A molecular phylogenetic study of *Deschampsia* (Poaceae: Aveneae) inferred from nuclear ITS and plastid *trnL* sequence data: support for the recognition of *Avenella* and *Vahlodea*

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The circumscription and phylogeny of *Deschampsia* were studied for the first time by parsimony analysis of nuclear ribosomal internal transcribed spacer (ITS) and plastid *trnL* intron sequences. The traditional sectional division based on morphology was not supported by sequence data, which showed differences between core *Deschampsia* s.str. (mainly represented by *D. cespitosa*), *D. atropurpurea* and *D. flexuosa*. Differences in the ITS marker included insertions in the sequence of *D. atropurpurea*; the *trnL* marker contained a deletion shared by all *Deschampsia* sequences, excluding *D. atropurpurea* and *D. flexuosa*, and an insertion in *D. flexuosa*. ITS sequences also differed in an insertion shared by Northern Hemisphere accessions. Both markers produced similar tree topologies but *D. klossi*, in spite of being morphologically close to *Deschampsia* s.str., fell with *D. flexuosa* outside the core of the genus in the *trnL* tree. Molecular evidence corroborates morphological and cytological data supporting exclusion of *D. atropurpurea* and *D. flexuosa* from *Deschampsia* and their treatment as separate genera. The position of *D. klossi* needs further investigation.

KEYWORDS: circumscription, *Deschampsia*, *Deschampsia atropurpurea*, *Deschampsia cespitosa*, *Deschampsia flexuosa*, ITS, phylogeny, *trnL*

INTRODUCTION

Deschampsia P. Beauv. is a genus of 37 perennial and few annual grass species commonly distributed in cold temperate regions and high mountains in the tropics. The main disagreements on the delimitation of *Deschampsia* are related to the morphological diversity and widespread distribution of *D. cespitosa* (L.). P. Beauv. and its relationships to *D. atropurpurea* (Wahlenb.) Scheele and *D. flexuosa* (L.) Trin. The overall morphological similarity between the two latter taxa and the main core of the genus (represented by *D. cespitosa*) have led to their inclusion in *Deschampsia* in many floras, treatments and catalogs (Parodi, 1949; Paunero, 1955; Hess & al., 1967; Hitchcock & al., 1969; Tzvelev, 1976; Holmgren & Holmgren, 1977; Clarke, 1980; Clayton & Renvoize, 1986; Conert, 1987; McVaugh, 1983; Schmeil, 1988; Rzedowski & Rzedowski, 1990; Stace, 1991; Zuloaga & al., 1994; Edgar & Connor, 2000).

Alternative views advocating the segregation of *Deschampsia atropurpurea* and *D. flexuosa* from *Deschampsia* s.l. and their treatment as separate genera have also been proposed. Hylander (1953) included D. atropurpurea in *Vahlodea* (= *V. atropurpurea*) but kept *D. flexuosa* in *Deschampsia*. Albers (1972a, 1972b, 1973, 1978, 1980a, 1980b, 1980c) published several studies on their cytology (but also morphology), showing different chromosome numbers for *D. atropurpurea* (2*n*=14, diploid) and *D. flexuosa* (2*n*= 28, tetraploid). Karyological variation in *D. cespitosa* (2*n*=26, 39, 52) is described as being the result of a process of fusion of smaller chromosomes and subsequent polyploidization (Albers, 1978). García-Suarez & al. (1997) presented chromosome C-banding, isozymes, genomic DNA and plastid DNA restriction data, also showing some differnences among the three taxa. This evidence and its logical conclusion, assigning the separate generic status to *D. flexuosa* and *D. atropurpurea*, has, however, rarely been followed (Frey, 1999; Soreng, 2003).

Holmberg (1926) used the length of the rachilla between the florets in relation to the length of the lemma of the lower floret and the shape of the tip of the lemma, to divide *Deschampsia* into three sections (Table 1): sect. *Campella*, with a long rachilla between the florets and 4-toothed lemmas with lateral teeth larger, including *D. cespitosa*, *D. media*, and *D. setacea*; sect. *Avenaria*, with shorter rachillas and 4-toothed lemmas with small, more or less equal teeth, including *D. flexuosa*; and sect. *Vahlodea* with the lemmas irregularly toothed and the teeth minute, including *D. atropurpurea*. Buschmann

Table 1. Generic delimitation of *Deschampsia* s.l. according to Holmberg (1926), Hylander (1953), Albers (1972a, b). This study supports the classification of Albers.

Taxa	Holmberg (1926)	Hylander (1953)	Albers (1972a, b)
Deschampsia cespitosa	*Deschampsia* sect. *Campella*	*Deschampsia* subgen. *Campella*	*Deschampsia*
Deschampsia atropurpurea	*Deschampsia* sect. *Vahlodea*	*Vahlodea*	*Vahlodea*
Deschampsia flexuosa	*Deschampsia* sect. *Avenaria*	*Deschampsia* subgen. *Avenella*	*Avenella*

(1950) added *D. argentea*, *D. elongata*, *D. calycina* (= *D. danthonioides*), *D. refracta* (= *D. cespitosa*) and a group of taxa (*D. alpina, D. bottnica, D. littoralis, D. wibeliana*) that have been referred to as subspecies of *D. cespitosa* (Clarke, 1980; Chiapella, 2000) to sect. *Campella*, and *D. stricta* (= *D. flexuosa*) and *D. foliosa* to sect. *Avenaria*. Sect. *Vahlodea* was retained with the single species, *D. atropurpurea*. A preliminary cladistic study based on morphology did not support this division and *Deschampsia* was depicted as a paraphyletic group (Chiapella, 2003).

DNA sequence data are now commonly used to resolve problems where taxonomists have not been able to agree on relationships using traditional characters. The internal transcribed spacer (ITS) region of the 18S-26S nuclear ribosomal DNA (rDNA) is a moderately conserved region that has been extensively used in phylogenetic studies in Poaceae (Hamby & Zimmer, 1988; Hsiao & al. 1994, 1995a, 1995b, 1999; Baldwin & al., 1995; Grebenstein & al., 1998; Hodkinson & al., 2000, 2002; Baumel & al., 2002). In spite of potential problems arising from multiple-copies markers (Small & al., 2004), its relative small size, with entire ITS sequences of over 200 grass species ranging between 584 and 633 bp (Hsiao & al., 1999), makes it a suitable marker for a first approach into the phylogenetic study of a not previously explored genus.

The plastid DNA *trnL* region has also been used in several molecular phylogenetic studies and, due to its maternally sided inheritance, in identifying the maternal parent in hybrid taxa in grasses (Ferris & al., 1997; Hodkinson & al., 2002). The region provides phylogenetic resolution at the generic level (Bakker & al., 2000) and reveals a slower evolutionary tempo than nuclear markers (Wolfe & al., 1987; Ingvarsson & al., 2003).

This study of nuclear and plastid sequences of *Deschampsia* s.l. was undertaken to: (1) circumscribe the genus and explore its phylogenetic relationships; (2) evaluate the division into sections proposed by Holmberg (1926) and Buschmann (1948, 1950); and (3) provide an hypothesis for the origin of the genus, considering its scattered intercontinental distribution with the highest concentration of species in southern South America.

MATERIALS AND METHODS

Taxon sampling and outgroup selection. — The 34 accessions representing 18 species of *Deschampsia* s.l. studied (Appendix), included representatives of all sections proposed by Holmberg (1926) and of all geographic regions with a high number of taxa. Species were classified following Parodi (1949) and Nicora (1978) for the South American taxa, Van Royen (1979) for *D. klossi*, Wagner & al. (1990) for *D. nubigena*, Groves (1981) for *D. christophersenii* and *D. mejlandii*, Chiapella (2000) for the subspecies of *D. cespitosa* and Edgar & Connor (2000) for *D. chapmanii* and *D. tenella*. Whereas the monophyly of *Deschampsia* s.l. has never been verified with molecular data, its inclusion in tribe Aveneae has rarely been doubted. Most important treatments using morphological data included it unequivocally in this tribe (Parodi, 1949; Clayton & Renvoize, 1986; Tzvelev, 1989). Molecular data showed, however, that the distinction between Aveneae and Poeae is not clear (Nadot & al., 1994; Catalán & al., 1997), and in a study using plastid DNA restriction sites and morphological data both tribes formed an unresolved single clade (Soreng & Davis, 1998). *Deschampsia cespitosa* was placed together with other Poeae taxa (Catalán & al., 2004), contradicting the conventional view, based on morphology, of *Deschampsia* belonging to Aveneae. Thus, and to start from a conventional standard, the outgroups were selected among the three main evolutionary lines depicted by Clayton & Renvoize (1986: 417) for tribe Aveneae subtribe Aveninae (the subtribe in which *Deschampsia* s.l. is placed): (1) the *Helictotrichon* group (*Arrhenatherum*, *Avena*); (2) the *Trisetum* group (*Trisetum*); and (3) the *Deschampsia* group (*Aira*, *Agrostis*). New sequences were obtained for *Arrhenatherum elatius* and *Aira caryophyllea*, and published sequences of *Agrostis capillaris*, *Trisetum flavescens* and *Poa pratensis* were retrieved from EMBL/GenBank. All the outgroups were used in all the analyses, except *Trisetum* wich was used only in the ITS analysis (see Appendix).

DNA isolation, amplification and sequencing. — DNA was isolated following a modification of the 2× CTAB method of Doyle & Doyle (1987). Leaf pieces were ground to powder and treated with 750 µl extraction buffer, and incubated at 60°C for 30 minutes. Then, 700 µl of SEVAG (chloroform: isoamyl alcohol 24 : 1) were added to the tissue homogenate. This was kept at 4°C for 2 hours and then centrifuged at 14000 rpm for 5 minutes. The clear upper phase was transferred to a clean Eppendorf tube, and 400 µl cold isopropanol were added to precipitate the DNA. The DNA pellet was rinsed with

70% ethanol, dried at 37°C, and stored in TE buffer until use. The entire ITS region was amplified with primers ITS 5 and ITS 4 (White & al., 1990), and the *trnL* intron with primers "c" and "d" (Taberlet & al., 1991). Thermal cycling for PCR consisted of 34 cycles, each with 1 min denaturation at 95°C, 1 min annealing at 48°C, 1 min extension at 72°C, and a final extension of 10 min. PCR products were purified with Qiaquick (Qiagen) spin columns according to the manufacturer's protocol. Purified PCR products were sequenced in an ABI Prism Dye Terminator Cycle Kit (Perkin-Elmer Applied Biosystems) and then visualized using an ABI Prism 377 Automated DNA Sequencer (Perkin-Elmer Applied Biosystems).

Phylogenetic analysis. — Sequences were edited with Autoassembler (Perkin-Elmer Corp.) and visually aligned with MacClade (Maddison & Maddison, 1992). Parsimony analysis was performed with PAUP version 4.0b4a (Swofford, 2000) on three different data sets: ITS, *trnL* and combined. Gaps were treated as missing data, characters were assumed to be unordered, and optimal trees were found using heuristic search with the following options: taxa addition closest, tree-bisection-reconnection (TBR) branch-swapping algorithm, Mul Trees option in effect, starting tree obtained via stepwise addition, trees held at each step = 1, MaxTrees setting = 100. Branch support for the groups found was estimated using bootstrap with 1000 replicates (Felsenstein, 1985). The combined analysis was done following verification of congruence of the data by using the character partition test as implemented in PAUP. It has been suggested that combinability of data may have a direct impact on the phylogeny accuracy (Cunningham, 1997), but agreement is lacking as to whether data should be combined or not (Huelsenbeck & al., 1996; Barker & Lutzoni, 2002).

RESULTS

Sequence variation and phylogenetic analyses. — The ITS sequences of *Deschampsia* s.l. ranged from 595 to 597 bp long, the difference being due to a 2 bp insertion (synapomorphic for clade "B" of Fig. 1) at positions 583–584 in the ITS 2 spacer. The ITS 1 spacer comprised positions 1–218 (218 nucleotides), the 5.8S gene 219–381 (162 nucleotides), and the ITS 2 spacer 382–595/597 (213/215 nucleotides). The aligned ITS region comprised 604 nucleotides (including outgroups), of which 443 (73.3%) were constant and 106 (17.6%) potentially parsimony-informative. The heuristic search with ITS data produced 1,989 trees with tree length = 314, consistency index (CI) = 0.64, and retention index (RI) = 0.80. The strict consensus tree with bootstrap values is shown in Fig. 1. *Deschampsia* s.l. is not monophyletic since *D. atropurpurea* and *D. flexuosa* are not grouped with the remaining species, which form a well-supported (92% bootstrap) monophyletic group, further divided in two clades with good bootstrap support, clade A (84%) and B (81%).

The plastid *trnL* intron region consisted of 584 aligned nucleotides, of which 532 (91%) characters were constant and 20 (3.5%) potentially parsimony-informative. All sequences of *Deschampsia* excepting *D. atropurpurea*, *D. flexuosa* and *D. klossi* had a 5 bp deletion at positions 216–220 relative to the other taxa; this gap is synapomorphic for *Deschampsia* s.str. *Deschampsia atropurpurea* also had a 9 bp deletion at positions 268–276. All *Deschampsia* s.l. sequences differed from the outgroup *Aira caryophyllea* by two deletions, 4 bp at positions 371–374 and 2 bp at positions 389–390. Another outgroup, *Agrostis capillaris*, differed from *Deschampsia* s.l. by a 5 bp deletion at positions 308–312. All accessions of *D. flexuosa* and *D. klossi* had a 25 bp insertion at positions 438–462, which is synapomorphic for the clade D formed by these two taxa (Fig. 2). The *trnL* analysis produced six trees of length = 58, CI = 0.94, and RI =

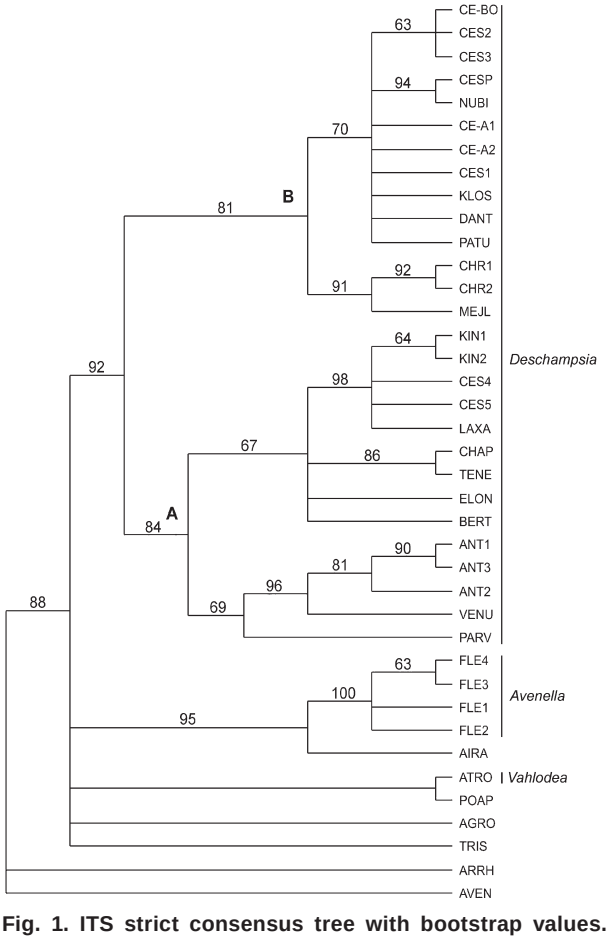

Fig. 1. ITS strict consensus tree with bootstrap values. Clade A, northern accessions; clade B, southern accessions. Species names as in Appendix.

0.97. As in the ITS tree, *Deschampsia* s.l. is not monophyletic because of the positions of *D. atropurpurea* and *D. flexuosa*. The other species are joined in a clade, which remains mostly unresolved but for a small clade comprising accessions of *D. antarctica* and *D. venustula*.

Combined analysis. — The pooled ITS-*trnL* data set comprised 1,188 characters after alignment, which were treated as unordered and equally weighted. Of these, 984 characters were constant, and 116 potentially parsimony-informative. Since the topologies resulting from the two markers differ, although sharing a common feature (the exclusion of *D. atropurpurea* and *D. flexuosa* from core *Deschampsia* s.l.) a character partition test was run on a combined matrix using a subset of 23 accessions of *Deschampsia* and 5 outgroups (*Aira*, *Agrostis*, *Arrhenatherum*, *Avena*, *Poa*). The test value was P = 0.002, suggesting incongruence between the two datasets. Analysis yielded 16 trees (tree length = 343, CI = 0.71, RI = 0.78, trees not shown). Since *D. klossi* was identified as showing different positions in the nuclear and plastid topologies, a second run was done without this species. The value of the new character partition test was P = 0.967, indicating no incongruence between the two data sets. The strict consensus of 16 trees (tree length = 356, CI = 0.69, RI = 0.76) is depicted in Fig. 3.

DISCUSSION

Delimitation and division into sections of Deschampsia. — The genus *Deschampsia* was proposed by Palisot de Beauvois (1812) based on *Aira cespitosa*. *Aira* was divided in two groups, one with muticous lemmas (Linné, 1753: 63), and the other with awned lemmas (Linné, 1753: 64), in which *A. cespitosa* and *A. flexuosa* were included. In addition to this character, Palisot described *Deschampsia* as having paniculate inflorescences, 2–3-flowered "glumes" longer than the spikelets, lemmas with several teeth, and straight awns, slightly longer than the lemmas, and inserted in or near the base. Early descriptions of planta taxa often do not meet modern standards (Irvine & Dixon, 1982) and repeatedly result in the need for revision (Cafferty & al., 2000); in *Deschampsia* the combination of characters listed above can be applied to the several forms of *D. cespitosa* common in Europe, and also to *D. atropurpurea* and *D. flexuosa*. The consequence was a loose generic concept that was widely adopted (see Introduction). The molecular evidence presented allows for a clear definition of the generic boundaries of *Deschampsia*, which are in agreement with cytological (Albers, 1972a, 1972b, 1973, 1978, 1980a, 1980b, 1980c; García-Suarez & al.,

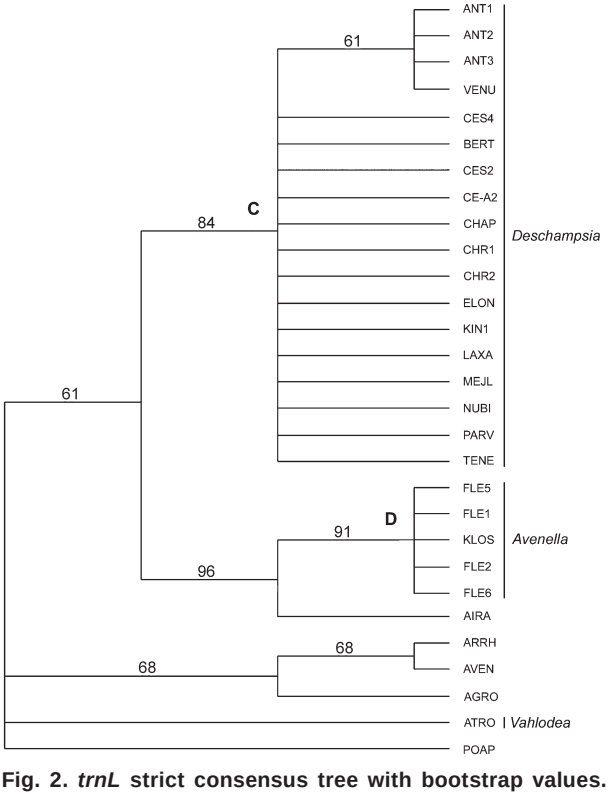

Fig. 2. *trnL* strict consensus tree with bootstrap values. Clade C, *Deschampsia* s.str.; clade D, *D. flexuosa* (= *A. flexuosa*) and *D. klossi*. Species names as in Appendix.

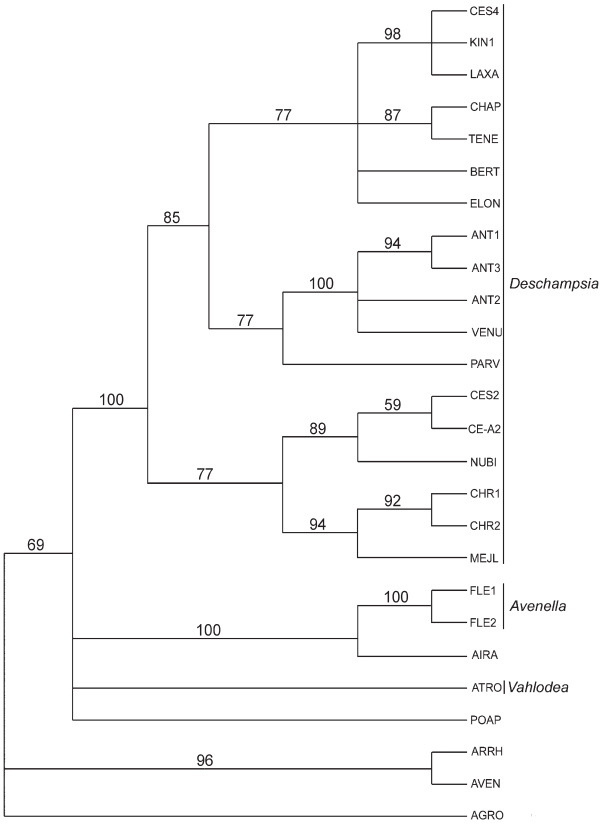

Fig. 3. Combined strict consensus tree with bootstrap values, excluding *D. klossi*. Species names as in Appendix.

1997) and some morphological (Chiapella, 2003) data, both implying the exclusion of *D. atropurpurea* and *D. flexuosa* from *Deschampsia*. Among the most commonly used morphological characters, only the ligules present clear differences in the three taxa, being acute in *Deschampsia*, obtuse in *D. flexuosa* and irregularly toothed to truncate in *D. atropurpurea*. Other characters such as the shape and size of spikelets, insertion and size of awns, and shape of panicles vary greatly and inconsistently. The species remaining in core *Deschampsia* form well-supported clades in both the separate analyses (ITS, 92%; *trnL*, 84%) and combined trees (including *D. klossi*, 85%; excluding it, 100%). Although delimitation of the genus seems clear with molecular data, this is not the case when using morphological data to differentiate among *D. atropurpurea*, *D. flexuosa* and core *Deschampsia*. Even species remaining in *Deschampsia* rarely differ in discrete characters but rather in a continuous way, which in the case of the most common species (*D. cespitosa*) implies frequent and simultaneous overlapping of morphological types and geographic distributions (Chiapella, 2000).

Concerning the delimitation of *Deschampsia* s.str., the ITS and *trnL* trees agree in the separation of *D. atropurpurea* and *D. flexuosa* from core *Deschampsia*, the ITS tree being better resolved than the *trnL* one. The position of *D. klossi* also differed between the nuclear and plastid trees. This species was excluded from core *Deschampsia*, and grouped with *D. flexuosa* in the *trnL* tree, suggesting introgression and its possible origin through reticulate evolution. The combined analysis, however, shows a circumscription of *Deschampsia* s.str. that is in agreement with the ITS tree, in which *D. klossi* falls with clade B ("Northern") of Fig. 1.

The division into sections proposed by Holmberg (1926) and emended by Buschmann (1948, 1950) is not supported by the molecular evidence, which excludes the only species of sect. *Vahlodea* Griseb. (*D. atropurpurea*) and the main species of sect. *Avenaria* Reichenb. (*D. flexuosa*) from *Deschampsia*. The species remaining in the genus belong to sect. *Campella* (Link) Griseb. (= *D.* sect. *Deschampsia*), which in the nuclear and combined trees is divided into two major clades that roughly correspond to the geographic origin of the accessions (Figs. 1, 3). Clade A comprises most southern taxa and southern accessions of *D. cespitosa*, clade B the northern accessions of *D. cespitosa*, *D. christophersenii* and *D. mejlandii* from Tristan da Cunha, and the southern *D. danthonioides* and *D. patula*. Clade A includes two subclades with moderate bootstrap support, one formed by the southernmost taxa *D. antarctica*, *D. parvula* and *D. venustula* (69%) and the other with the remaining southern taxa, *D. kingii* and *D. laxa* (mainly in Tierra del Fuego and Patagonia), *D. berteroana* (central Chile), *D. elongata* and the two New Zealandic species *D. chapmanii* and *D. tenella* (67%). In this group, two well-supported clades are resolved, one containing the exclusively South American taxa and the southern accessions of *D. cespitosa* (98%) and another with the endemic New Zealand taxa (86%). The Chilean annual *D. berteroana* and *D. elongata* remain unresolved. The well-supported (96%) clade comprising all the accessions of *D. antarctica* and *D. venustula* has *D. parvula* as sister group. In clade B resolution is generally lower than in clade A but two groups are noticeable, one including the Tristan da Cunha species (bootstrap support 91%) and the other with the remaining taxa (70%). The resolution in this last group, which includes mostly northern hemisphere taxa but also the southern *D. danthonioides* and *D. patula*, is low, but reveal affinities between *D. cespitosa* and *D. cespitosa* subsp. *bottnica* (63%) and the accession of *D. cespitosa* retrieved from GenBank (L36513) and *D. nubigena* (94%).

Phylogeny of Deschampsia. — The estimation of phylogeny by using a combination of sequences of nuclear and plastid markers, frequently ITS and *trnL*, is common in studies using DNA sequence data (e.g., Baumel & al., 2002; Hodkinson & al., 2002; Catalán & al., 2004; Nickrent & al., 2004); nuclear data provides usually more potentially informative sites. This was also the case in Deschampsia s.l., where ITS provided 17.6% against 3.5% of *trnL*, and each dataset yielded a different history. The ITS data highlight the existence of two main lineages as represented by clades "A" and "B" in Fig. 1, whereas in the plastid tree (Fig. 2) these clades collapse and form a single large polytomy; nevertheless, *Deschampsia*—excluding *D. atropurpurea* and *D. flexuosa*—is depicted as monophyletic with good bootstrap-support (84%), suggesting a close relationship of the plastid genomes. The 5.8S region of the ITS has a length of 163 bp in all studied species, similar to the 164 bp observed by Hsiao & al. (1994), whereas the ITS1 and ITS2, with 218 bp and 213–215 bp, respectively, were shorter than those accounted for in Hsiao & al. (1994). This minor variation in sequence length was due to indels, most notably a 2 bp insertion in a group of mainly northern hemisphere and two southern (*D. danthonioides* and *D. patula*) accessions. Variation among sequences of the same species but from distant geographic regions was remarkable in *D. cespitosa*. Comparable results of intra-specific variation in ITS sequences also have been reported so far for a few genera including *Calycadenia*, *Sinapis* and *Vicia* (Baldwin, 1993).

Comparisons between the combined tree (Fig. 3) and the single-marker trees (Figs. 1 and 2) are possible only with ITS, because of the large polytomy in the plastid tree. The only group formed in the latter is, however, recognisable in the nuclear single marker tree and in the

combined tree, that between *D. antarctica* and *D. venustula*. *Deschampsia* s.str. is depicted as a monophyletic clade with bootstrap support ranging between 84% and 100%, and the accessions of *D. flexuosa* are also monophyletic with 100% bootstrap support. *Deschampsia atropurpurea* remains unresolved. The combined tree has different topology but supports the abovegeneric circumscription. *Aira* is consistently resolved as the sister group of *D. flexuosa* whereas the other outgroups are more distantly related or unresolved.

Biogeography of *Deschampsia*. — The ITS tree (Fig. 1) depicts *D. antarctica*, *D. venustula* and *D. parvula* of southern Argentina and Chile as sister to the clade comprised of *D. kingii*, *D. laxa*, *D. berteroana* from central Chile, *D. tenella* of New Zealand and the South American accessions of *D. cespitosa*. In clade B the two species endemic to the Tristan da Cunha archipelago, *D. christophersenii* and *D. mejlandii*, are sister to a clade, which includes most of the Euroasiatic accessions of *D. cespitosa*. Thus while the molecular data hint at a close relationship to northern taxa, the southern geographical position of Tristan da Cunha suggests an origin of *D. christophersenii* and *D. mejlandii* by long-distance dispersal from South America. At least two facts support the feasibility of the latter event. First, pollen of *Nothofagus pumilio*, a key species of the Patagonian temperate forests, has been found in Pleistocene peat bog samples of Tristan da Cunha (Hafsten, 1960). Second, the fern flora of the islands is rich in taxa characteristic of the Andean Patagonic forests (De la Sota & Ponce, 1998) including *Blechnum penna-marina* (Tryon, 1966), and the genera *Asplenium*, *Hymenophyllum*, *Hypolepis* and *Ophioglossum*. The hypothesis of a South American origin for some elements of the Tristan da Cunha flora is further sustained in the position of the islands, which lies in the pathway of a westerly wind system. Dispersal against these prevailing winds from other regions seems highly improbable.

Although a subject that covers vast tracts of time and space as plant migration, is often an activity "inevitably speculative" (Clayton, 1981), and a more inclusive sampling is needed to achieve unambiguous results. The existence of diversification centres in southern South America (11 species) and New Zealand (4 species), the presence of *D. antarctica* in several southern seas islands and of *D. cespitosa* in southern Argentina, Brazil and Chile, and the ITS evidence for a southern clade (Fig. 1, clade A) suggest a major radiation of *Deschampsia* in the southern Hemisphere. How dispersion among such distant regions has happened remains unclear but some long-distance event has evidently occurred. The ability for long-distance dispersal in *D. antarctica* has been rated as low as suggested by its low genetic diversity (Holderegger & al., 2003), which is probably due to vegetative propagation. But the capacity to disperse has been high enough to account for the presence of the species in southern islands. Seeds of Antarctic populations of *D. antarctica* have a relatively low but rapid germination ability (Corte, 1961), indicating that long-distance dispersal might well result in successful establishment. Moreover, *Deschampsia* species are non-invasive and very restricted to their original habitats, and their ranges may thus well reflect past migration events.

The accessions of *D. flexuosa* (= *A. flexuosa*), regardless of their geographic origin, form a well-supported clade in all trees, falling with *D. klossi* in the plastid tree. The relative geographic proximity between *D. klossi*, common in the mountains of New Guinea (Van Royen, 1979), and *D. ligulata* (= *D. flexuosa* var. *ligulata*), endemic to Mount Kinabalu in Borneo (Buschmann, 1950), makes a hybridisation event likely. The similar habitats in which both taxa are found further support this.

Deschampsia and its allies *D. atropurpurea* (= *Vahlodea atropurpurea*) and *D. flexuosa* (= *Avenella flexuosa*) are a complex group (Table 2), whose members are morphologically difficult to separate, and may have been prone to hybridisation and polyploidisation. Although providing a first insight into the phylogeny of the genus, ITS sequence data are sometimes not sufficient for resolving the relationships of related taxa (Sang, 2002), making necessary the use of single-copy nuclear genes. Further sampling of taxa of different geographic origins and ploidy levels, and inclusion of more molecular markers, is needed to achieve a clearer picture of the phylogeny of the genus.

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Table 2. Comparison among the three genera accepted in this study. Type species are indicated below genus name.

	***Deschampsia* (L.) P. Beauv.** ***D. cespitosa* (L.) P. Beauv.**	***Avenella* (Bluff & Fingerh.) Drejer** ***A. flexuosa* (L.) Drejer**	***Vahlodea* Fr.** ***V. atropurpurea* (Wahlenb.) Fr. ex Hartm.**
Leaf blade			
shape	involute to flat	filiform	flat
width	1.5–5 mm	up to 1.5 mm	2–4 mm
Spikelet			
shape	lanceolate	oblong	ovoidal
number	(1–)2(–3)-flowered	2-flowered	2-flowered
Glumes			
shape	lanceolate	lanceolate	broadly lanceolate
colour	green, yellow (or a mix)	purple to silver	green to violaceous
Lemma			
shape	narrowly oblong	oblong	oblong
apex	4-toothed, lateral teeth larger	4-toothed, teeth minute	erose
size	2.5–4 mm	4–5 mm	2–4 mm
awn insertion	basal-medial third	basal third	medial-upper third
Ligule			
shape	acute	obtuse	truncate
length	2–12 mm	2.5–3 mm	3.5–5 mm
Chromosome no.	$2n$ = 26, 39, 52 (polyploid series)	$2n$ = 28 (tetraploid)	$2n$ = 14 (diploid)
No. of species	ca. 35	1	1
Distribution	cold and cold-temperate regions of both hemispheres; high mountains in tropics	cold-temperate North and South America; Europe; scattered in North Africa	cold-temperate North and South America; Europe

LITERATURE CITED

Albers, F. 1972a. Cytotaxonomie und B-Chromosomen bei *Deschampsia cespitosa* (L.) P.B. und verwandten Arten. *Beitr. Biol. Pflanzen* 48: 1–62.

Albers, F. 1972b. Cytosystematische Untersuchungen in der Subtribus Deschampsiineae Holub (Tribus Aveneae Nees). II. Die Gattungen *Vahlodea* Fr. und *Avenella* Koch. *Ber. Deutsch. Bot. Ges.* 85: 279–285.

Albers, F. 1973. Cytosystematische Untersuchungen in der Subtribus Deschampsiinae Holub (Tribus Aveneae Nees). I. Zwei Arten der Gattung *Corynephorus* P.B. *Preslia* 45: 11–18.

Albers, F. 1978. Karyologische und genomatische Veränderungen innerhalb der Gräser-Subtriben Aristaveninae und Airinae. *Ber. Deutsch. Bot. Ges.* 91: 693–697.

Albers, F. 1980a. Systematik, variation und Entwicklungstendenzen der Subtriben Aristaveninae und Airinae (Gramineae-Aveneae). *Phyton (Horn)* 20: 95–116.

Albers, F. 1980b. Vergleichende Karyologie der Gräser-Subtriben Aristaveninae und Airinae (Poaceae-Aveneae). *Pl. Syst. Evol.* 136: 137–167.

Albers, F. 1980c. Karyogeobotanik der Gräser-Subtriben Aristaveninae und Airinae (Aveneae). *Flora* 169: 150–167.

Bakker, F.T., Culham, A., Gomez-Martinez, R., Carvalho, J., Compton, J. Dawtrey, R. & Gibby, M. 2000. Patterns of nucleotide substitution in angiosperm cpDNA *trnL* (UAA)-*trnF* (GAA) regions. *Molec. Biol. Evol.* 17: 1146–1155.

Baldwin, B.G. 1993. Molecular phylogenetics of *Calycadenia* (Compositae) based on its sequences of nuclear ribosomal DNA: chromosomal and morphological evolution re-examined. *Amer. J. Bot.* 80: 222–238.

Baldwin, B.G., Sanderson, M.J., Porter, J.M., Wojciechowski, M.F., Campbell, C.S. & Donoghue, M.J. 1995. The ITS region of nuclear ribosomal DNA: a valuable source of evidence on angiosperm phylogeny. *Ann. Missouri Bot. Gard.* 82: 247–277.

Barker, F.K. & Lutzoni, F.M. 2002. The utility of the incongruence length difference test. *Syst. Biol.* 51: 625–637.

Baumel, A., Ainouche, A.L., Bayer, R.J., Ainouche, A.K. & Misset, M.T. 2002. Molecular phylogeny of the genus *Spartina* Schreb. (Poaceae). *Molec. Phylog. Evol.* 22: 303–314.

Buschmann, A. 1948. Charakteristik und Systematische Stellung von *Deschampsia setacea* (Huds.) Hack. *Phyton* 1: 24–41.

Buschmann, A. 1950. Die makaronesischen *Deschampsia*-Arten. *Phyton* 2: 276–287.

Cafferty, S., Jarvis, C.E. & Turland, N.J. 2000. Typification of Linnean plant names in the Poaceae (Gramineae). *Taxon* 49: 239–260.

Catalán, P., Kellogg, E.A. & Olmstead, R.G. 1997. Phylogeny of Poaceae subfamily Pooideae based on chloroplast *ndhF* gene sequences. *Molec. Phylog. Evol.* 8: 150–166.

Catalán, P., Torrecilla, P., Lopez Rodríguez, J.A. & Olmstead, R.G. 2004. Phylogeny of the festucoid grasses of subtribe Loliinae and allies (Poeae, Pooideae) inferred from ITS and *trnL-F* sequences. *Molec. Phylog. Evol.* 31: 517–541.

Chiapella, J. 2000. The *Deschampsia cespitosa* complex in Central and Northern Europe: a morphological analysis. *Bot. J. Linn. Soc.* 134: 495–512.

Chiapella, J. 2003. Infrageneric classification and phylogeny of *Deschampsia* (Poaceae: Aveneae). Pp. 219–230 in:

Kryukov A. & Yakimenko, L. (eds.), *Problems in Evolution*, vol. 5. Dal'Nauka Publishers, Vladivostok.

Clarke, G.C.S. 1980. Deschampsia. Pp. 225–227 in: Tutin, T.G., Heywood, V.H., Moore, D.M., Valentine, D.H., Walters, S.M. & Webb, D.A. (eds.), *Flora Europaea*, 5. Cambridge Univ. Press, Cambridge.

Clayton, W.D. 1981. Evolution and distribution of grasses. *Ann. Missouri Bot. Gard.* 68: 5–14.

Clayton, W.D. & Renvoize, S.A. 1986. Genera Graminum. *Kew Bull. Addit. Ser.* 13.

Conert, H.J. 1987. Deschampsia. Pp. 302–317 in: Hegi, G., *Illustrierte Flora von Mitteleuropa*. Parey Buchverlag, Berlin.

Corte, A. 1961. Fertilidad de las semillas en fanerógamas que crecen en Cabo Primavera (Costa de Danco), Península Antártica. *Contr. Inst. Antarc. Argent.* 65: 1–16.

Cunningham, C.W. 1997. Is congruence between data partitions a reliable predictor of phylogenetic accuracy? Empirically testing an iterative procedure for choosing among phylogenetic methods. *Syst. Biol.* 46: 464–478.

De la Sota, E.R. & Ponce, M.M. 1998. Pteridophyta. Pp. 282–369 in: Correa, M.N. (dir.), *Flora Patagónica*, Parte I. INTA, Buenos Aires.

Doyle, J.J. & Doyle, J.A. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochem. Bull.* 19: 11–15.

Edgar, E. & Connor, H.E. 2000. *Flora of New Zealand*, vol. V: *Grasses*. Manaaki Whenua Press, Lincoln.

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791.

Ferris, C.R., King, R.A. & Hewitt, G.M. 1997. Evidence for the maternal parentage in the hybrid of *Spartina anglica*. *Molec. Ecol.* 6: 185–187.

Frey, L. 1999. *Avenella*—a genus of the Aveneae (Poaceae) worthy of recognition. *Fragm. Flor. Geobot. Suppl.* 7: 27–32.

García-Suarez, R., Alonso-Blanco, C., Fernandez-Carvajal, M.C., Fernadez-Prieto, J.A., Roca, A. & Giraldez, R. 1997. Diversity and systematics of *Deschampsia* sensu lato (Poaceae), inferred from karyotypes, protein electrophoresis, total genomic DNA hybridization and chloroplast DNA analysis. *Pl. Syst. Evol.* 205: 99–110.

Gaut, B.S., Tredway, L.P., Kubik C., Gaut, R.L. & Meyer, W. 2000. Phylogenetic relationships and genetic diversity among members of the *Festuca-Lolium* complex (Poaceae) based on ITS sequence data. *Pl. Syst. Evol.* 224: 33–53.

Gielly, L. & Taberlet, P. 1994. The use of chloroplast DNA to resolve plant phylogenies: noncoding versus *rbcL* sequences. *Molec. Biol. Evol.* 11: 769–777.

Grebenstein, B., Röser, M., Sauer, W. & Hemleben, V. 1998. Molecular phylogenetic relationships in Aveneae (Poaceae) species and other grasses as inferred from ITS 1 and ITS 2 rDNA sequences. *Pl. Syst. Evol.* 213: 233–250.

Groves, E.W. 1981. Vascular plant collections from the Tristan da Cunha group of Islands. *Bull. Brit. Mus. (Nat. Hist.), Bot.* 8: 333–420.

Hafsten, U. 1960. Pleistocene development of vegetation and climate in Tristan da Cunha and Gough Island. *Univ. Bergen Árbok Naturvidensk.* 20: 1–45.

Hamby, R.K. & Zimmer, E.A. 1988. Ribosomal RNA sequences for inferring phylogeny within the grass family (Poaceae). *Pl. Syst. Evol.* 160: 29–37.

Hess, H.E., Landolt, E. & Hirzel, R. 1967. *Flora der Schweiz*. Birkhäuser Verlag, Basel.

Hitchcock, C.L., Cronquist, A., Ownbey, M. & Thompson, J.W. 1969. *Vascular Plants of the Pacific Northwestern*, part 1. Univ. of Washington Press, Seattle.

Hodkinson, T.R., Renvoize, S.A., Chonghaile, G.N., Stapleton, C.M.A. & Chase, M.W. 2000. A comparison of ITS nuclear DNA sequence data and AFLP markers for phylogenetic studies in *Phyllostachys* (Bambusoideae, Poaceae). *J. Pl. Res.* 113: 259–269.

Hodkinson, T.R., Chase, M.W., Takahashi, C., Leitch, I.J., Bennet, M.D. & Renvoize, S.A. 2002. The use of DNA sequencing (ITS and *trnL-F*), AFLP, and fluorescent in situ hybridization to study allopolyploid *Miscanthus* (Poaceae). *Amer. J. Bot.* 89: 279–286.

Holderegger, R., Stehlik, I., Lewis-Smith, R.I. & Abbott, R.J. 2003. Populations of Antarctic Hairgrass (*Deschampsia antarctica*) show low genetic diversity. *Arctic Antarc. Alpine Res.* 35: 214–217.

Holmberg, G. 1926. Gruppindelningen inom släkted *Deschampsia* med särskild hänsyn till *D. setacea*. *Bot. Not.* 1926: 259–262.

Holmgren, A.H. & Holmgren, N.H. 1977. Poaceae. Pp. 175–464 in: Cronquist, A., Holmgren, A.H., Holmgren, N.H., Reveal, J.L. & Holmgren, P.K. (eds.), *Intermountain Flora*. Columbia Univ. Press, New York.

Hsiao, C., Chatterton, N.J., Asay, K.H. & Jensen, K.B. 1994. Phylogenetic relationships of 10 grass species: an assessment of phylogenetic utility of the internal transcribed spacer region in nuclear ribosomal DNA in monocots. *Genome* 37: 112–120.

Hsiao, C., Chatterton, N.J., Asay, K.H. & Jensen, K.B. 1995a. Phylogenetic relationships of the monogenomic species of the wheat tribe, Triticeae (Poaceae), inferred from nuclear rDNA (ITS) sequences. *Genome* 38: 211–223.

Hsiao, C., Chatterton, N.J., Asay, K.H. & Jensen, K.B. 1995b. Molecular phylogeny of the Pooideae (Poaceae) based on nuclear rDNA sequences. *Theor. Appl. Genet.* 90: 389–398.

Hsiao, C., Jacobs, S.W.L., Chatterton, N.J. & Asay, K.H. 1999. A molecular phylogeny of the grass family (Poaceae) based on the sequences of nuclear ribosomal DNA (ITS). *Austral. Syst. Bot.* 11: 667–688.

Huelsenbeck, J.P., Bull, J.J. & Cunningham, C.W. 1996. Combining data in phylogenetic analysis. *Tree* 11: 152–158.

Hylander, N. 1953. *Nordisk kärlväxtflora*. Almqvist & Wiksell, Stockholm.

Ingvarsson, P.K., Ribstein, S. & Taylor, D.R. 2003. Molecular evolution of insertions and deletions in the chloroplast genome of *Silene*. *Molec. Biol. Evol.* 20: 1737–1740.

Irvine, L.M. & Dixon, P.S. 1982. The typification of Hudson's algae: a taxonomic and nomenclatural reappraisal. *Bull. Brit. Mus. (Nat. Hist.), Bot.* 10: 91–105.

Linné, C. 1753. *Species Plantarum*. Laurentii Salvii, Holmiæ.

Maddison, W.P. & Maddison, D.R. 1992. *MacClade* version 3.04. *Analysis of Phylogeny and Character Evolution*. Sinauer, Sunderland.

McVaugh, R. 1983. *Flora Novo-Galiciana: a Descriptive Account of the Vascular Plants of Western Mexico*. University of Michigan Press, Ann Arbor.

Moon, C.D., Craven, K.D., Leuchtmann, A., Clement, S.L. & Schardl, C.L. 2004. Prevalence of interspecific hybrids amongst asexual fungal endophytes of grasses. *Molec. Ecol.* 13: 1455–1467.

Nadot, S., Bajon, R. & Lejeune, B. 1994. The chloroplast gene *rps4* as a tool for the study of Poaceae phylogeny. *Pl. Syst. Evol.* 191: 27–38.

Nicora, E. 1978. Deschampsia. Pp. 225–238 in: Correa, M.N. (dir.), *Flora Patagónica*, VIII. INTA, Buenos Aires.

Nickrent, D.L., Garcia, M.A., Martin, M.P. & Mathiasen, R.L. 2004. A phylogeny of all species of *Arceuthobium* (Viscaceae) using nuclear and chlorplast DNA sequences. *Amer. J. Bot.* 91: 125–138.

Palisot de Beauvois, A.M.F.J. 1812. Essai d une nouvelle Agrostographie, ou nouveau genres des Graminées, avec figures représentant les caracters de tous les genres. Chez l'auteur, Paris.

Parodi, L.R. 1949. Las gramíneas sudamericanas del género *Deschampsia*. *Darwiniana* 8: 415–475.

Paunero, E. 1955. Las Aveneas Españolas I. *Anales Inst. Bot. Cavanilles* 13: 149–229.

Ridgway, K.P., Duck, J.M. & Young, J.P.W. 2003. Identification of roots from grass swards using PCR-RFLP and FFLP of the plastid *trnL* (UAA) intron. BMC Ecology 3: 8, doi: 10.1186/1472-6785-3-8.

Rzedowski, J. & Rzedowski, G. 1990. *Flora Fanerogámica del Valle de Mexico* 2. Publicaciones del Instituto de Ecologia, Michoacán.

Sang, T. 2002. Utility of low-copy nuclear gene sequences in plant phylogenetics. *Crit. Rev. Biochem. Molec. Biol.* 37: 121–147.

Schmeil, O. 1988. *Flora von Deutschland.* Quelle & Meyer Verlag, Heidelberg.

Small, R.J., Cronn, R.C. & Wendel, J.F. 2004. L.A.S. Johnson Review No. 2. Use of nuclear genes for phylogeny reconstruction in plants. *Austral. Syt. Bot.* 17: 145–170.

Soreng, R.J. 2003. Vahlodea. Pp 687–688 in: Soreng, R.J., Peterson, P.M., Davidse, G., Judziewicz, E.J., Zuloaga, F.O., Filgueiras, T.S. & Morrone, O. (eds.), *Catalogue of New World Grasses (Poaceae): IV. Subfamily Pooideae. Contr. U.S. Natl. Herb.* 48: 1–730.

Soreng, R.J. & Davis, J.I. 1998. Phylogenetics and character evolution in the Grass family (Poaceae): simultaneous analysis of morphological and chloroplast DNA restriction site data character sets. *Bot. Rev.* 64: 1–85.

Stace, C.A. 1991. *New Flora of the British Isles.* Cambridge University Press, Cambridge.

Subbotin, S.A., Krall, E.L., Riley, I.T., Chizhov, V.N., Staelens, A., De Loose, M. & Moens, M. 2004. Evolution of the gall-forming plant parasitic nematodes (Tylenchida: Anguinidae) and their relationships with hosts as inferred from Internal Transcribed Spacer sequences of nuclear ribosomal DNA. *Molec. Phylog. Evol.* 30: 226–235.

Swofford, D.L. 2000. *PAUP: Phylogenetic analysis using parsimony*, version 4.0. Sinauer, Sunderland.

Taberlet, P, Gielly, L., Pautou, G. & Bouvet, J. 1991. Universal primers for amplification of three non-coding regions of chlorplast DNA. *Pl. Molec. Biol.* 17: 1105–1109.

Tryon, A.F. 1966. Origin of the fern flora of Tristan da Cunha. *Brit. Fern Gaz.* 9: 269–276.

Tzvelev, N.N. 1976. *Grasses of the Soviet Union.* Nauka Publishing House, Leningrad.

Tzvelev, N.N. 1989. The system of grasses (Poaceae) and their evolution. *Bot. Rev.* 55: 141–204.

Van Royen, P. 1979. *The Alpine Flora of New Guinea.* J. Cramer, Vaduz.

Wagner, W.L., Herbst, D.L. & Sohmer, S.H. 1990. *Manual of the flowering plants of Hawaii.* Univ. of Hawaii Press, Honolulu.

White, T.J., Bruns, T., Lee, S. & Taylor, J. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Pp. 315–322 in: Innis, M.A., Gelfand, D.H., Sninsky, J.J. & White, T.J. (eds.), *PCR protocols. A Guide to Methods and Applications.* Academic Press, San Diego.

Wolfe, K.H., Li, W.-H. & Sharp, P.M. 1987. Rates of nucleotide substitution vary greatly among plant mitochondrial, chloroplast and nuclear DNAs. *Proc. Natl. Acad. Sci. U.S.A.* 84: 9054–9058.

Zuloaga, F.O., Nicora, E.G., Rúgolo Z., Morrone, O., Pensiero, J. & Cialdella, A.M. 1994. Catálogo de la Familia Poaceae en la República Argentina. *Mongr. Syst. Bot. Missouri Bot. Gard.* 47: 1–178.

Appendix. Taxa included, voucher information and EMBL accessions for DNA sequences used in this paper. Accessions marked [1] included only in ITS analysis; marked [2] included only in *trnL* analysis; marked [3] retrieved from EMBL/GenBank; references for retrieved accessions: [4] Hsiao & al. 1995a, CESP; [5] Subbotin & al. 2004, [6] Moon & al. 2004, AGRO; [7] Grebenstein & al. 1998; [8] Gilley & Taberlet 1994, AVEN; [9] Gaut & al. 2000, [10] Ridgway & al. 2003, POAP; [11] Grebenstein & al. 1998, TRIS.

Taxa, geographic origin, voucher specimen, EMBL accession (ITS, *trnL*), code (more than one entry after a species name indicates multiple accessions for that species)

***Deschampsia antartica* (Hook. f.) E. Desv**, Malvinas (Falklands), Stanley Harbour, *D. Broughton s.n.* (WU), AM041213, AM041248, ANT1; Argentina, Tierra del Fuego, Estancia Maria Cristina, *F. Roig 15984* (MERL), AM041214, AM041249, ANT2; Argentina, Tierra del Fuego, turbera Terra Australis, *F. Roig 15969* (MERL), AM041215, AM041250, ANT3; ***Deschampsia atropurpurea* (Wahlenb.) Scheele**, Argentina, Tierra del Fuego, Ushuaia, *MERL 44026* (MERL), AM041216, AM041251, ATRO; ***Deschampsia berteroana* (Kunth) Trin.**, Chile, Santiago, Batuco, *S. Bliss 601* (CONC), AM041217, AM041252, BERT; ***Deschampsia cespitosa* subsp. *alpina* (L.) Tzvelev**, Sweden, Torne Lappmark, Abisko, *F. Vierhafen s.n.* (WU), AM041218[1] (ITS), CE-A1; Norway, Sør Trøndelag, Oppland, *A. Brysting 02-5* (WU), AM041219, AM041255, CE-A2; ***Deschampsia cespitosa* subsp. *botnica* (Wahlenb.) Tzvelev**, Sweden, Kappelskär, *J. Chiapella 788* (WU), AM041220[1] (ITS), CE-BO; ***Deschampsia cespitosa* (L.) P. Beauv.**, Sweden, Färingsö, *J. Chiapella 783* (WU), AM041221[1] (ITS), CES1; Sweden, Rättvik, *J. Chiapella 787* (WU), AM041222, AM041253, CES2; Norway, Hedmark, Opphus, *J. Chiapella 767* (WU), AM041223[1] (ITS), CES3; Argentina, Mendoza, Malargüe, *F. Roig 15811* (MERL), AM041224, AM041254,

Appendix. Continued.

CES4; Argentina, Río Negro, Estancia El Condor, *S. Chichizola s.n.* (MERL), AM041225[1] (ITS), CES5; ***Deschampsia chapmanii* Petrie**, New Zealand, Eyre Mts., George Burn, *A. Druce S141 25-32* (CHR), AM041226, AM041256, CHAP; ***Deschampsia christophersenii* C.E. Hubb.**, Tristan da Cunha, Green Hill, *G. Jakubowsky 285* (WU), AM041227, AM041257, CHR1; Tristan da Cunha, Burntwood, *G. Jakubowsky 290* (WU), AM041228, AM041258, CHR2; ***Deschampsia danthonioides* (Trin.) Benth**, Chile, O'Higgins, Termas de Cauquenes, *A. Pfister 13102* (CONC), AM041229[1] (ITS), DANT; ***Deschampsia elongata* (Hook.) Benth.**, Argentina, Río Negro Lago Mascardi, *J. Chiapella 763* (WU), AM041230, AM041259, ELON; ***Deschampsia flexuosa* (L.) Trin.**, Sweden, Härjedalen, Idre, *J. Chiapella 775* (WU), AM041231, AM041260, FLE1; Malaysia, Mt. Kinabalu, *J. van Valkenburg 1452* (WAG), AM041232, AM041261, FLE2; Argentina, Tierra del Fuego, Estancia Ushuaia, *P. Quiroga & al. s.n.* (WU), AM041233[1] (ITS), FLE3; Argentina, Tierra del Fuego, Tolhuin, *F. Roig 14929* (MERL), AM041234[1] (ITS), FLE4; New Zealand, Otago, Ross Creek Reserve, *P.N. Johnson 995* (CHR), AM041262[2] (*trnL*), FLE5; Finland, Nauvo Haverö, Pajula, *T. Lempiäinen & V. Laine s.n.* (WU), AM041263[2] (*trnL*), FLE6; ***Deschampsia kingii* (Hook. f.) E. Desv.**, Argentina, Tierra del Fuego, Parque Nacional Tierra del Fuego, *P. Quiroga & al. s.n.* (WU), AM041235, AM041264, KIN1; Argentina, Tierra del Fuego, Estancia Ushuaia, *V. Lencinas & G. M. Pastur s.n.* (WU), AM041236 (ITS), KIN2; ***Deschampsia klossi* Ridl.**, Indonesia, Irian Jaya, Mt. Jaya, *J. Mardsen & al. 186* (L), AM041237, AM041265, KLOS; ***Deschampsia laxa* Phil.**, Chile, Palena, Pampa Pichanco, *F. Roig 13007* (MERL), AM041238, AM041266, LAXA; ***Deschampsia mejlandii* C.E. Hubb.**, Tristan da Cunha, Green Hill, *G. Jakubowsky 287* (WU), AM041239, AM041267, MEJL; ***Deschampsia nubigena* Hillebr.**, U.S.A., Hawaii, East Maui, *K.R. Wood 4259* (WU), AM041246, AM041268, NUBI; ***Deschampsia parvula* (Hook. f.) E. Desv.**, Argentina, Tierra del Fuego, Río Moat, F. Roig 14920 (MERL), AM041240, AM041269, PARV; ***Deschampsia patula* (Phil.) Skottsb.**, Argentina, Santa Cruz, Estancia Punta Alta, *TBPA 744* (MERL), AM041241 (ITS), PATU; ***Deschampsia tenella* Petrie**, New Zealand, Southland, Upper Wanganui, *P. Wardle & R.P. Buxton 94-153* (CHR), AM041244, AM041270, TENE; ***Deschampsia venustula* Parodi**, Argentina, Santa Cruz, Lago Argentino, *F. Roig 14477* (MERL), AM041245, AM041271, VENU; ***Aira caryophyllea* L.**, Chile, Bío Bío, Concepción, *K.H. Rechinger 63093* (W), AM049252, AM049254, AIRA; ***Arrhenatherum elatius* (L.) J. Presl & C. Presl**, Austria, Lower Austria, Gutenstein, *W. Till s.n.* (WU), AM049253, AM049255, ARRH; ***Deschampsia cespitosa***[1, 3], L36513[4] (ITS), CESP; ***Agrostis capillaris* L.**[3], AF498395[5], AY450948[6], AGRO; ***Avena sativa* L.**[3], Z96890[7], Z96893[7], X75695[8], AVEN; ***Poa pratensis* L.**[3], AF171183[9], AY177349[10], POAP; ***Trisetum flavescens* (L.) P. Beauv.**[1, 3], Z96896[11], Z96897[11], TRIS.