on TreeBASE (study number of S2019).

RESULTS

Molecular Perspective—Of the 253 herbarium specimens sampled, 129 yielded useful sequence data. The 129 samples represented 88 taxa, 71 of which were different species. Of these species, 30 are native to South America, two of which have disjunct populations in southern North America, seven are native in northern Mexico or the southern United States, and 15 in other parts of North America. Of the remainder, 12 were from Eurasia or the Mediterranean region, and seven from Australia. Voucher information for the samples is provided in the appendix.

The 129 samples yielded 102 cpDNA haplotypes and 91 different ITS sequences. BLAST analysis demonstrated that none of the sequences corresponded to fungal sequences. Combining the three cpDNA regions, there were 2,156 characters of which 1,721 were constant, 229 variable but uninformative, and 206 both variable and parsimoniously informative. Of the 363 ITS characters, 208 were constant, 44 variable but uninformative, and 111 variable and parsimony informative. The ITS sequence traces revealed no polymorphic sites, nor were any of the peaks irregular, as has been found in other polyploid groups (Wendel et al. 1995).

The ILD indicated significant incongruence between ITS and cpDNA when all the samples were included and when the samples that fell out in markedly different portions of the cpDNA and ITS trees were excluded. These samples were *Achnatherum stillmanii*, *Austrostipa stipoides*, *Jarava plumosa* 5, *Nassella trichotoma* 2, and *Stipa (Pappostipa) speciosa* 1, 2, 4, 5, 7, 9, 10, 11. When examined separately, neither of the partitions exhibited any area of incongruence that had BS > 70 except the above list of species. Since hard incongruence was not detected (Seelanan et al. 1997), we combined data with the species listed above excluded (Seelanan et al. 1997; Soltis et al. 1998; Smith 2000). Maximum parsimony analysis of cpDNA and ITS sequences alone resulted in 217,000 trees of 566 steps each, CI = 0.505, RI = 0.896 (Fig. 1), and 235,200 trees of 423 steps each, CI = 0.427, RI = 0.789 (Fig. 2), respectively. The combined data resulted in 215,900 trees of 949 steps each, CI = 0.443, RI = 0.824 (Fig. 3a, b).

The tree shown for the combined data (Fig. 3a, b) is a majority-rule tree based on the combined data analysis with a different model for ITS and cpDNA as selected by Modeltest using LRT. Duplicate runs with altered taxon order and with models selected using AIC differed only slightly in posterior probability values. Two minor differences were recovered with trees using a single model for all data. The clade marked with an asterisk is not supported with the model selected by AIC and the dotted line shows the relationship of *Ptilagrostis porteri* with the model selected by LRT.

Strongly Supported Clades—Hall and Salipante (2007b), in a retraction of their earlier paper (Hall and Salipante 2007a) reported that, using sequences obtained from an evolutionary model that included indels and allowed for both mutations and selection, there is a strong correlation between the validity of a clade and measures of clade confidence such as posterior probabilities and bootstrap support. Table 2 presents a summary of the strongly supported clades (ssc; PP > 95 and BS > 70) on each of the trees. The cpDNA sequences yielded more ssc than the ITS sequences. Combining sequences from specimens that were placed in similar locations on the two trees yielded the greatest number of ssc.

The largest ssc on the cpDNA tree included most North American species of *Achnatherum*, most North American accessions of *Stipa (Pappostipa) speciosa*, *Amelichloa*, *Nassella*, *Jarava*, *Ptilagrostis pelliottii*, the Eurasian species of *Achnatherum*, some species of *Piptatherum*, *Stipa parviflora*, and most species of *Austrostipa*. It did not include the South American species of *Pappostipa*. There is a somewhat similar, but more weakly supported (PP = 94, BS = 61) clade on the ITS tree. It differs in excluding two southern North American species of *Achnatherum* and the North American species of *S. (Pappostipa) speciosa* that were placed, with very weak support (PP < 50, BS < 50), in a clade with the South American members of *Pappostipa* and the Mediterranean *Stipa parviflora*.

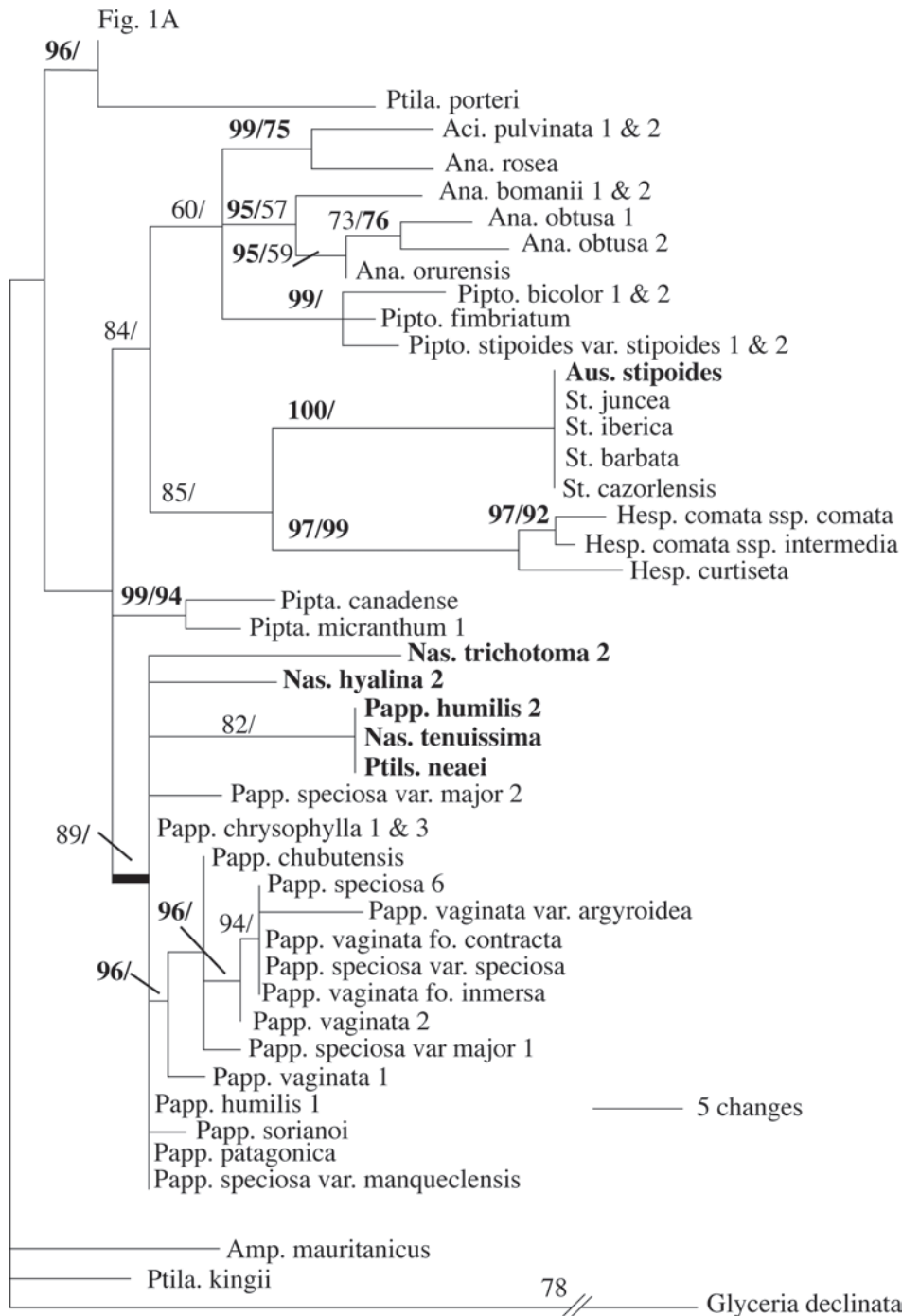


FIG. 1. Majority Rule tree of cpDNA sequences using Bayesian Inference and a model of K81uf + I + G. Numbers along branches are posterior probabilities before the slash, BS values >50 after. Clades that collapse in the strict consensus of all MP trees are marked with a C after the slash. Taxa in bold are accessions for which either only cpDNA was available or position differs compared to ITS (Fig. 2). Branch in bold represents discrepant clade compared to ITS (Fig. 2). Ach - *Achnatherum*, Aci. - *Aciachne*, Ame. - *Amelichloa*, Amp. - *Ampelodesmus*, Ana. - *Anatherostipa*, Aus. - *Austrostipa*, Jar. - *Jarava*, Hesp. - *Hesperostipa*, Nas. - *Nassella*, Papp. - *Stipa* subg. *Pappostipa* Pipto. - *Piptatherum*, Pipto. - *Piptochaetium*, Ptila. - *Ptilagrostis*, Ptils. - *Stipa* subg. *Ptilostipa*, St. - *Stipa*.

The combined tree places most North American species of *Achnatherum*, *Amelichloa*, *Nassella*, and *Jarava* in a single ssc within the above clade. It is weakly supported (PP = 88, BS < 50) as sister to *Austrostipa*. Within this large ssc, *Ach. occidentale* and *Ach. nelsonii* form an ssc, supporting Maze's (1962) recommendation that the two taxa be treated as a single species. *Amelichloa* also forms an ssc, but is paraphyletic with respect to *Nassella*. There are ssc within *Nassella* but their relationships to each other and *Amelichloa* are not resolved.

Jarava forms a clade sister to the *Amelichloa* - *Nassella* clade, but with PP = 98 and BS < 50.

The South American representatives of *Pappostipa* plus one of the North American specimens of *S. speciosa* formed an ssc on the combined tree. Within this clade, the North American specimen formed an ssc with *Stipa vaginata* var. *argyroides* on both the ITS and combined tree. On the cpDNA tree, this North American specimen is shown as having an identical haplotype to three other *S. vaginata* specimens and the South

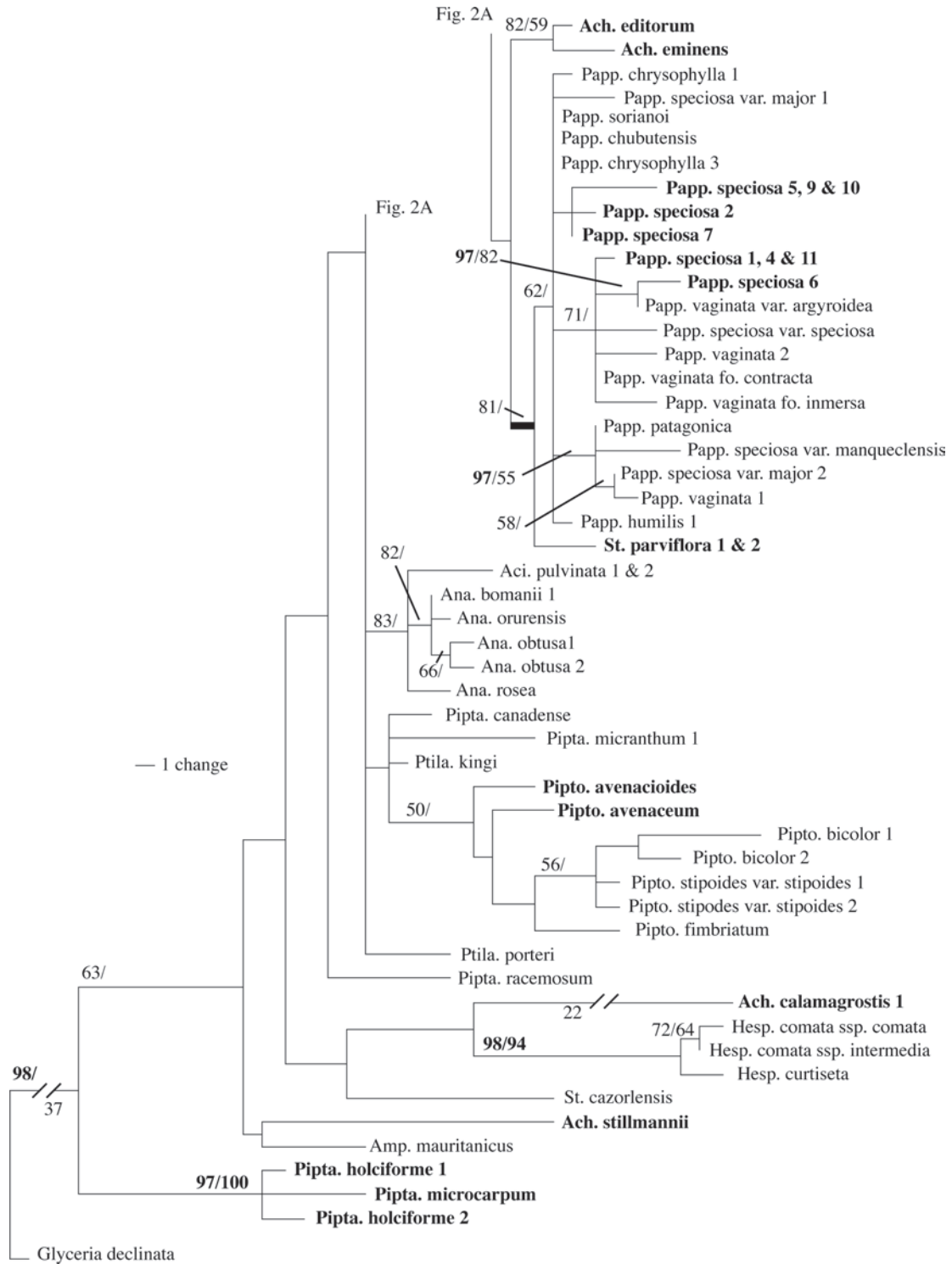
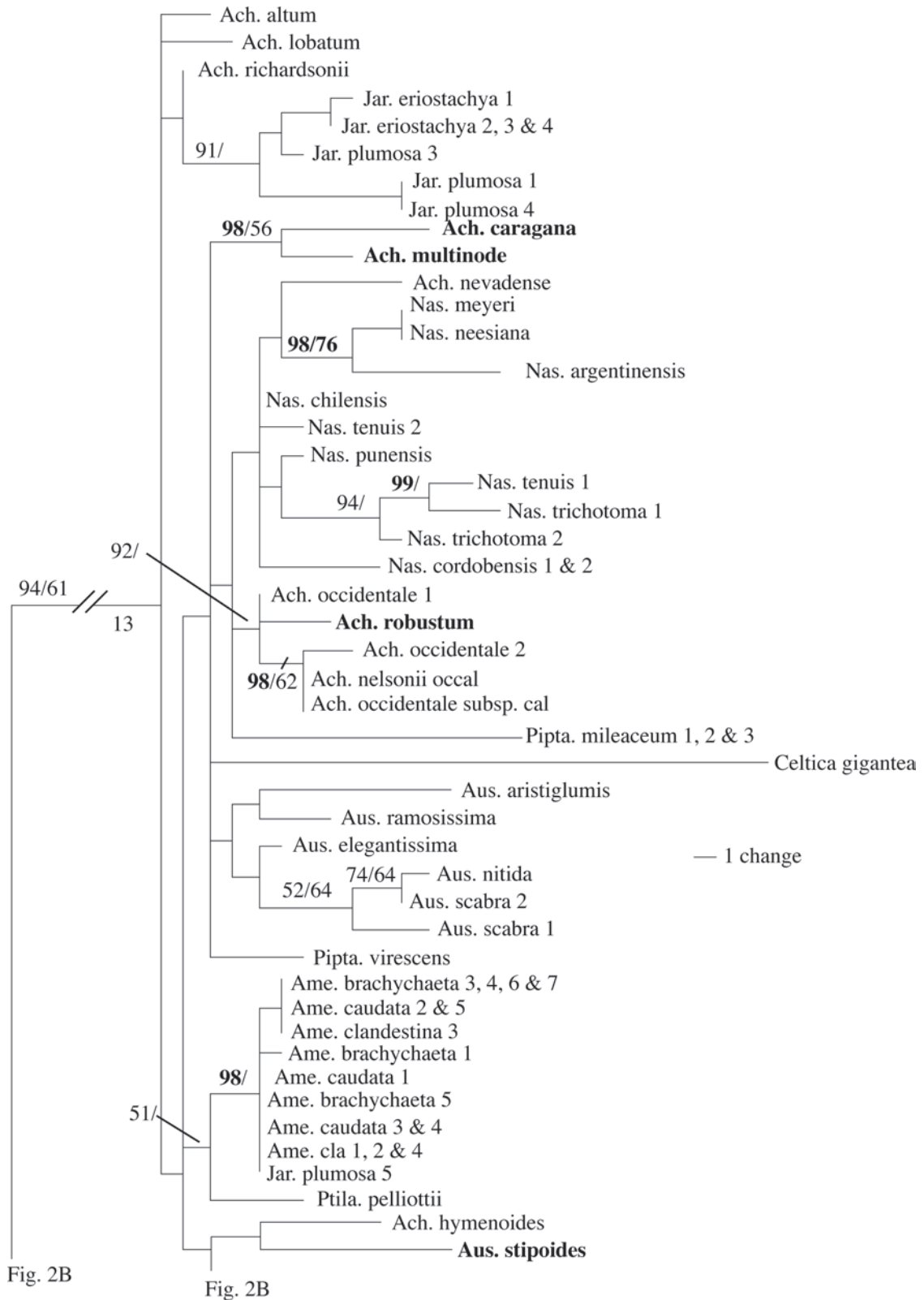


FIG. 2. Majority Rule tree of ITS sequences using Bayesian Inference and a model of TIM + I + G. Numbers along branches are posterior probabilities before the slash, BS values >50 after. Clades that collapse in the strict consensus of all MP trees are marked with a C after the slash. Taxa in bold are accessions for which either only ITS was available or position differs compared to cpDNA (Fig. 1). Branch in bold represents discrepant clade compared to cpDNA (Fig. 1). *Achnatherum*, Aci. - *Aciachne*, Ame. - *Amelichloa*, Amp. - *Ampelodesmus*, Ana. - *Anatherostipa*, Aus. - *Austrostipa*, Jar. - *Jarava*, Hesp. - *Hesperostipa*, Nas. - *Nassella*, Papp. - *Stipa* subg. *Pappostipa* Pipta. - *Piptatherum*, Pipto. *Piptochaetium*, Ptila. - *Ptilagrostis*, St. - *Stipa*.

American *S. speciosa* var. *speciosa*. *Stipa vaginata* differs from *S. speciosa* in its lemma vestiture and, usually, in having a shorter anthoecium and awn (Nicora 1978). The North American specimen has the lemma vestiture of *S. speciosa* but anthoecium and awn lengths that are more typical of *S. vaginata*, although not outside the range for *S. speciosa*. We con-

clude, therefore, that it is a somewhat atypical example of *S. speciosa*.

Hesperostipa forms an ssc on all three trees, the only currently recognized taxon to do so. *Piptochaetium* does so on the combined tree, but not on either the cpDNA or ITS tree. *Aciachne pulvinata* and *Anatherostipa rosea* form an ssc on both



cp and combined trees, with the other species of *Anatherostipa* in the study forming a separate ssc on the combined tree.

With the exception of *Austrostipa stipoides*, *Austrostipa* formed an ssc on the cpDNA and combined trees. *Austrostipa stipoides* was excluded from the combined analysis because the position based on the cpDNA and ITS data sets was

strikingly different. Jacobs et al. (2007), who examined only ITS data and included a high proportion of *Austrostipa* taxa, also found *Austrostipa* to be monophyletic with the exception of a sample from a duplicate of the specimen that we used.

Conflicts Within and Between the cpDNA and ITS Trees—As noted earlier, the location of *Achnatherum stillmanii*, *Aus-*

TABLE 2. Strongly supported clades (clades with Posterior Probability >95 and Bootstrap >70). Samples excluded from the combined tree because of strong conflict between their cpDNA and ITS data were *Achnatherum stillmanii*, *Austrostipa stipoides*, *Jarava plumosa* 5, *Nassella trichotoma* 2, and *Stipa* (*Pappostipa*) *speciosa* 1, 2, 4, 5, 7, 9, 10, 11. NA – North American; SA – South America.

cpDNA (Fig. 1a, b)	ITS (Fig. 2a, b)	Combined (Majority Rule) (Fig. 3a, b)
NA <i>Achnatherum</i> (exc. <i>A. stillmanii</i>) & NA <i>Stipa</i> (<i>Pappostipa</i>) <i>speciosa</i> (exc. 6) & <i>Nassella</i> & <i>Amelichloa</i> & <i>Jarava</i> & <i>Ptilagrostis pelliottii</i> & <i>Austrostipa</i> (exc. <i>Aus. stipoides</i>) & <i>Celtica gigantea</i>		NA <i>Achnatherum</i> (exc. <i>A. robustum</i>) & <i>Amelichloa</i> & <i>Nassella</i> & <i>Jarava</i> (<i>Ach. stillmanii</i> excluded)
		<i>Jarava eriostachya</i> (all 4 specimens) <i>Jarava plumosa</i> (2 of 3 specimens)
	NA <i>Stipa</i> (<i>Pappostipa</i>) <i>speciosa</i> 6 & <i>S. (Pappostipa) vaginata</i> var. <i>argyroides</i>	SA <i>Stipa</i> (<i>Pappostipa</i>) <i>speciosa</i> 6 NA <i>Stipa</i> (<i>Pappostipa</i>) <i>speciosa</i> 6 & <i>S. (Pappostipa) vaginata</i> var. <i>argyroides</i>
NA <i>Stipa</i> (<i>Pappostipa</i>) <i>speciosa</i> (exc.6) <i>Hesperostipa</i>	<i>Hesperostipa</i> <i>Nassella argentinensis</i> & (<i>N. meyeri</i> & <i>N. neesiana</i>)	[Excluded from combined analysis] <i>Hesperostipa</i> <i>Nassella argentinensis</i> & (<i>N. meyeri</i> & <i>N. neesiana</i>)
<i>Aciachne pulvinata</i> & <i>Anatherostipa rosea</i>		<i>Nassella tenuis</i> 1 & <i>N. trichotoma</i> 1 <i>Nassella cordobensis</i> (both specimens) <i>Aciachne pulvinata</i> & <i>Anatherostipa rosea</i> <i>Anatherostipa bomanii</i> & (<i>A. obtusa</i> & <i>A. orurensis</i>)
<i>Achnatherum calamagrostis</i> & <i>A. caragana</i>		<i>Achnatherum nelsonii</i> & <i>A. occidentale</i> <i>Austrostipa</i> and two internal clades (<i>Aus. stipoides</i> excluded)
<i>Austrostipa</i> exc. <i>Aus. stipoides</i>		<i>Stipa parviflora</i> <i>Piptatherum holciforme</i> & <i>P. microcarpum</i>
<i>Stipa parviflora</i> (specimens identical) <i>Piptatherum holciforme</i> & <i>P. microcarpum</i>	<i>Piptatherum holciforme</i> & <i>P. microcarpum</i>	<i>Piptatherum holciforme</i> & <i>P. microcarpum</i>
<i>Piptatherum canadense</i> & <i>P. micranthum</i>		<i>Piptatherum canadense</i> & <i>P. micranthum</i> <i>Piptatherum miliaceum</i> (all 3 specimens) <i>Piptochaetium</i>

Thomasson (1978, 1979) hypothesized that there are two distinct lineages in American Stipeae, with one lineage encompassing the fossil genus *Berriochloa*, *Hesperostipa*, *Piptochaetium*, and *Stipa*, the other *Nassella*, *Achnatherum*, and *Piptatherum*. Our results provide some support for this picture so far as the American taxa are concerned. The *Hesperostipa-Piptochaetium-Anatherostipa-Aciachne* clade formed one of the earliest diverging clades on the combined tree (Fig. 3a). As in the study by Cialdella et al. (2007), the Andean genera *Anatherostipa* and *Aciachne* formed a somewhat weakly supported clade. Unlike those authors, we found this clade to be sister to, rather than embedded in, *Piptochaetium*, and that these two clades were sister to *Hesperostipa*. Our combined results also place *Nassella*, *Achnatherum*, and *Jarava* s.st., but not *Piptatherum*, in a single, strongly supported clade. Evaluation of Tsvelev's (1977) hypothesis that the tribe as a whole originated in Australia will require more intensive sampling, both geographic and molecular, as will development of a more robust phylogeny for the South American members of the tribe.

Note added in proof: Romaschenko et al. (2008) recently published *Pappostipa* as a generic name, after demonstrating that it is monophyletic. They have provided the appropriate combinations in *Pappostipa* for the taxa here treated as members of *Stipa* subg. *Pappostipa*.

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APPENDIX 1. Voucher information and GenBank numbers for the samples used in constructing the trees. The names of the species are followed by their native range, then information about the voucher specimen(s). The voucher information presented is the herbarium code and accession number, the name of the collector and the collection number (or, if there is no accession number, the collection date), source, and then the ITS5a2c, *trnL*, *trnH-psbA*, *trnK-rps16* and GenBank codes. Names in *Pappostipa* were added in proof.

MELICEAE Link ex Lindl. *Glyceria declinata* Bréb., Eurasia, introduced elsewhere: HSC 94245, G.H. Hrusa 10935, California (Introduced), USA, EF674555, EU223364, DQ665480 DQ665571.

STIPEAE Dumort. *Achnatherum* P. Beauv.: *Achnatherum altum* (Swallen) Hoge & Barkworth, Southern North America: UTC 208903, J. Valdés Reyna VR 1503 & L. Rodríguez; Coahuila, Mexico, EU194677, EU200805, EU204651, EU204779; *Achnatherum calamagrostis* Beauv., Europe: 1 - UTC 217668, S. García & F.M. Vázquez 10 Aug 1991, Spain, EU194678, EU200806, EU204652, EU204780; *Achnatherum caragana* (Trin. & Rupr.) Nevski, Asia: UTC 210086, Cultivated - origin Iran, 24 Jul 1984, Utah, USA, EU194680, EU200808, EU204654, EU204782; *Achnatherum editorum* (Fourn.) Valdés-Reyna & Barkworth, southern North America: UTC 207031, P.S. Hoge 250 et al., Coahuila, EU194681, EU200809, EU204655, EU204783; *Achnatherum eminens* (Cav.) Barkworth, southern North America: UTC 204771, M.E. Barkworth 5138 et al., Coahuila, Mexico, EU194682, EU200810, EU204656, EU204784; *Achnatherum hymenoides* (Roem. & Schult.) Barkworth, North America: BA 80144, M.E. Barkworth 99.123, Colorado, USA, EU194683, EU200811, EU204657, EU204785; *Achnatherum lobatum* (Swallen) Barkworth, southern North America: UTC 229511, R.D. Worthington 28001, New Mexico, USA, EU194684, EU200812, EU204658, EU204786; *Achnatherum multinode* (Scribn.) Valdés-Reyna & Barkworth, southern North America: BA 76529, P.S. Hoge 259 et al., Coahuila, Mexico, EU194685, EU200813, EU204659, EU204787; *Achnatherum nelsonii* (Scribn.) Barkworth, western North America: BA 80137, L. Firestone 8333 & H. Firestone, California, USA, EU194686, EU200814, EU204660, EU204788; *Achnatherum nevadense* (B.L. Johnson) Barkworth, western North America: BA 80138, M.E. Barkworth 4060, California, USA, EU194687, EU200815, EU204661, EU204789; *Achnatherum occidentale* (Thurb.) Barkworth, western North America: 1 - UTC 208822, S. Haultain-Tweed, 1988, California, USA, EU194688, EU200816, EU204662, EU204790; 2-BA 80141, L. Firestone 8320 & H. Firestone, California, USA, EU194689, EU200817, EU204663, EU204791; *Achnatherum occidentale* subsp. *californicum* (Merr. & Burt Davy) Barkworth, western North America: UTC 200442, M.E. Barkworth 4097 & L.R. Firestone, California, USA, EU194690, EU200818, EU204664, EU204792; *Achnatherum richardsonii* (Link) Barkworth, North America: BA 80148, M.E. Barkworth 99.100, Wyoming, USA, EU194691, EU200819, EU204665, EU204793; *Achnatherum robustum* (Vasey) Barkworth, western North America: BA 76528, P.S. Hoge 285, Coahuila, Mexico, EU194692, EU200820, EU204666, EU204794; *Achnatherum stillmanii* (Bol.) Barkworth, California: UTC 235202, M.E. Barkworth 2003/12 S.W.L. Jacobs, & B. Jacobs, California, USA, EU194679, EU200807, EU204653, EU204781. **ACIACHNE** Benth. *Aciaclne pulvinata* Benth., South America: 1 - UTC 210601, P.M. Peterson 13203, R.J. Soreng, & S. Laegaard, La Paz, Bolivia, EU194693, EU200821, EU204667, EU204795; 2 - UTC 203408, T. Killeen 2541, La Paz, Bolivia, EU194694, EU200822, EU204668, EU204796. **AMELICHLOA** Arriaga & Barkworth: *Amelichloa brachychaeta* (Godr.) Arriaga & Barkworth: South America: 1 - BA 81137, Wells 19 & Erb, Entre Ríos, Argentina, EU194695, EU200823, EU204669, EU204797; 3 - UTC 229515, T.H. Gantenbein May 1996, California (Introduced), USA, EU194696, EU200824, EU204670, EU204798; 4 - CDFA, G.D. Barbe 4262 & J.L. Johnson, California (Introduced), USA, EU194697, EU200825, EU204671, EU204799; 5 - CDFA, B. Oliver, 29 Sep 1998, California (Introduced), USA, EU194698, EU200826, EU204672, EU204800; 6 - CDFA, J.L. Schall, 3 Aug 1960, California, USA, EU194699, EU200827, EU204673, EU204801; 7 - CDFA, E. Finley & B. Oliver, 14 Nov 1995, California (Introduced), USA, EU194700, EU200828, EU204674, EU204802; *Amelichloa caudata* (Trin.) Arriaga & Barkworth, South America: 1 - BA 80535, M.O. Arriaga 616, Buenos Aires, Argentina, EU194701, EU200829, EU204675, EU204803; 2 - CDFA, T. Gantenbein, 4 May 1996, California (Introduced), USA, EU194702, EU200830, EU204676, EU204804; 3 - UTC 237914, M.O. Arriaga 616, Buenos Aires, Argentina, EU194703, EU200831, EU204677, EU204805; 4 - BA 81417, M.O. Arriaga 623, Chubut, Argentina, EU194704, EU200832, EU204678, EU204806; 5 - UTC 206571, M. Curto 631, California, USA, EU194705, EU200833, EU204679, EU204807; *Amelichloa clandestina* (Hack.) Arriaga & Barkworth, northern Mexico: 1 - UTC 207071, P.S. Hoge 286, M.E. Barkworth, & M.A. Carranza, Coahuila, Mexico, EU194706, EU200834, EU204680, EU204808; 2 - UTC 203120, E.G. Aguilera, 19 May 1986, Coa-

huila, Mexico, EU194707, EU200835, EU204681, EU204809; 3 - UTC 226683, V. Yadon, 9 July 1999, California (Introduced), USA, EU194708, EU200836, EU204682, EU204810; 4 - UTC 203139, M.E. Barkworth 5115 & P.S. Hoge, Coahuila, Mexico; EU194709, EU200837, EU204683, EU204811. **AMPELODESMOS** Link: *Ampelodesmos mauritanicus* Dur. & Sch. Mediterranean: UTC 246449, M.E. Barkworth 2007.001, Utah (Cultivated), USA, EU194710, EU200838, EU204684, EU204812. **ANATHEROSTIPA** (Hack. ex Kuntze) Peñailillo: *Anatherostipa bomanii* (Hauman) Peñailillo, western South America: 1 - UTC 210632, P.M. Peterson 13071, R.J. Soreng, & S. Laegaard, La Paz, Bolivia, EU194711, EU200839, EU204685, EU204813; 2 - UTC 210711, P.M. Peterson 13056, R.J. Soreng, & S. Laegaard, La Paz, Bolivia, No ITS, EU200840, EU204686, EU204814; *Anatherostipa obtusa* (Nees & Meyen) Peñailillo, western South America: 1 - UTC 136726, R. Lara 6-A & K. Parker, Antaquira, Bolivia; EU194712, EU200841, EU204687, EU204815; 2 - UTC 210684, P.M. Peterson 12632 et al., La Paz, Bolivia, EU194745, EU200881, EU204728, EU204856; *Anatherostipa orurensis* F. Rojas, western South America: UTC 210617, P.M. Peterson 13117, R.J. Soreng, & S. Laegaard, La Paz, Bolivia, EU194713, EU200842, EU204688, EU204816; *Anatherostipa rosea* (Hitchc.) Peñailillo, western South America: UTC 208042, P.M. Peterson 8880, C.R. Annable, M.E. Poston, Ecuador; EU194714, no *trnL*, EU204689, EU204817. **AUSTROSTIPA** S.W.L. Jacobs & J. Everett: *Austrostipa aristigulum* (F. Muell.) S.W.L. Jacobs & J. Everett, Australia: BA 80562, M. Robb 1E, New South Wales, Australia, EU194715, EU200843, EU204690, EU204818; *Austrostipa bigeniculata* (Hughes) S.W.L. Jacobs & J. Everett, Australia: BA 80568, M. Robb 1B, New South Wales, Australia, No ITS, EU200844, EU204691, EU204819; *Austrostipa elegantissima* (Labill.) S.W.L. Jacobs & J. Everett, Australia: BA 80554, M.F. Porteners 9510049, New South Wales, Australia, EU194716, EU200845, EU204692, EU204820; *Austrostipa nitida* (Summerh. & C.E. Hubb.) S.W.L. Jacobs & J. Everett, Australia: BA 77735, P. Canty for NWPS 2007, South Australia, Australia, EU194717, EU200846, EU204693, EU204821; *Austrostipa ramosissima* (Trin.) S.W.L. Jacobs & J. Everett: UTC 246450, M.E. Barkworth 2007.002, Utah (Cultivated), USA, EU194718, EU200847, EU204694, EU204822; *Austrostipa scabra* (Lindl.) S.W.L. Jacobs & J. Everett, Australia: 1 - BA 80578, J. Everett 1563, Easter Island, Chile, EU194719, EU200848, EU204695, EU204823; 2 - BA 77641, F.J. Badman 4538, South Australia, Australia, EU194720, EU200849, EU204696, EU204824; *Austrostipa stipoides* (Hook. f.) S.W.L. Jacobs & J. Everett, Australia: BA 80567, J. Everett 451, New South Wales, Australia, EU194721, EU200850, EU204697, EU204825. **CELTICA** F.M. Vázquez & Barkworth: *Celtica gigantea* (Link) F. M. Vázquez & Barkworth, western Mediterranean: UTC 246451, M.E. Barkworth 2007.003, Utah (Cultivated), USA, EU194722, EU200851, EU204698, EU204826. **HESPEROSTIPA** (M.K. Elias) Barkworth: *Hesperostipa comata* ssp. *comata* (Trin. & Rupr.) Barkworth, North America: UTC 218764, J.F. Smith 2553, Idaho, USA, EU194723, EU200852, EU204699, EU204827; *Hesperostipa comata* ssp. *intermedia* (Scribn. & Tweedy) Barkworth, western North America: UTC 173684, M.E. Barkworth 3461, N. Gay, & L. Greene, California, USA, EU194724, EU200853, EU204700, EU204828; *Hesperostipa curtisetata* (A.S. Hitchc.) Barkworth, North America: UTC 200479, H. Marriott 11 Jul 1984, Wyoming, USA, EU194725, EU200854, EU204701, EU204829. **JARAVA** Ruiz & Pav.: *Jarava eriostachya* (Kunth) Peñailillo, South America: 1 - BA 90993, Faggi s.n., Córdoba, Argentina, EU194726, EU200855, EU204702, EU204830; 2 - BA 90995, Faggi s.n., Córdoba, Argentina, EU194727, EU200856, EU204703, EU204831; 3 - BA 90997, Faggi s.n., Jujuy, Argentina, EU194728, EU200857, EU204704, EU204832; 4 - BA 90998, Faggi s.n., Tucumán, Argentina, EU194729, EU200858, EU204705, EU204833; *Jarava plumosa* (Spreng.) S.W.L. Jacobs & J. Everett, South America: 1 - BA 80531, M.O. Arriaga 612, Buenos Aires, Argentina, EU194731, EU200860, EU204707, EU204835; 2 - BA 80537, M.O. Arriaga 618, Buenos Aires, Argentina, No ITS, EU200861, EU204708, EU204836; 3 - BA 80072, M.O. Arriaga 596, Buenos Aires, Argentina, EU194732, EU200862, EU204709, EU204837; 4 - UTC 237902, M.O. Arriaga 618, Buenos Aires, Argentina, EU194733, EU200863, EU204710, EU204838; 5 - BA 78932, Faggi & Cannon s.n., Buenos Aires, Argentina, EU194730, EU200859, EU204706, EU204834. **NASSELLA** (Trin.) E. Desv.: *Nassella argentinensis* (Speg.) Peñailillo, South America: BA 80068, M.O. Arriaga 602, Córdoba, Argentina, EU194734, EU200864, EU204711, EU204839; *Nassella cordobensis* (Speg.) Barkworth, South America: 1 - BA 90992, Faggi s.n., Córdoba, Argentina, EU194736, EU200866, EU204713, EU204841; 2 - BA 90994, Faggi s.n., Córdoba, Argentina, EU194737, EU200867, EU204714, EU204842; *Nassella hyalina* (Nees) Barkworth, South America: 1 - BA 79991, M.O. Arriaga & D. Montero, Buenos Aires, Argentina, no ITS, EU200868, EU204715, EU204843; 2 - BA 91107, M.O. Arriaga 681, Argentina, no ITS, EU200869, EU204716, EU204844; 3 - BA 73087, M.O. Arriaga 305, Capital Federal, Argentina, no ITS, EU200870, EU204717, EU204845; *Nassella meyeri*

- Torres, South America: BA 91099, M.O. Arriaga 673, Jujuy, Argentina, EU194738, EU200871, EU204718, EU204846; *Nassella neesiana* (Trin. & Rupr.) Barkworth, South America: 1 - BA 80071, M.O. Arriaga 595, Buenos Aires, Argentina, EU194739, EU200872, EU204719, EU204847; 2 - BA 91004, M.O. Arriaga 670, Chubut, Argentina, no ITS, EU200873, EU204720, EU204848; *Nassella pampeana* (Speg.) Barkworth, South America: BA 81425, M.O. Arriaga 629, Chubut, Argentina, no ITS, EU200874, EU204721, EU204849; *Nassella punensis* Torres, South America: UTC 210644, P.M. Peterson 12893 et al., La Paz, Bolivia, EU194740, EU200875, EU204722, EU204850; *Nassella tenuis* (Phil.) Barkworth, South America: 1 - BA 81427, M.O. Arriaga 631, Chubut, Argentina, EU194741, EU200876, EU204723, EU204851; 2 - BA 81506, M.O. Arriaga 639, Chubut, Argentina, EU194742, EU200877, EU204724, EU204852; *Nassella tenuissima* (Trin.) Barkworth, South America and southern North America (disjunct): BA 91106, M.O. Arriaga 680, San Luis, Argentina, no ITS, EU200878, EU204725, EU204853; *Nassella trichotoma* Hack. ex Arech., South America: 1 - BA 81421, M.O. Arriaga 625, Chubut, Argentina, EU194743, EU200879, EU204726, EU204854; 2 - BA 91103, M.O. Arriaga 677, Córdoba, Argentina, EU194744, EU200880, EU204727, EU204855. **PIPTATHERUM** P. Beauv.: *Piptatherum canadense* (Poir.) Dorn, North America: UTC 238734, L.B. Gerdes 4812, Minnesota, USA, EU194770, EU200906, EU204754, EU204882; *Piptatherum holciforme* (M. Bieb) Roem. & Schult., Eurasia: 1 - UTC 234499, A. Badarau & S. Dezsi, May 2001, Mehendinti, Romania, EU194771, EU200907, EU204755, EU204883; 2 - UTC 239273, M.E. Barkworth et al.; 27 Jun 2003, Armenia, EU194772, EU200908, EU204756, EU204884; *Piptatherum micranthum* (Trin. & Rupr.) Barkworth, North America: 1 - UTC 191276, J.S. Tuhy 1527, Utah, USA, EU194773, EU200909, EU204757, EU204885; *Piptatherum microcarpum* (Pilg.) Tzvelev, Eurasia: UTC 234734, B. Crampton T.O. 2430, California (Cultivated), USA, EU194774, EU200910, EU204758, EU204886; *Piptatherum miliaceum* (L.) Coss., Eurasia and Mediterranean: 1 - BA 81515, M.O. Arriaga 648 et al., Andalucía, Spain, EU194775, EU200911, EU204759, EU204887; 2 - UTC 123956, A.A. Beetle R-330, Morocco, EU194776, EU200912, EU204760, EU204888; 3 - UTC 226846, S.W.L. Jacobs 8403 & M.E. Barkworth, South Australia (Introduced), Australia, EU194777, EU200913, EU204761, EU204889; *Piptatherum racemosum* (Sm.) Eaton, North America: UTC 225634, S.J. Darbyshire 4416, Ontario, Canada, EU194778, EU200914, EU204762, EU204890; *Piptatherum vire-scens* (Trin.) Boiss., Eurasia: UTC 234515, A.S. Badarau & S. Dezsi, May 2001, Mehendinti, Romania, EU194779, EU200915, EU204763, EU204891. **PIPTOCHAETIUM** J. Presl: *Piptochaetium avenacioides* (Nash) Valencia & Costas, southeastern North America: UTC 247722, L.C. Anderson 22818, Florida, USA, ITS, no *trnL*, EU223361, EU223362; *Piptochaetium avena-ceum* (L.) Parodi, southeastern North America: UTC 247724, Lorán C. Anderson 22835, Florida, USA, EU627627, no *trnL*, no *trnH*, EU223363; *Piptochaetium bicolor* (Vahl) E. Desv., South America: 1 - BA 91108, M.O. Arriaga 682, Argentina, EU194780, EU200916, EU204764, EU204892; 2 - BA 80508, M.O. Arriaga 609, Buenos Aires, Argentina, EU194781, EU200917, EU204765, EU204893; *Piptochaetium fimbriatum* (Kunth) Hitchc., southern North America: BA 76525, P.S. Hoge 629 et al., Coahuila, Mexico, EU194782, EU200918, EU204766, EU204894; *Piptochaetium sti-poides* (Trin. & Rupr.) Hack. ex Arechav. var. *stipoides*, South America: 1 - BA 80510, M.O. Arriaga 611, Buenos Aires, Argentina, EU194783, EU200919, EU204767, EU204895; 2 - BA 80070; M.O. Arriaga 594, Buenos Aires, Argentina, EU194784, EU200920, EU204768, EU204896. **PTILAGROS-TIS** Griseb.: *Ptilagrostis kingii* (Bol.) Barkworth, California: UTC 173686, M. Barkworth 3462, N. Gay & L. Greene, California, USA, EU194785, EU200921, EU204769, EU204897; *Ptilagrostis pelliottii* (Danguy) Grubov, Asia: UTC 244387, V.I. Yarubov 1735, L. Leueldaeyev, & Sh. Dakse-neie, Mongolia, EU194786, EU200922, EU204770, EU204898; *Ptilagrostis porteri* (Rydb.) W.A. Weber, Colorado, North America: UTC 227957, M.E. Barkworth 99.117, Colorado, USA, EU194787, EU200923, EU204771, EU204899. **STIPA** L.: **STIPA** subg. **PAPPOSTIPA** Speg.: *Stipa (Pappostipa) chrysophylla* E. Desvaux [= *Pappostipa chrysophylla* (E. Desvaux) Romaschenko], South America: 1 - BA 91003, M.O. Arriaga 669, Chubut, Argentina, EU194747, no *trnL*, EU204730, EU204858; 3 - BA 81429, M.O. Arriaga 633, Chubut, Argentina, EU194746, EU200882, EU204729, EU204857; *Stipa (Pappostipa) chubutensis* Speg. [= *Pappostipa chubutensis* (Speg.) Romaschenko], South America: BA 81509, M.O. Arriaga 642, Chubut, Argentina, EU194748, EU200883, EU204731, EU204859; *Stipa (Pappostipa) humilis* (Cav.) Peñailillo [= *Pappostipa humilis* (Cav.) Romaschenko], South America: 1 - BA 81510, M.O. Arriaga 643, Chubut, Argentina, EU194749, EU200884, EU204732, EU204860; 2 - BA 80063, M.O. Arriaga 598, Mendoza, Argentina, no ITS, EU200885, EU204733, EU204861; *Stipa (Pappostipa) patagonica* Speg. [= *Pappostipa pata-gonica* (Speg.) Romaschenko], South America: BA 81431, M.O. Arriaga 635, Río Negro, Argentina, EU194750, EU200886, EU204734, EU204862; *Stipa (Pappostipa) sorianoii* Parodi [= *Pappostipa sorianoii* (Parodi) Romaschenko], South America: BA 81512, M.O. Arriaga 645, Santa Cruz, Argentina, EU194751, EU200887, EU204735, EU204863; *Stipa (Pap-postipa) speciosa* Trin. & Rupr. [= *Pappostipa speciosa* (Trin. & Rupr.) Romaschenko], South America and southern North America: 1 - UTC 242801, C.W. Cook 20, Arizona, USA, EU194759, EU200895, EU204743, EU204871; 2 - UTC 244479, W. Fertig 21656, Utah, USA, EU194759, EU200895, EU204743, EU204871; 4 - UTC 193388, E. Zurcher, C. Gilbert, J.A. MacMahon, 19 March 1985, Baja California, Mexico, EU194754, EU200890, EU204738, EU204866; 5 - UTC 204754, J.S. Tuhy 3179 & J.S. Holland, Utah, USA, EU194755, EU200891, EU204739, EU204867; 6 - UTC 176714, S. Goodrich 16965, Utah, USA, EU194756, EU200892, EU204740, EU204868; 7 - UTC 196539, S. Goodrich 11389, Nevada, USA, EU194757, EU200893, EU204741, EU204869; 9 - UTC 233015, N.D. Atwood 27510 & L.C. Higgins, Arizona, USA, EU194758, EU200894, EU204742, EU204870; 10 - UTC 95468, L.C. Anderson 769, Arizona, USA, EU194752, EU200888, EU204736, EU204864; 11 - UTC 173598, M.E. Barkworth 3406, California, USA, EU194753, EU200889, EU204737, EU204865; *Stipa (Pappostipa) speciosa* var. *major* (Speg.) Parodi [= *Pappostipa major* (Speg.) Romaschenko], South America: 1 - BA 81432, M.O. Arriaga 636, Neuquén, Argentina, EU194762, EU200898, EU204746, EU204874; 2 - BA 91006, M.O. Arriaga 672, Chubut, Argentina, EU194759, EU200895, EU204743, EU204871; *Stipa (Pappostipa) speciosa* var. *manqueclensis* F.A. Roig [= *Pappostipa speciosa* var. *manqueclensis* (F.A. Roig) Romaschenko], South America: BA 81428, M.O. Arriaga 682, Chubut, Argentina, EU194763, EU200899, EU204747, EU204875; *Stipa (Pappostipa) speciosa* Trin. & Rupr. var. *speciosa* [= *Pappostipa speciosa* (Trin. & Rupr.) Romaschenko var. *speciosa*], South America: BA 81507, M.O. Arriaga 640, Chubut, Argentina, EU194764, EU200900, EU204748, EU204876; *Stipa (Pappostipa) vaginata* Phil. [= *Pappostipa vaginata* (Phil.) Romaschenko], South America: 1 - BA 91002, M.O. Arriaga 668, Chubut, Argentina, EU194765, EU200901, EU204749, EU204877; 2 - UTC 210656, P.M. Peterson 12750 et al., La Paz, Bolivia, EU194766, EU200902, EU204750, EU204878; *Stipa (Pappostipa) vaginata* fo. *contracta* F.A. Roig [= *Pap-postipa vaginata* fo. *contracta* (F.A. Roig) Romaschenko], South America: BA 80064; M.O. Arriaga 599, Mendoza, Argentina, EU194768, EU200904, EU204752, EU204880; *Stipa (Pappostipa) vaginata* fo. *immersa* F.A. Roig [= *Pappostipa vaginata* fo. *immersa* (F.A. Roig) Romaschenko], South America: BA 80062, M.O. Arriaga 597, Mendoza, Argentina, EU194769, EU200905, EU204753, EU204881; *Stipa (Pappostipa) vaginata* var. *argyroidea* F.A. Roig [= *Pappostipa vaginata* var. *argyroidea* (F.A. Roig) Romaschenko], South America: BA 81418, M.O. Arriaga 624, Chubut, Argentina, EU194766, EU200902, EU204750, EU204878. **STIPA** subg. **PTILOSTIPA** Speg.: *Stipa (Ptilostipa) neaei* Nees ex Steud., South America: BA 81433, M.O. Arriaga 637, Neuquén, Argentina, no ITS, EU200924, EU204772, EU204900; *Stipa barbata* Desf., Eurasia: BA 81518, M.O. Arriaga 651 et al., Toledo, Spain, no ITS, EU200925, EU204773, EU204901; *Stipa cazorensis* (F.M. Vázquez & Devesa) F.M. Vázquez, H. Scholz, & Sonnentag, Mediterranean: BA 81517, M.O. Arriaga 650 et al., Andalucía, Spain, EU194788, EU200926, EU204774, EU204902; *Stipa iberica* Martinovsky, Mediterranean: BA 81520, M.O. Arriaga 653 et al., Castilla La Nueva, Spain, no ITS, EU200927, EU204775, EU204903; *Stipa juncea* L., Mediterranean: BA 81519, M.O. Arriaga 652 et al., Castilla La Nueva, Spain, no ITS, EU200928, EU204776, EU204904; *Stipa parviflora* Desf. Mediterranean: 1 - BA 81521, M.O. Arriaga 654 et al., Toledo, Spain, EU194789, EU200929, EU204777, EU204905; 2 - BA 81516, M.O. Arriaga 649 et al., Andalucía, Spain, EU194790, EU200930, EU204778, EU204906.