Research Article

Phylogeny, biogeography, reticulation, and classification of *Agrostis* (Poaceae: Pooideae: Poeae: Agrostidinae) with expansion of *Polypogon* to include *Lachnagrostis* (in part)

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Abstract To investigate the evolutionary relationships and biogeographical history among the species of *Agrostis* and allied genera within the subtribe Agrostidinae, we generated a phylogeny based on sequences from nuclear ribosomal DNA (ITS) and three plastid regions (*rpl32-trnL* spacer, *rps16-trnK* spacer, and *rps16* intron). We also aimed to assess the generic limits of *Agrostis*, characterize possible subgeneric relationships among species in the genus, identify hypothesized reticulation events, and present our biogeographical theory. Based on our phylogeny of 198 samples, representing 138 species (82 from *Agrostis* as currently recognized, 10 from *Polypogon*, and 10 from *Lachnagrostis*), we identify two strongly supported clades within *Agrostis*: clade Longipaleata (*Agrostis* subg. *Vilfa*) and clade Brevipaleata (*A.* subg. *Agrostis*). The species of *Agrostis* in clade Longipaleata usually have florets with paleas 2/5 to as long as the lemma, whereas species in clade Brevipaleata have florets with paleas less than 2/5 as long as the lemma, minute, or absent. Core (species with congruent alignment using ITS and plastid data) phylogenetic analysis of *Agrostis* reveals three strongly supported clades within Longipaleata (European-Northwest African, Asian, and African), three strongly supported clades within Brevipaleata (Asian, North American, and South American), and a European grade leading to the latter two. Of the six genera commonly associated with *Agrostis*, that is, *Bromidium*, *Polypogon*, *Lachnagrostis*, *Linkagrostis*, *Chaetopogon,* and *Chaetotropis*, only *Polypogon* maintained its status as a separate genus, while the remaining genera are subsumed within *Agrostis* or *Polypogon*. *Polypogon* is identified as an intergeneric hybrid originating via ancient hybridization between unknown representatives of *Agrostis* clade Longipaleata (plastid DNA) and *Calamagrostis* clade Americana (nrDNA). We include several species of *Lachnagrostis*, including the type (*L. filiformis*), that follow the same pattern in *Polypogon*, while the remaining species of *Lachnagrostis* in our study are identified as ancient intersubgeneric hybrids within *Agrostis*. We propose nine new combinations in *Polypogon*: *P. adamsonii* (Vickery) P.M. Peterson, Soreng & Romasch.; *P. aemulus* (R. Br.) P.M. Peterson, Soreng & Romasch.; *P. billardierei* (R. Br.) P.M. Peterson, Soreng & Romasch.; *P. bourgaei* (E. Fourn.) P.M. Peterson, Soreng & Romasch.; *P. filiformis* (G. Forst.) P.M. Peterson, Soreng & Romasch.; *P. littoralis* P.M. Peterson, Soreng & Romasch.; *P. exaratus* (Trin.) P.M. Peterson, Soreng & Romasch.; *P. polypogonoides* (Stapf) P.M. Peterson, Soreng & Romasch.; and *P. reuteri* (Boiss.) P.M. Peterson, Soreng & Romasch. We designate lectotypes for the names *Agrostis* sect. *Aristatae* Willd., *Agrostis barbuligera* Stapf, *A. bourgaei* E. Fourn., *A. eriantha* Hack., *A. exarata* Trin., *A. lachnantha* Nees, *A. polypogonoides* Stapf, *Chaetotropis chilensis* Kunth, *Polypogon elongatus* Kunth, *P. inaequalis* Trin., *P. suspicatus* Willd., and *Vilfa muricata* J. Presl.

Key words: *Agrostis*, *Calamagrostis*, *Chaetopogon*, *Chaetotropis*, genomic introgression, ITS, *Linkagrostis*, phylogenetic analysis, plastid DNA sequences, taxon duplication approach, taxonomy.

1 Introduction

The genus *Agrostis* L. includes ca. 198 species worldwide and is placed in subtribe Agrostidinae Fr., supersubtribe Agrostidodinae Soreng, tribe Poeae R.Br., and supertribe Poodae L. Liu in subfamily Pooideae Benth. (Soreng et al., 2022). The conserved type of the genus is *A. canina* L. based on a lectotype selected by Philipson (1937); this supersedes the lectotypification on *A. stolonifera* L. by Hitchcock (1920) [Jarvis, 1992; Brummitt, 1995; Portal, 2009]. Trinius (1820, 1824) recognized the length of the palea as an important character in separating species of *Agrostis* into two groups. He placed species with short paleas in *A.* sect. *Trichodium* (Michx.) Trin. (lectotype *Trichodium laxiflorum* Michx. = *Agrostis scabra* Willd.) and those with longer paleas in *A.* sect. *Vilfa* (Adans.) Roem. & Schult. [lectotype *Vilfa stolonifera* (L.) P. Beauv. = *A. stolonifera* L.].

Since Trinius's classification, researchers have attempted to identify additional lineages within the genus. Björkman (1960) recognized four groups in *Agrostis* differing in lemma epidermal morphology: (1) species with a lemmatal network (*Trichodium* net) present on lemma (in 91 species); (2) species with a lemmatal network fragmentarily developed (in nine species); (3) species with a tendency toward having a lemmatal network (in five species); and (4) species with a lemmatal network wanting (in 13 species). Björkman (1960) found that all but one (78 of 79) species with short paleas (ca. ≤ 1/3 the lemma length) had a *Trichodium* net (group 1), while 15 species with long paleas (ca. >1/3 the lemma length) also had a *Trichodium* net (group 1). Of the latter, 11 were species from the mountains of tropical Africa. Group 2 included *Agrostis stolonifera* L., a species with variable lemma epidermal morphology, and Group 3 included *A. gigantea* Roth. Group 4 included some Australian taxa commonly recognized in *Lachnagrostis* Trin. (e.g., Widén, 1971; Edgar, 1995; Jacobs, 2001; Brown, 2013), two Mediterranean annuals, including *Agrostula truncatula* (Parl.) P.M. Peterson, Romasch., Soreng & Sylvester [syn. ≡ *Neoschischkinia truncatula* (Parl.) Valdés & H. Scholz] (Valdés & Scholz, 2006; Peterson et al., 2020), and a few other species. Widén (1971) refined this classification and recognized seven types of epidermal surface structures, but maintained the traditional classification of the genus, placing species in *Agrostis* sects. *Agrostis* (including *Agrostis* sect. *Trichodium*) and *Vilfa*. Finot et al. (2011) studied the micromorphology of lemmas in species of *Agrostis* and *Polypogon* Desf. in Chile and came to similar conclusions that *Agrostis* could be separated into two distinct groups. In the former Soviet Union, Tzvelev (1976, 1983) recognized four sections in the genus: (1) *Agrostis* sect. *Agrostis*, with species with paleas 1/2–2/3 the length of a usually unawned lemma; (2) *A.* sect. *Pentatherum* (Nábělek) Tzvelev [type *Calamagrostis olympica* Boiss. = *A. olympica* (Boiss.) Bor], with paleas 2/3–1 the length of a dorsally awned lemma (Doğan, 1985; Clayton et al., 2006); (3) *A.* sect. *Agraulus* (P. Beauv.) Tzvelev, *nom. superfl.* for *A.* sect. *Agrostis* [lectotype *Agraulus caninus* (L.) P. Beauv. = *A. canina*, designated by Hitchcock, 1937], with paleas <1/3 the length of a dorsally awned lemma; and (4) *A.* sect. *Trichodium*, with paleas absent or <1/6 the length of a usually unawned lemma. Romero García et al. (1988a, 1988b) divided *Agrostis* into two subgenera in the Iberian Peninsula:

(1) *A.* subg. *Zingrostis* A.T. Romero García, G. Blanca López & C. Morales Torres (type *A. reuteri* Boiss.), containing species that have diffuse panicles with widely spreading, capillary, and divaricate branches and paleas 1/2−1 the length of an unawned lemma; (2) *A.* subg. *Agrostis*, consisting of three sections: *A.* sect. *Agrostis* [= *A.* sect. *Trichodium*, *A.* sect. *Agraulus* (P. Beauv.) Tzvelev], with paleas <1/3 the length of the lemma; *A.* sect. *Vilfa*, with paleas 1/2−2/3 the length of a usually unawned lemma; and *A.* sect. *Aperopsis* Asch. & Graeb. [= *Neoschischkinia* Tzvelev], with paleas <1/6 the length of the awned or unawned lemma and an annual lifecycle. Kurchenko (2010) formed an evolutionary hypothesis within *Agrostis* and classified the genus found in Russia and neighboring countries into four sections: *Vilfa, Agrostis, Pseudopolypogon* Kurchenko [type *A. hissarica* Roshev. = *Polypogon hissaricus* (Roshev.) Bor] with disarticulation below the scabrous and muticous glumes, and *Trichodium*. Tzvelev & Probatova (2019) followed this system, with the exclusion of *A.* sect. *Pseudopolypogon*, which is absent from modern Russia.

Several additional infrageneric names have been proposed in *Agrostis* that remain in *Agrostis*: *A.* sect. *Agrostiotypus* Asch. & Graebn. (type *A. stolonifera*, *nom. superfl. pro A.* sect. *Vilfa*), *A.* sect. *Dolichagrostis* Honda (type *A. nipponensis* Honda = *A. valvata* Steud.), *A.* sect. *Microphyllae* Beetle (type *A. microphylla* Steud.), *A.* sect. *Quinquesetum* Parodi (type *A. ramboi* Parodi; syn. *Bromidium ramboi* Nees & Meyen = *Agrostis ramboi*), and *A.* sect. *Bromidium* (Nees & Meyen) E. Desv. (type *A. hygrometrica* Nees; = *Agrostis hygrometrica*). *Bromidium* Nees & Meyen was separated from *Agrostis* as having lemma usually pubescent, nerves extended as four setae, dorsal awn well developed, and caryopsis thin or liquid (with lipid) (Rúgolo de Agrasar, 2012); however, DNA data place the genus within *Agrostis* (da Silva et al., 2020).

Several other infrageneric names in *Agrostis* apply to other genera as currently understood: *A.* sect. *Airagrostis* Griseb. [type *A. trichoclada* Griseb., syn. *A.* subg. *Airagrostis* (Griseb.) Schischk. = *Colpodium biebersteinii* (Boiss.)], *A.* sect. *Apera* (Adans.) Dumort. [type *Apera spica-venti* (L.) P. Beauv., syn. *A.* subg. *Apera* (Adans.) Rchb. = *Apera* Adans.], *A.* sect. *Aristatae* Willd. [lectotype, **designated here**: *Apera spica-venti* (L.) P. Beauv.], *A.* sect. *Deyeuxia* (Clarion ex P. Beauv.) Hook. f. (type *Deyeuxia montana* P. Beauv. = *Calamagrostis* Adans.), *A.* sect. *Lachnagrostis* (Trin.) E. Desv. (type *Avena filiformis* G. Forst. = *Lachnagrostis* Trin.), *A.* sect. *Nardagrostis* Asch. & Graebn. (type *A. curtisii* Kerguélen = *Alpagrostis* P.M. Peterson, Romasch., Soreng & Sylvester), *A.* sect. *Podagrostis* Griseb. [type *A. canina* var. *aequivalvis* Trin. = *Podagrostis* (Griseb.) Scribn. & Merr.], and *A.* subg. *Vilfoidea* Rouy [type *A. verticillata* Vill. = *Polypogon viridis* (Gouan) Breist. = *Polypogon* sect. *Vilfoidea* (Rouy) Tzvelev].

In recent years, several species formerly recognized in *Agrostis* have been moved to other genera, in most cases based on phylogenetic evidence, including *Agrostula* (monotypic: *Agrostula truncatula* = *Neoschischkinia truncatula* (Parl.) Valdés & H. Scholz = *Agrostis truncatula*) [Peterson et al., 2020]; *Alpagrostis*, with four species distributed in Europe and the Mediterranean formerly considered part of the *Agrostis alpina* Scop. complex (Peterson et al., 2020); and *Podagrostis*, now with 12

recognized species, including five species transferred from *Agrostis* by Sylvester et al. (2020) and two by Molina et al. (2021). By contrast, phylogenetic data have shown that four of the five species formerly recognized within *Agrostis* that subsequently had been moved to *Neoschischkinia* Tzvelev [i.e., *N. reuteri* (Boiss.) Valdés & H. Scholz = *A. reuteri*, *N. pourretii* (Willd.) Valdés & H. Scholz = *A. pourretii* Willd., *N. elegans* (Thore) Tzvelev = *A. tenerrima* Trin., *N. nebulosa* (Boiss. & Reut.) Tzvelev = *A. nebulosa* Boiss. & Reut.] are nested within the *Agrostis* lineage and best recognized in that genus (Peterson et al., 2020).

Polypogon [type *Alopecurus monspeliensis* L. = *P. monspeliensis* (L.) Desf.], with approximately 22 species, differs from *Agrostis* in having spikelets that disarticulate below the glumes (vs. above the glumes), a broader and more truncate lemma, awned glumes (vs. unawned), photosynthetic tissue of the lemma covering most of the lemma (vs. continuous in the lower part of the lemma and extending along the nerves distally), paleas with a bundle of small elongated cells in each tip if two-tipped (vs. palea tips single-pointed if two-tipped, or rarely ca. aristate), and caryopses broadest above the middle (vs. broadest at or below the middle) (Björkman, 1960; Kellogg, 2015; Romero García, 2021d). Ascherson & Graebner (1899) divided *Polypogon* into two sections: *Polypogon* sect. *Eupolypogon* (*nom. inval.* = *Polypogon* sect. *Polypogon*) and *Polypogon* sect. *Polypogonagrostis* Asch. & Graebn (lectotype *P. elongatus* Kunth, designated by Tzvelev, 1976). *Polypogon* sect. *Polypogonagrostis* originally included two species: *P. littoralis* Sm. [= *P. lutosus* (Poir.) Hitchc. ≡ × *Agropogon lutosus* (Poir.) P. Fourn., the type of × *Agropogon* P. Fourn (*Agrostis* × *Polypogon*)] and *P. elongatus* Kunth [syn. ≡ *Chaetotropis elongatus* (Kunth) Björkman, syn. = *Nowodworskya* J. Presl]. Four species have been recognized in the section (Tzvelev, 1976, 1983), all of which have a *Trichodium* net on their lemma epidermises in addition to having 1-flowered stipitate spikelets with awned or unawned glumes exceeding the floret and paleas 1/2 to as long as the lemma (Björkman, 1960; Barkworth, 2007; Saarela et al., 2010, 2017; Tkach et al., 2020; Soreng et al., 2022). Species of *Polypogon* sect. *Polypogonagrostis* are similar to *Agrostis* in having relatively small paleas, elongated caryopses, sparse photosynthetic tissue on the lemma, and glossy lemma surfaces (Björkman, 1960). The species of this section have also been included in *Agrostis* (Röser & Tkach, 2024). Alternatively, some authors have recognized species of *Polypogon* sect. *Polypogonagrostis* in the genus *Chaetotropis* Kunth (Kunth, 1829–1835; Björkman, 1960; Nicora, 1970, 1978; Nicora & Rúgolo de Agrasar, 1987; Rúgolo de Agrasar, 2012; Soreng et al., 2017).

Numerous researchers have documented discordance between nuclear and plastid sequence data of species of *Agrostis* and *Polypogon,* suggesting reticulate hybridization events or chloroplast capture among the species (Reichman et al., 2006; Rotter et al., 2010; Saarela et al., 2010, 2017; Honig et al., 2015). For example, in their plastid tree, Saarela et al. (2017) found that all species of *Polypogon* that they sampled, representing both sections, form a strongly supported clade also including *Agrostis capillaris* L. and *A. gigantea* that was sister to a larger *Agrostis* clade. In their nuclear (ITS and ITS + ETS) trees, however, their sample of *P.* sect. *Polypogonagrostis* (*P. elongatus*) was nested in the

Agrostis clade among species with a *Trichodium* net on their lemma epidermises, whereas the other species of *Polypogon* formed a strongly supported clade, also including *Agrostis exarata* and one (ITS + ETS) or more (ITS) species of *Lachnagrostis*, that were more closely allied with *Calamagrostis* than the main *Agrostis* clade. Recently, it has been suggested that all species of *Polypogon* should be subsumed within *Agrostis* (Röser & Tkach, 2024).

Lachnagrostis is a genus of ca. 40 species of annuals and perennials with inflorescences often shedding and dispersing as a whole, spikelets 1-to (sometimes) 2-flowered with a rachilla extension, glumes longer than the florets, callus with hairs up to ca. 2/3 the length of the lemma, and lemmas with minute teeth at the apex, unawned or with an abaxial awn, the awn straight or geniculate (Kellogg, 2015—20 spp. of Australasia, and considered polyphyletic based on sampling of Saarela et al., 2010, 2017; Soreng et al., 2022—ca. 40 spp. mainly from Australasia, but six or more from Africa and one endemic to South America). *Lachnagrostis* has been linked to *Agrostis* and has often been placed as a synonym of *Agrostis* (e.g., Clayton & Renvoize, 1986). Saarela et al. (2017) sampled a few *Lachnagrostis* species, but as there was no overlap in the species sampled in their ITS and *matK* trees, they were unable to make conclusions about their affinities. However, with a much broader sampling of *Lachnagrostis*, Brown (2013, 2015) found the genus to be non-monophyletic based on nuclear and plastid data and found some incongruence between these genomes.

Chaetopogon Janchen is a monotypic genus (*C. fasciculatus* Link) characterized by having an annual habit, panicles moderately dense, spikelets lacking a rachilla extension and falling entire, and lower glumes becoming a long slender awn (Clayton & Renvoize, 1986; Soreng et al., 2015). Some researchers have included *Chaetopogon* in *Polypogon* [*P. fasciculatus* (Link) Pers.], with which it shares some morphological features (awned glumes, spikelets falling entire), while Kellogg (2015) and Soreng et al. (2017, 2022) treated *Chaetopogon* as a synonym of *Agrostis* based on the ITS phylogeny in Saarela et al. (2010, 2017). However, in their plastid *trnL-trnF* tree (Saarela et al., 2017, suppl. material 11), *Chaetopogon* is excluded from a strongly supported *Agrostis* p.p. clade and allied with *Polypogon*, *Agrostis capillaris* p.p., *A. gigantea* p.p., and a few other taxa, congruent with the plastid tree in Quintanar et al. (2007). The incongruence between nrDNA and plastid data of *C. fasciculatus* indicates that the genus likely has a hybrid origin (Saarela et al., 2017).

Bromidium is a small genus of four annual and one perennial species distributed in South America characterized by having 5-veined lemmas with the lateral veins clearly aristate (mucronate or short-awned) [Rúlogo de Agrasar, 1982, 2007, 2012]. These five species have at one time on another been placed in *Agrostis* or *Deyeuxia* (Jacobs, 2009; Peterson & Harvey, 2012).

Calamagrostis Adans., a large genus with 130 species (including *Deyeuxia* Clarion ex P. Beauv. s.s., but excluding American species transferred to *Cinnagrostis* Griseb., *Deschampsia* P. Beauv., *Greeneochloa* P.M. Peterson, Soreng, Romasch. & Barberá, *Laegaardia* P.M. Peterson, Soreng, Romasch. & Barberá, *Paramochloa* P.M. Peterson, Soreng, Romasch. & Barberá, and *Peyritschia* E. Fourn., and Australasian species transferred to *Echinopogon* and *Pentapogon* R. Br.)

with 1-flowered spikelets, lemmas with a callus of a crown of hairs, and usually with a single dorsally attached awn, is closely related to *Agrostis* (Saarela et al., 2017; Peterson et al., 2019, 2020, 2021). In the Eastern Hemisphere and Australasia, species morphologically similar to *Calamagrostis* and *Deyeuxia* (when recognized) were also historically placed in *Agrostis* (Vickery, 1940; Zotov, 1965; Edgar, 1995). Most of these have not yet been investigated phylogenetically.

Cytologically, most species of *Agrostis* are polyploid, and the species that have been investigated, which mostly are turf, pasture, and erosion control grasses, are principally allopolyploids (Rotter et al., 2010; Honig et al., 2015; Saarela et al., 2017). Based on a literature survey of chromosome numbers in *Agrostis,* the following 12 species are the only known diploids ($2n = 14$) in the genus: *Agrostis atlantica* Maire & Trab. *A. canina, A. flaccida* Hack. (= *Podagrostis*?), *A. juressi* Link, *A. kurczenkoae* Prob., *A. nebulosa, A. pourretii, A. reuteri, A. sozanensis* Hayata (= *A. infirma* Buse), *A. tenerrima, A. tilenii* N. Fel. & Castrov., and *A. trinii* Turcz (= *A. vinealis* Schreb.) (Rice et al., 2014; Tzvelev & Probatova, 2019). No diploids are known in *Calamagrostis. Polypogon maritimus* Willd. is the only known diploid in that genus. Diploids are reported for all or most counted species of other accepted Agrostideae genera (*Agrostula, Alpagrostis, Gastridium* P. Beauv., *Podagrostis,* and *Triplachne* Link.) and two others accepted in *Agrostis* (*Linkagrostis* Romero García & C. Morales, and *Neoschischkinia*) [Rice et al., 2014].

The main goals of this study are to estimate the phylogenetic relationships among species of *Agrostis* based on ITS and three plastid DNA regions (*rpl32-trnK, rps16* intron, and *rps16-trnK*) and determine their relationships with species of *Bromidium, Calamagrostis, Chaetopogon, Chaetotropis, Lachnagrostis, Linkagrostis, Neoschischkinia,* and *Polypogon.* In addition, we aim to assess the generic limits of *Agrostis,* characterize possible subgeneric relationships among species in the genus, identify hypothesized reticulation events, and include phylogeographical interpretations of the evolutionary history of *Agrostis.*

This study was designed as a sequel to our previous study on the phylogeny of the closely related genus *Calamagrostis* (Peterson et al., 2021), using similar methods and based on the same principles. Here, we continue to advance the concept of core phylogeny and its usefulness, especially in phylogenetic studies of large genera with complex relationships among their members, using conventional genetic data such as cpDNA and ITS nrDNA sequences. We consider a core phylogeny to represent an evolutionary pattern among species based only on direct decent, excluding taxa or individuals with genomes of multiple origins. Following this concept in our phylogenetic studies, we split the analysis into two main phases. First, we develop a phylogenetic tree using only the "core" set of available taxa or individuals presumably having a single origin, and then we rerun the analysis with the addition (usually one taxon at a time) of taxa or individuals with genetic data (plastid or nuclear) for which multiple origins were detected. This taxon duplication approach (Pirie et al., 2008; Pelser et al., 2010; Peterson et al., 2015a, 2016, 2020, 2021) uses the core phylogeny as a framework to test the affinities of species based on different types of genetic data.

Eventually, these affinities can be characterized, providing inferences about the species origins and geographical distribution. Our core phylogeny of *Calamagrostis* (Peterson et al., 2021) demonstrated a better-developed topology of the species in the phylogeny and higher support for phylogenetic groups than did previous studies on *Calamagrostis* (Saarela et al., 2017), allowing for more meaningful biogeographic definitions of the groups. We attribute this to the elimination from analysis of incongruent data, including confounding ITS data that likely result from incomplete genomic introgression, gene flow, or incomplete concerted evolution. The feature of nrDNA to homogenize during different stages of genomic introgression and to reflect in various degrees the affinities with parental species is well documented (Fuertes Aguilar et al., 1999; Bailey et al., 2003; Liu et al., 2020; Wang et al., 2023). When compared to low-copy gene analysis, ITS data can sometimes indicate an intermediate position for hybrid species, that is, between locations of presumable parental taxa (Romaschenko et al., 2013), or provide an erroneous phylogenetic position for such species (Peterson et al., 2021). In a recent study of *Calamagrostis* (Peterson et al., 2021), the inclusion in phylogenetic analyses of a few possibly confounding ITS sequences significantly reduced the backbone support of the phylogeny. In the meantime, the application of the same set of ITS sequences, as part of the taxon duplication approach, was crucial in identification of the monophyletic "floating" group *Calamagrostis* subsect. *Deschampsiagrostis* V.N. Vassil. (whose affinities within the genus were unstable among analyses) displaying several morphological synapomorphies, which would have been difficult to interpret otherwise (Peterson et al., 2021). These challenges with ITS in phylogenetic reconstructions, which we encountered in our studies on Poeae and Stipeae, point to the necessity of using the taxon duplication approach, which can be a powerful tool for reconstruction of complex phylogenetic relationships among species.

2 Material and Methods

2.1 Taxon sampling
We sampled 198 samples, representing 138 species (82 species from *Agrostis* as currently recognized; see Soreng et al., 2022; Röser & Tkach, 2024) and eight genera representing Agrostidinae. A complete list of taxa including authorities, voucher information, and GenBank numbers can be found in Appendix S1. In many cases, we extracted DNA from silica-dried material collected by the authors. The remaining samples were obtained from specimens in the United States National Herbarium (US) and the Real Jardín Botánico (MA). In three cases, we used ITS data from GenBank.

It is necessary to include the types of genera and other higher taxa when conducting molecular studies and revising taxonomic classifications based on phylogenetic results so that names of higher taxa can be correctly applied to lineages. The following species included in our analyses are the types of their respective genus: *Agrostis canina* L. (conserved name), *Calamagrostis canescens* (Weber) Roth, *Chaetopogon fasciculatus* (Link) Hayek, *Chaetotropis chilensis*

Kunth, *Chascolytrum subaristatum* (Lam.) Desv., *Deyeuxia pyramidalis* (Host.) Veldkamp [= *Calamagrostis arundinacea* (L.) Roth], *Gastridium australe* (L.) P. Beauv. [= *G. ventricosum* (Gouan) Schinz & Thell.], *Greeneochloa coarctata* (Eaton) P.M. Peterson, Soreng, Romasch. & Barberá, *Lachnagrostis filiformis* (G. Forst.) Trin., *Laegaardia ecuadoriensis* (Laegaard) P.M. Peterson, Soreng, Romasch. & Barberá, *Linkagrostis juressi* (Link) Romero García, Blanca & Morales (= *Agrostis juressi*), *Neoschischkinia elegans* (Thore) Tzvelev (= *Agrostis tenerrima*), *Paramochloa effusa* (Kunth) P.M. Peterson, Soreng, Romasch. & Barberá, *Podagrostis aequivalvis* (Trin.) Scribn. & Merr., *Polypogon monspeliensis*, *Relchela panicoides* Steud., *Trichodium laxiflorum* Michx. (= *Agrostis scabra* Willd.), *Triplachne nitens* (Guss.) Link, and *Vilfa stolonifera* (L.) P. Beauv. (= *Agrostis stolonifera*).

We designed our study to characterize relationships among species of *Agrostis* and relatives, namely, *Bromidium*, *Calamagrostis*, *Chaetopogon*, *Chaetotropis*, *Lachnagrostis*, *Linkagrostis*, *Neoschischkinia*, and *Polypogon*. We also sampled the more distantly related genera *Alpagrostis*, *Chascolytrum*, *Echinopogon*, *Gastridium*, *Greeneochloa*, *Laegaardia*, *Linkagrostis*, *Paramochloa*, *Pentapogon*, *Podagrostis*, *Relchela* Steud., and *Triplachne*. All these genera have been found in a clade in several molecular studies (Saarela et al., 2017; Barberá et al., 2019a, 2019b, 2024; Peterson et al., 2019, 2020, 2021; da Silva et al., 2020, 2021) and are classified in four of the six subtribes of tribe Poeae supersubtribe Agrostidodinae (Soreng et al., 2017, 2022; Tkach et al., 2020; da Silva et al., 2021).

2.2 Phylogenetic methods
All procedures related to the sequencing of the plastid and ITS regions were performed in the Laboratory of Analytical Biology at the Smithsonian Institution. Detailed methods for DNA extraction, amplification, and sequencing are described in Romaschenko et al. (2012) and Peterson et al. (2010a, 2010b, 2012, 2014a, 2014b, 2015a, 2015b). We used Geneious Prime v.2020.1.4 (Kearse et al., 2012) for contig assembly of bidirectional sequences and Muscle (Edgar, 2004) to align consensus sequences and adjust the final alignment. The Bayesian trees were constructed using MrBayes v3.2.7 (Huelsenbeck & Ronquist, 2001; Ronquist et al., 2012). All compatible branches were saved. The Maximum Likelihood parameters for each region were estimated using GARLI 2.0 (Zwickl, 2006) and were used as priors in Bayesian calculations (Table 1). The combined data set was split into four partitions containing the ITS, *rpL32-trnL*, *rps16-trnK*, and *rps16* intron sequences.

Bayesian analysis was initiated with random starting trees and was run for eight million generations with the sampling frequency of trees set at the 100th iteration. Upon completion of the analyses, the variance of split sequences was less than 0.01 and the potential scale reduction factor was close or equal to 1.0, indicating convergence of the chains (Huelsenbeck & Ronquist, 2001). The search was also monitored using Tracer v1.7 (Rambaut et al., 2018). The effective sample size (ESS) value was greater than 100, and 25% of the sampled values were discarded. Posterior probabilities (PP) of ≥0.95 indicate a credible interval of probability, so we consider this as strong support.

We used the program IQ-Tree 2.3.5 to estimate ultrafast bootstrap approximation (with 10000 bootstrap replicates) to assess branch supports (Minh et al., 2013; Hoang et al., 2018). We used a partition model (Chernomor et al., 2016) to run the bootstrap analysis. We specified the gamma model for the among-site rate variation for each DNA

Table 1 Characteristics of the four regions, *rps16-trnK*, *rps16* intron, *rpL32-trnL*, ITS, and parameters used in Bayesian analyses indicated by the Akaike Information Criterion (AIC)

	rps16-trnK	rps16 intron	rpL32-trnL	Combined plastid data	ITS	Overall
Total aligned characters	1044	1075	1513	3632	761	4393
Number of sequences/success	121 (62.1%)	83 (42.6%)	189 (95.5%)	393 (66.2%)	193 (97.5%)	586 (74.0%)
Number of new sequences/ratio	86 (71.1%)	52 (62.7%)	141 (74.6%)	278 (70.7%)	142 (73.6%)	419 (71.5%)
Likelihood score (-lnL)	3371.75	1339.42	2243.13		9024.84	
Number of substitution types	6	6	6	–	6	–
Model for among sites rate variation	gamma	gamma	gamma	–	gamma	–
Substitution rates	1.03554	0.72196	1.32138	–	1.53923	–
	2.53139	0.84357	0.81336		2.24230	
	0.06426	0.17519	0.31943		3.25513	
	0.85125	0.67863	0.71533		0.44914	
	1.79013	1.49975	0.72263		5.77997	
	1.00000	1.00000	1.00000		1.00000	
Character state frequencies	0.38584	0.36329	0.36744	–	0.21981	–
	0.11038	0.12935	0.15251		0.28816	
	0.17846	0.17029	0.13357		0.29788	
	0.32531	0.33708	0.34646		0.19415	
Proportion of invariable sites	0.37997	0.00000	0.65562	–	0.65732	–
Substitution model	TVM + G	GTR + I + G	GTR + G	–	GTR + I + G	–
Gamma shape parameter (α)	0.90075	0.82870	1.08240	–	1.84000	–

region (Table 1), which was identified by IQ-Tree in preliminary runs. Bootstrap (BS) values of 95%–100% were interpreted as strong support.

2.3 Principles and phases of phylogenetic reconstruction

Phylogenetic reconstructions were performed in two main phases. The first phase included Bayesian preliminary searches (trees from preliminary searches are not shown) designed to detect hard incongruences between ITS and plastid data, construction of the preliminary core phylogeny, individual testing of the specimens with incongruences against the preliminary core phylogeny, and construction of the final core phylogeny (Fig. 1). The second phase included a series of individual searches of the incongruent species to identify the correct affiliation of their ITS and plastid sequences, characterize patterns among discordant splits between the ITS and plastid data, and construction of phylogenies identifying the incongruent ITS and plastid sequences tested against the core phylogeny. Procedurally, the two-phased core phylogenetic analysis of *Agrostis* can be presented in the 10 following steps: (1) creation of two separate data sets of ITS and plastid data for 198 specimens; (2) determination of bootstrap values for each data set; (3) selection of the specimens with similar phylogenetic positions in both data sets supported by bootstrap values of 95 and above and creation of the preliminary core phylogeny data set with these samples; (4) testing of each remaining specimen in a phylogenetic analysis against the preliminary core data set; (5) addition of any newly detected specimens with similar or noncontradictory affiliations of ITS and plastid sequences to the preliminary core data set, and creation of the final core data set comprising 116 specimens (set 1, see Appendix S1); (6) determination of bootstrap values and Bayesian phylogenetic analyses for the core data set (Fig. 1); (7) repetition of the test phylogenetic analysis for the each of the 82 remaining specimens showing alignment split between ITS and plastid data against the core data set; (8) characterization of the discordant splits between ITS and plastid data; (9) creation of the four expanded data sets combining specimens of the core data set and specimens with the characteristic alignment split between ITS and plastid data (sets 2–5, see Appendix S1); and (10) performing the bootstrap analysis and Bayesian phylogenetic analyses for the expanded data sets, and finally creating the phylogenies demonstrating different types of alignment splits between ITS and plastid data.

2.4 Assessment of incongruence and data combining strategy

Combining all congruent data provides better resolution of phylogenetic trees, strengthens support for the nodes, and maximizes the informativeness and explanatory power of the character data used in the analysis (Huelsenbeck & Cunningham, 1996). The plastid and ITS topologies resulting from bootstrap analysis were inspected for conflicting nodes with support (BS) ≥ 0.95. If no supported incongruences were found, plastid and ITS sequences were combined and used in the core phylogenetic analysis (Fig. 1). This analysis (combined plastid and ITS sequences) included a subset of the American, Eurasian, Australian, and Pacific species of *Calamagrostis* and representatives of nineteen other genera.

We did not include *Agrostula truncatula* in our analysis, which we previously found to be allied with other genera in Agrostidinae (Peterson et al., 2021), and sister to *Calamagrostis* (Peterson et al., 2020). Our unpublished data suggest a complex origin of *Agrostula truncatula* and further study is required. *Phalaris arundinacea* L. (Phalaridinae Fr.), *Amphibromus scabrivalvis* (Trin.) Swallen (Torreyochloinae Soreng & J.I. Davis), and *Torreyochloa pauciflora* (J. Presl) G.L. Church (Torreyochloinae) were chosen as outgroups, since they all lie outside the Agrostidodinae but within the tribe Poeae R. Br. Chloroplast Group 1 (Aveneae type) [Saarela et al., 2017; Soreng et al., 2017, 2022; Tkach et al., 2020]. We excluded 80 specimens representing 48 species in *Agrostis* (24 species), *Chaetotropis* (3 species), *Lachnagrostis* (10 species), *Linkagrostis* (1 species), and *Polypogon* (10 species) from the core phylogeny based on the incongruence of their plastid and ITS data.

2.5 Taxon duplication approach

A taxon duplication approach (Pirie et al., 2008; Pelser et al., 2010; Peterson et al., 2015a, 2016, 2020, 2021) was applied to 83 specimens representing 48 species for which incongruence of plastid and ITS data were detected (sets 2–5, Appendix S1). Each of these specimens was assigned two entries in our matrices: one containing only ITS and one containing only plastid sequences. This technique allowed us to identify the placements of the incongruent ITS and plastid sequences in the context of the *Agrostis* core phylogeny. To avoid the mutual influence of confounding ITS sequences, each specimen was analyzed separately before being assigned to one of the four expanded data sets (sets 2–5, Appendix S1), each including samples with a similar pattern of incongruence between ITS and plastid data representing characteristic ITS/plastid discordant splits. The number of specimens added to the core data set (data set 1–115 specimens) to form extended data sets is the following: data set 2–36 specimens, data set 3–18 specimens, data set 4–17 specimens, and data set 5–12 specimens. The outgroup set included the same species as those used in core phylogeny (Fig. 1).

We used this taxon duplication approach to resolve our phylogenetic tree, minimizing the diffusing effects of taxa with strongly supported incongruence between plastid and ITS data but showing the placements of the plastid and ITS sequences in relation to the taxa in the core phylogeny. This allowed us to hypothesize multiple origins and elucidate complex evolutionary histories within phylogenetic groups.

3 Results

3.1 Phylogenetic analyses

Sixty-two percent (426/689) of the sequences in our study are newly reported in GenBank and 38% (263) are previously published sequences (Appendix S1) generated for earlier studies (Peterson et al., 2020, 2021). All but five sequences in our study were generated in our laboratory. Thirteen percent (105/792) of the sequences (ITS & plastid) in our data set are missing. Total aligned characters for individual regions and other parameters are shown in Table 1.
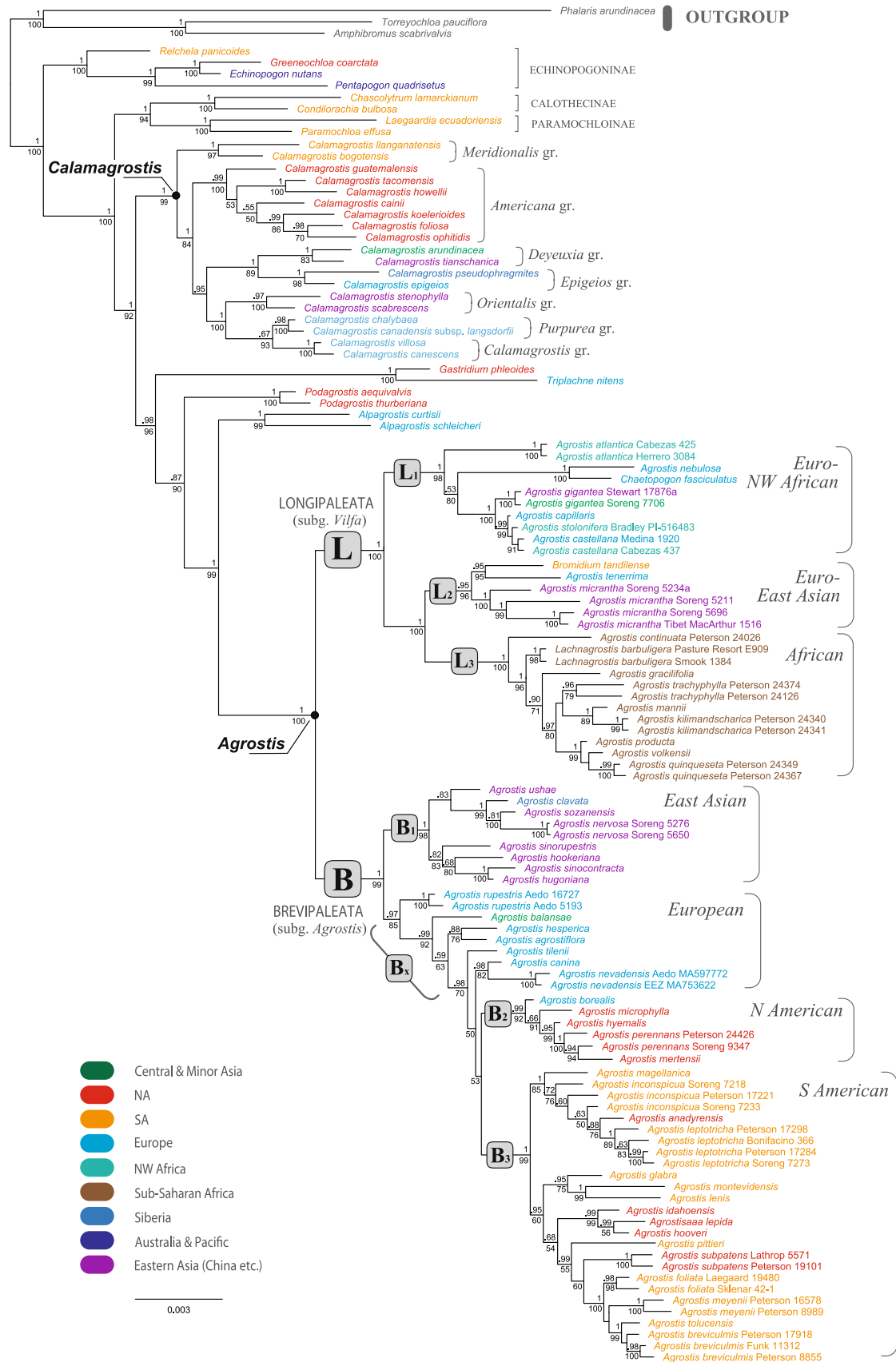
Fig. 1. Continued

3.2 Core phylogenetic (samples with congruent ITS and plastid data)

The Bayesian tree from combined, congruent plastid (*rpl32-trnL*, *rps16-trnK*, and *rps16*), and ITS regions (Fig. 1) is well resolved, and many major clades are strongly supported. The clade corresponding to *Agrostis* is maximally supported (PP = 1, BS = 100) and is sister to *Alpagrostis* (PP = 1, BS = 99). The *Agrostis* clade is divided into two major clades, both with strong support (PP = 1, BS = 100 or 99). We refer to these clades informally as the Longipaleata (L) clade and the Brevipaleata (B) clade. The species of *Agrostis* included in the Longipaleata clade usually have florets with paleas 2/5 to as long as the lemma, whereas species in the Brevipaleata clade have florets with paleas less than 2/5 as long as the lemma, minute, or absent.

The Longipaleata clade comprises three strongly supported clades (PP = 0.95, BS = 96–100): one (L$_1$; PP = 1, BS = 98) includes *Chaetopogon fasciculatus* and six species of *Agrostis* (including *A. stolonifera*, the type of *Vilfa* Adans.), all primarily distributed in Europe and northwest Africa. Another of these clades (L$_2$; maximally supported) includes four accessions of the Asian species *A. micrantha* Steud. sister to *Bromidium tandilense* (Kuntze) Rúgolo (= *Agrostis tandilensis* (Kuntze) Parodi + *A. tenerrima*). The third clade (L$_3$; maximally supported) includes eight species of *Agrostis* and *Lachnagrostis barbuligera* (Stapf) Rúgolo & A.M. Molina (sometimes treated as *A. barbuligera* Stapf), all distributed in Africa. Clades L$_2$ and L$_3$ are maximally supported as sister groups.

The Brevipaleata clade comprises three strongly supported clades that we refer to as B$_1$, B$_2$, and B$_3$ and a grade of five lineages that we refer to as B$_x$. Clade B$_1$ (PP = 1, BS = 98) comprises seven species distributed in eastern Asia and one species, *A. clavata* Trin., distributed in eastern Asia, North America, and northern Europe. Clade B$_1$ is sister to all other species of the Brevipaleata clade, which form a moderately to strongly supported lineage (PP = 0.97, BS = 85). The B$_x$ grade occurs at the base of this lineage, and branch support among the five lineages of the grade varies from weak to strong. It comprises seven species distributed in Europe, one of which, *A. balansae* (Boiss.) Tzvelev, extends into Asia Minor. Clade B$_2$ (PP = 0.99, BS = 92) includes six species primarily distributed in North America, although *A. mertensii* Trin. is cosmopolitan and known from the Americas, Europe, and Asia, and *A. borealis* Hartm. is Scandinavian. Clade B$_3$ (PP = 1, BS = 99) includes 11 species distributed in South America and five species that occur in North America, two of which (*A. pallens* Trin., *A. subpatens* Hitchc.) extend into Central America.

Within Agrostidodinae, *Podagrostis* is sister to *Agrostis* + *Alpagrostis* and, together, these three genera are sister to *Gastridium* + *Triplachne*. Successive sisters to the previous clade include *Calamagrostis*, Calothecinae Soreng + Para-mochloinae L.N. Silva & Saarela, and Echinopogoninae Soreng (Fig. 1). *Calamagrostis* is monophyletic (PP = 1, BS = 99) based on limited species sampling representing each of the seven groups (gr.) identified by Peterson et al. (2021).

3.3 Phylogenetic trees with taxon duplication (including species or samples with incongruent ITS and plastid sequences)

The four taxon duplication trees (Figs. 2–5) include species or samples with incongruent plastid and ITS DNA along with the samples from the core phylogeny. Each of these trees focuses on one of the four main patterns of incongruence between plastid and ITS data in the samples that we studied.

Our first taxon duplication tree including a subset of the incongruent taxa provides insight into plastid- and ITS-based relationships of some *Agrostis*, *Polypogon*, and *Lachnagrostis* species. Based on ITS data, three *Agrostis* species (*A. bourgaei* E. Fourn., *A. exarata* Trin., *A. reuteri*), all sampled species of *Polypogon* (*P. australis*, *P. interruptus* Kunth, *P. fugax* Nees, *P. griquensis*, *P. maritimus*, *P. monspeliensis*, *P. tenellus* R. Br., *P. tenuis* Brongn., *P. viridis*), and six *Lachnagrostis* species (*L. adamsonii* (Vickery) S.W.L. Jacobs, *L. aemula* (R. Br.) Trin., *L. billardieri* (R. Br.) Trin., *L. filiformis*, *L. littoralis* (Hack.) Edgar, *L. polypogonoides* (Stapf) A.J. Br.) form a strongly supported clade (PP = 1, BS = 100) that is nested in the *Calamagrostis* Americana group clade (Fig. 2). Among these taxa, *L. polypogonoides* (clade ITS$_{C1}$) and *A. reuteri* (clade ITS$_{C2}$) are successive sister groups to a large, strongly supported lineage divided into two strongly supported clades: ITS$_{C3}$ and ITS$_{C4}$. Clade ITS$_{C3}$ includes *Agrostis bourgaei*, *A. exarata*, *Polypogon fugax*, *P. maritimus*, *P. monspeliensis*, and *P. viridis*. Clade ITS$_{C4}$ includes *Polypogon australis*, *P. griquensis*, *P. interruptus*, *P. tenellus*, *P. tenuis*, *L. adamsonii*, *L. aemula*, *L. billardieri*, *L. filiformis*, and *L. littoralis* ssp. *littoralis*. Affinities of these taxa differ based on plastid data: *A. reuteri* (PL$_{L1-1}$) is placed in *Agrostis* Longipaleata clade L$_1$, *L. polypogonoides* (PL$_{L3-1}$) is placed in *Agrostis* Long-ipaleata clade L$_3$; *A. bourgaei* (PL$_{B3}$) is placed in *Agrostis* Brevipaleata clade B$_3$ sister to *A. subpatens*; *P. fugax, P. monspeliensis, P. viridis*, and *P. tenuis* form a strongly supported clade (PL$_{L1-3}$) that is part of *Agrostis* Longipaleata clade L1; *A. exarata* (PL$_{B2}$) is placed in *Agrostis* Brevipaleata clade B$_2$ sister to *A. microphylla* Steud.; and *P. australis, P. linearis* Trin. (only plastid data exists), *P. interruptus, P. griquensis, L. adamsonii, L. billardieri, L. filiformis*, and *L. aemula* are all part of *Agrostis* Longipaleata clade L$_1$, but relationships among most of these taxa are poorly supported. Among them, *P. australis, P. linearis,* and *P. interruptus* form a strongly supported clade and *L. filiformis* and *L. aemula* form a strongly supported clade (Fig. 2).

Our second taxon duplication tree (Fig. 3) including a subset of the incongruent taxa provides insights into plastid- and ITS-based relationships of *Bromidium* and

Fig. 1. Core Bayesian tree inferred from combined plastid (*rpl32-trnL, rps16-trnK,* and *rps16* intron) and ITS sequences of *Agrostis* with major groups and their geographic interpretations. Brevipaleata (B) and Longipaleata (L) clades correspond to *Agrostis* subg. *Agrostis* and *A.* subg. *Vilfa*, respectively. *Agrostis* is represented by the core data set excluding specimens with detected incongruence of ITS and plastid markers. Numbers (0.50–1) above the branches indicate posterior probabilities and numbers (50–100) below the branches indicate bootstrap. Scale bar = 0.3% substitutions per site.
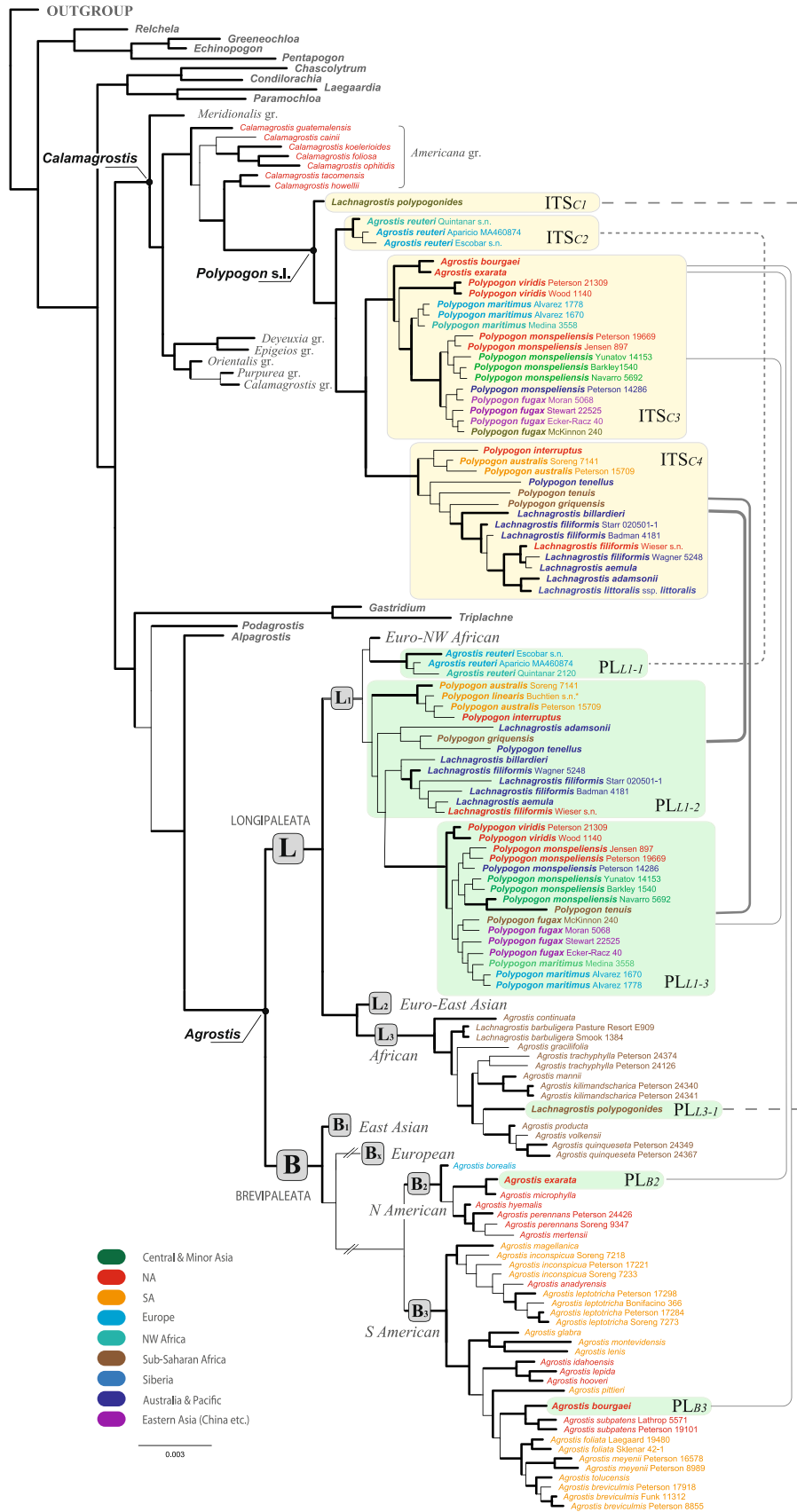
OUTGROUP

Relchela
Greeneochloa
Echinopogon
Pentapogon
Chascolytrum
Condilorachia
Laegaardia
Paramochloa

Calamagrostis

Meridionalis gr.

Calamagrostis guatemalensis
Calamagrostis cainii
Calamagrostis koelerioides
Calamagrostis foliosa
Calamagrostis ophitidis
Calamagrostis tacornensis
Calamagrostis howellii

Americana gr.

Polypogon s.l.

Lachnagrostis polypogonides ITS*C1*

Agrostis reuteri Quintanar s.n.
Agrostis reuteri Aparicio MA460874
Agrostis reuteri Escobar s.n.
ITS*C2*

Deyeuxia gr.
Epigeios gr.
Orientalis gr.
Purpurea gr.
Calamagrostis gr.

Agrostis bourgaei
Agrostis exarata
Polypogon viridis Peterson 21309
Polypogon viridis Wood 1140
Polypogon maritimus Alvarez 1778
Polypogon maritimus Alvarez 1670
Polypogon maritimus Medina 3558
Polypogon monspeliensis Peterson 19669
Polypogon monspeliensis Jensen 897
Polypogon monspeliensis Yunatov 14153
Polypogon monspeliensis Barkley1540
Polypogon monspeliensis Navarro 5692
Polypogon monspeliensis Peterson 14286
Polypogon fugax Moran 5068
Polypogon fugax Stewart 22525
Polypogon fugax Ecker-Racz 40
Polypogon fugax McKinnon 240
ITS*C3*

Polypogon interruptus
Polypogon australis Soreng 7141
Polypogon australis Peterson 15709
Polypogon tenellus
Polypogon tenuis
Polypogon griquensis
Lachnagrostis billardieri
Lachnagrostis filiformis Starr 020501-1
Lachnagrostis filiformis Badman 4181
Lachnagrostis filiformis Wieser s.n.
Lachnagrostis filiformis Wagner 5248
Lachnagrostis aemula
Lachnagrostis adamsonii
Lachnagrostis littoralis ssp. *littoralis*
ITS*C4*

Gastridium
Triplachne

Podagrostis
Alpagrostis

Euro-NW African

Agrostis reuteri Escobar s.n.
Agrostis reuteri Aparicio MA460874
Agrostis reuteri Quintanar 2120
PL*L1-1*

L1

Polypogon australis Soreng 7141
Polypogon linearis Buchtien s.n.*
Polypogon australis Peterson 15709
Polypogon interruptus
Lachnagrostis adamsonii
Polypogon griquensis
Polypogon tenellus
Lachnagrostis billardieri
Lachnagrostis filiformis Wagner 5248
Lachnagrostis filiformis Starr 020501-1
Lachnagrostis filiformis Badman 4181
Lachnagrostis aemula
Lachnagrostis filiformis Wieser s.n.
PL*L1-2*

LONGIPALEATA

L

Polypogon viridis Peterson 21309
Polypogon viridis Wood 1140
Polypogon monspeliensis Jensen 897
Polypogon monspeliensis Peterson 19669
Polypogon monspeliensis Peterson 14286
Polypogon monspeliensis Yunatov 14153
Polypogon monspeliensis Barkley 1540
Polypogon monspeliensis Navarro 5692
Polypogon tenuis
Polypogon fugax McKinnon 240
Polypogon fugax Moran 5068
Polypogon fugax Stewart 22525
Polypogon fugax Ecker-Racz 40
Polypogon maritimus Medina 3558
Polypogon maritimus Alvarez 1670
Polypogon maritimus Alvarez 1778
PL*L1-3*

L2 *Euro-East Asian*

L3
Agrostis continuata
Lachnagrostis barbuligera Pasture Resort E909
Lachnagrostis barbuligera Smook 1384
African
Agrostis graclifolia
Agrostis trachyphylla Peterson 24374
Agrostis trachyphylla Peterson 24126
Agrostis mannii
Agrostis kilimandscharica Peterson 24340
Agrostis kilimandscharica Peterson 24341
Lachnagrostis polypogonides PL*L3-1*

Agrostis

B1 *East Asian*
Agrostis producta
Agrostis volkensii
Agrostis quinqueseta Peterson 24349
Agrostis quinqueseta Peterson 24367

B
B4 *European*
Agrostis borealis

BREVIPALEATA

B2
Agrostis exarata PL*B2*
Agrostis microphylla
Agrostis hyemalis
Agrostis perennans Peterson 24426
Agrostis perennans Soreng 9347
Agrostis mertensii

N American

Agrostis magellanica
Agrostis inconspicua Soreng 7218
Agrostis inconspicua Peterson 17221
Agrostis inconspicua Soreng 7233
Agrostis anadyrensis
Agrostis leptotricha Peterson 17298
Agrostis leptotricha Bonifacino 366
Agrostis leptotricha Peterson 17284
Agrostis leptotricha Soreng 7273
Agrostis glabra

B3
Agrostis montevidensis
Agrostis lenis
Agrostis idahoensis
Agrostis lepida
Agrostis hooveri
Agrostis pittieri

S American

Agrostis bourgaei PL*B3*
Agrostis subpatens Lathrop 5571
Agrostis subpatens Peterson 19101
Agrostis foliata Laegaard 19480
Agrostis foliata Sklenar 42-1
Agrostis meyenii Peterson 16578
Agrostis meyenii Peterson 8989
Agrostis tolucensis
Agrostis breviculmis Peterson 17918
Agrostis breviculmis Funk 11312
Agrostis breviculmis Peterson 8855

Central & Minor Asia
NA
SA
Europe
NW Africa
Sub-Saharan Africa
Siberia
Australia & Pacific
Eastern Asia (China etc.)

0.003

Fig. 2. Continued

Chaetotropis among some species of *Agrostis* and *Lachnagrostis*. *Bromidium ramboi* (ITS only) pairs with *B. tandilense*, and together, they are sister to *A. tenerrima* in the Longipaleata clade L_2. Based on ITS data, *C. chilensis*, *C. elongata* (Kunth) Björkman, and *C. imberbis* (Kunth) Björkman are nested within *Agrostis* Brevipaleata clade B_3 (ITS_{B3-1}). Relationships among these species are poorly supported. The plastid data, by contrast, place these three species in a strongly supported clade (PL_{L1-4}) sister to *Agrostis* Longipaleata clade L_1. Based on ITS data, *Agrostis bergiana* Trin., *A. olympica* (our sample is from the Russian Caucasus, but the species is mainly west Asian), one of the two accessions of *A. pilosula* Trin. (*Koelz 21857*, from India), and four African taxa, namely, *A. schimperiana* Hochst. ex Steud., *Lachnagrostis eriantha* (Hack.) A.J. Br., *L. lachnantha* (Nees) Rúgolo & A.M. Molina, and *L. schlechteri* (Rendle) Rúgolo & A.M. Molina, form a clade (unsupported; ITS_{Bx}), which also includes *A. nevadensis*, within the B_x grade (Fig. 3). The other accession of *A. pilosula* (*Rodin 5581*, from Pakistan) is included in Brevipaleata clade B_3, within a clade of North and South America species, in the ITS tree. Based on plastid data, these seven species align in four locations within the Longipaleata clade: *A. schimperiana* and *L. lachnantha* form a strongly supported clade (PL_{Lx}) sister to clades L_2 and L_3 (Fig. 3); both accessions of *A. pilosula* form a strongly supported clade (PL_{L2}) sister to *A. micrantha* in clade L_2; *A. olympica* (PL_{L3-2}) is sister to all remaining taxa in clade L_3, but this relationship is weakly supported; *A. bergiana* (PL_{L3-3}) is nested in clade L_3, sister (poorly supported) to *A. gracilifolia* C.E. Hubb.; and *L. eriantha* (PL_{L3-4}) is nested within clade L_3, sister to a strongly supported clade comprising the African species *A. producta* Pilg., *A. volkensii* Stapf, and *A. quinqueseta* (Steud.) C.E. Hubb.

Our third taxon duplication tree (Fig. 4) including a subset of the incongruent taxa provides insights into plastid- and ITS-based relationships of some Euro-Siberian, Pacific, and Australian species of *Agrostis*. Based on ITS data (Fig. 4), our four accessions of *A. vinealis* (three from Europe and one from Siberia; ITS_{B1}) form a weakly supported clade within East Asian clade B_1 sister (again, weakly supported) to *A. hugoniana* Rendle–*A. sinocontracta* S.M. Phillips & S.L. Lu (Fig. 4, Based on plastid data, however, *A. vinealis* accessions (PL_{Bx-1} and PL_{Bx-2}) are placed among the grade (B_x) and the four samples are not recovered as monophyletic (separated by unsupported branches). Based on ITS data, six species of *Agrostis* from the Pacific and Australia (*A. australensis* Mez, *A. dyeri* Petrie, *A. muelleriana* Vickery, *A. parviflora* R. Br., *A. venusta* Trin.; ITS_{B2-2} in part; see Fig. 5 for other part) form a weakly supported clade that is nested in Brevipaleata clade B_2, whereas based on plastid data, these species form a strongly supported clade (PL_{B1}) nested in the East Asian clade B_1. Similarly, based on ITS data, *A. infirma* (ITS_{B2-1}) falls within Brevipaleata clade B_2, whereas, based on plastid data, it falls within Brevipaleata

clade B_1 (PL_{B2}). Based on ITS data, *A. elliottiana* Schult. (ITS_{Lx}) is included in the Longipaleata clade, weakly supported as sister to Longipaleata clades L_2 and L_3, and *A. pourretii* (ITS_{L2}) is also included in the Longipaleata clade, sister to Longipaleata clade L_2. Based on plastid data, these two species (PL_{By} and PL_{Bz}) are closely related (or part of) to the Brevipalaeta clade, as they are placed outside the lineage including clades B_1, B_2, and B_3 and the grade of taxa that is basal to clades B_2 and B_3. *Linkagrostis juressi*, based only on ITS data, is found between Longipaleata L_1 and L_2 clades (Fig. 4).

Our fourth (Fig. 5) analysis including a subset of the incongruent taxa provides insights into plastid- and ITS-based relationships of some North American species of *Agrostis* within the Brevipaleata clade. Based on plastid sequences, *A. sandwicensis* Hillebr. (from Hawaii, USA), *A. pallens, A. oregonensis* Vasey, and *A. swalalahos* Otting (Oregon, USA), *A. variabilis* Rydb., *A. pallens* var. *foliosa* Hitchc., *A. gigantea* (Europe) and *A. scabra* p.p. (eastern USA, *Peterson 21980*) form a strongly supported clade (PL_{Bx-3}, but excluding *A. hendersonii*). Within this clade, strongly supported subclades include *A. variabilis* and *A. pallens* ssp. *diegoensis*; *A. gigantea* and *A. scabra* p.p.; and *A. sandwicensis*, *A. pallens* p.p., *A. oregonensis*, and *A. swalalahos*. Based on ITS data, however, these taxa are placed in different parts of the tree: *A. gigantea* (Europe) is sister to another accession of *A. gigantea* (Kyrgyzstan) in clade L_1, (Fig. 5, ITS_{L1}); *A. pallens–A. pallens* var. *foliosa, A. oregonensis*, and *A. swalalahos* form a strongly supported lineage within clade B_3 sister to *A. lepida* Hitchc. (Tulare Co., CA, USA; usually treated as a synonym of *A. pallens*) [ITS_{B3-7}]; *A. sandwicensis* (ITS_{B3-6}) and *A. variabilis* (ITS_{B3-5}) fall within different parts of Brevipaleata clade B_3; and *A. scabra* (*Peterson 21980*) is part of Brevipaleata clade B_2. Based on ITS data, *A. hendersonii* Hitchc. (ITS_{B3-4}) is part of a strongly supported clade including *A. magellanica* Lam., *A. inconspicua* Kunze ex E. Desv., *A. anadryensis* Soczava, and *A. leptotrica* E. Desv. within Brevipaleata clade B_3, whereas based on plastid data, *A. hendersonii* (PL_{Bx-3}) is part of the grade B_x that is basal to Brevipaleata clades B_2 and B_3. Based on plastid data, three accessions of *A. stolonifera* (Europe) form a weakly supported clade in Longipaleata clade L_1, whereas based on ITS data, two of these (*Castroviejo 17902* and *Lazaro s.n.*, PL_{L1-5}) form a clade sister to *A. scabra* (*Peterson 21980*, ITS_{B2-2}) in Brevipaleata clade B_2. Based on plastid markers, *A. scabra* (*Soreng 6078*, PL_{B2-1}) is sister to *A. mertensii* within Brevipaleata clade B_2, whereas based on ITS data, it falls within Brevipaleata clade B_3 (ITS_{B3-3}).

3.4 Phylogenetic distribution of plastid lineages
We hypothesize the origin of plastid lineages, referred to as "plastid donor", in relation to the biogeographically defined lineages that "received" the plastid genes. The species nested within the *Calamagrostis* Americana group

Fig. 2. Intergeneric origins of *Polypogon* and some additional species of *Agrostis* and *Lachnagrostis* with incongruent split between plastid and ITS data. *Polypogon* s.l. is represented by the ITS-derived clade within the *Calamagrostis* Americana group. Brevipaleata (B) and Longipaleata (L) clades correspond to *Agrostis* subg. *Agrostis* and *A.* subg. *Vilfa*, respectively. Thick black branches in the phylogram indicate posterior probabilities of 0.95–1 and/or bootstrap of 95–100. Scale bar = 0.3% substitutions per site.
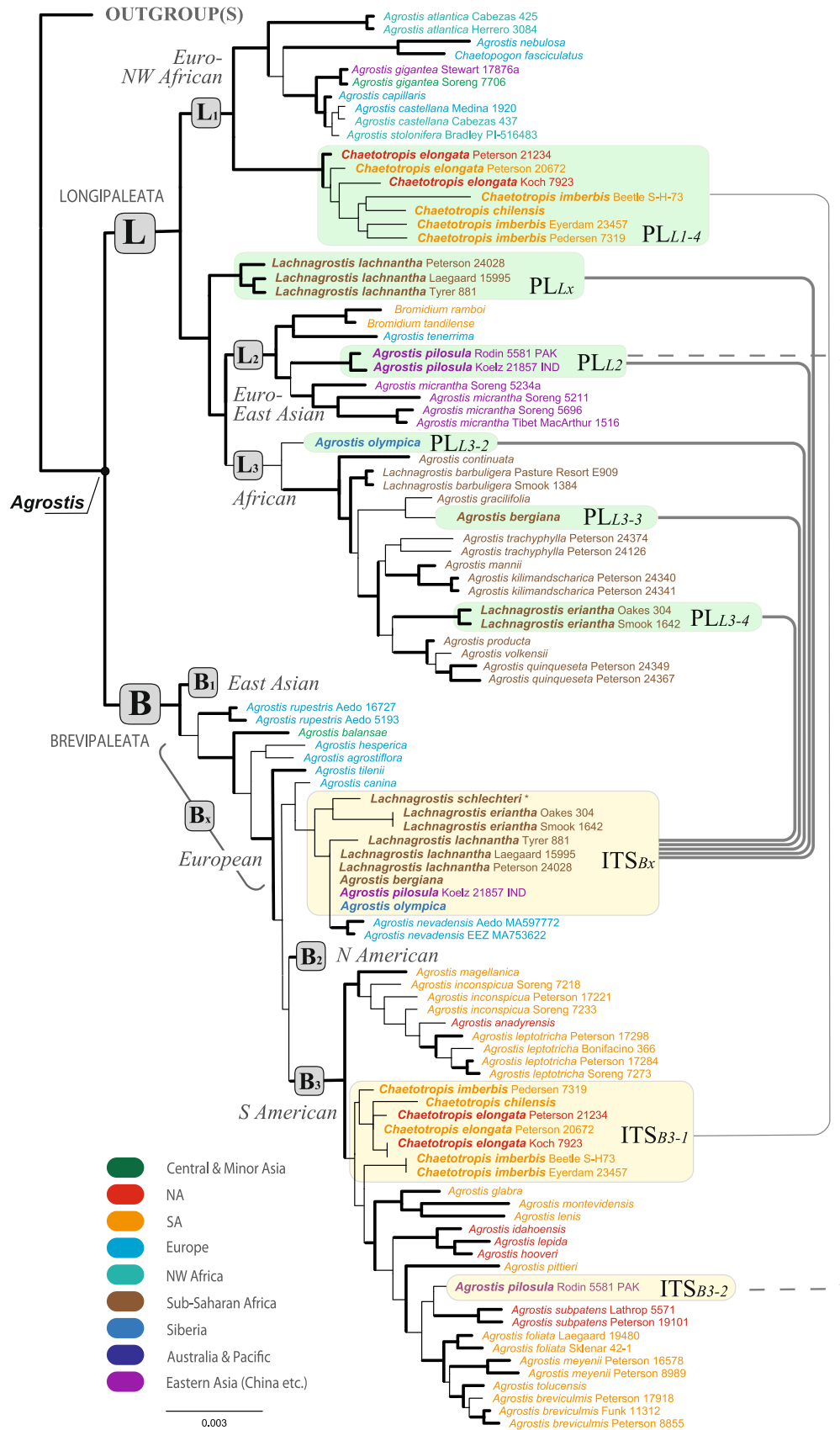
Fig. 3. Continued

(receiver), based on ITS data, currently found in Europe or northwestern Africa, that is, *Agrostis reuteri* (PL_{L1-1}); *Polypogon australis*, *P. griquensis*, *P. interruptus*, *P. linearis*, *P. tenellus*, *Lachnagrostis adamsonii*, *L. aemula*, *L. billardieri*, and *L. filiformis* (PL_{L1-2}); and *P. fugax*, *P. maritima*, *P. monspeliensis*, *P. viridis*, and *P. tenuis* (PL_{L1-3}), received their plastid haplotype from the *Agrostis* Longipaleata clade. Likewise, *Chaetotropis elongata*, *C. chilensis*, and *C. imberbis*, which are part of Brevipaleata clade B_3 based on ITS data, received their plastid haplotype from the Longipaleata L_1 clade, where the nrDNA ITS type aligns within species found in South America, whereas *A. stolonifera* (PL_{L1-5}) received the plastid haplotype from the Longipaleata L_1 clade and its ITS signal aligns within the Brevipaleata B_2 clade with species from North America (Fig. 3). One accession of *Agrostis gigantea* received its plastid haplotype from the Brevipaleata B_x and its ITS signal aligns with the Longipaleata L_1 clade, with other species primarily distributed in Europe and northwestern Africa (Fig. 5).

Lachnagrostis polypogonoides received its plastid haplotype from the Longipaleata L_3 clade (PL_{L3-1}), endemic to South Africa, and its ITS signal aligns with the *Calamagrostis* Americana group (Fig. 2). *Agrostis olympica* (PL_{L3-2}) (endemic to southwest Asia), *A. bergiana* (PL_{L3-3}), and *Lachnagrostis eriantha* (PL_{L3-4}) (endemic to southern Africa) received their plastid haplotype from the Longipaleata L_3 clade distributed in Africa, and their ITS signal aligns with Brevipaleata B_x containing species primarily found in Europe (Fig. 3). African species *Lachnagrostis lachnantha* (PL_{Lx}) received its plastid haplotype from Longipaleata LP_{Lx} and its ITS signal aligns with Brevipaleata B_x (Fig. 3). *Agrostis elliottiana* (North America) (PL_{Bz}) and *A. pourretii* (southwest Europe and northwest Africa) (PL_{By}) received their plastid haplotypes from near the base of the Brevipaleata and their ITS signal aligns with the Longipaleata L_x grade and the Longipaleata L_2 clade, respectively (Fig. 4). *Agrostis pilosula*, from mountainous regions of southeast Asia near the Tibetan Plateau, received its plastid haplotype from the Longipaleata PL_{L2} clade and its ITS signal aligns with the Brevipaleata B_x grade (Fig. 3).

Agrostis dyeri, *A. muelleriana*, *A. australensis*, *A. venusta*, *A. parviflora* (PL_{B1}), and *A. infirma* and *A infirma* ssp. *remota* (PL_{B2}), found in Australia and the Pacific, received their plastid haplotypes from Brevipaleata B_1 and their ITS signal aligns with the Brevipaleata B_2 clade with other species from North America (Fig. 4). *Agrostis vinealis* ($PL_{Bx1,2}$) found in Europe and Siberia received its plastid haplotype from the Brevipaleata B_1 clade and its ITS signal aligns at the base of the Brevipaleata B_2 clade with East Asian species (Fig. 4). *Agrostis hendersonii*, *A. oregonensis*, *A. pallens*, *A. pallens* var. *foliosa*, *A. sandwicensis*, *A. scabra*, *A. swalalahos*, and *A variabilis* (PL_{Bx-3}), all from North America, received their plastid haplotypes from the Brevipaleata Bx grade and their ITS signal aligns with the Brevipaleata B_3 clade (Fig. 5). North American *Agrostis exarata* (PL_{B2}) and *A. bourgaei* (PL_{B3}),

found within *Polypogon* embedded within the *Calamagrostis* Americana Group (ITS signal), received their plastid haplotypes from the Longipaleata L_1 clade (Fig. 2). North American *Agrostis scabra* received its plastid haplotype from the Brevipaleata B_2 clade and its ITS signal aligns in Brevipaleata B_3 (Fig. 5).
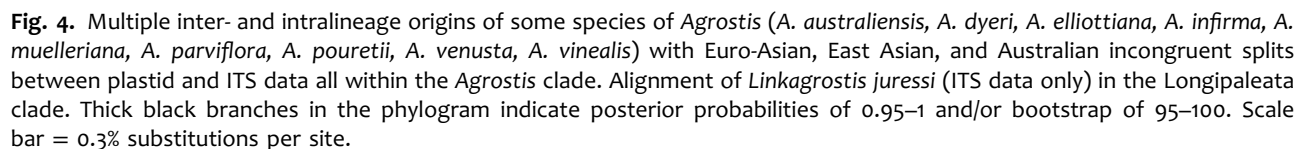
4 Discussion

4.1 Phylogeny
Our overall topology among subtribes Agrostidinae, Calothecinae, Paramochloinae, and Echinopogoninae is consistent with previous studies (Saarela et al., 2017; Tkach et al., 2020; Peterson et al., 2020, 2021; da Silva et al., 2021). Our study was focused on estimating relationships among species of *Agrostis* and allied genera, including *Bromidium*, *Chaetopogon*, *Chaetotropis*, *Lachnagrostis*, and *Polypogon*, all of which have been linked with or attributed to *Agrostis* (Reichman et al., 2006; Rotter et al., 2010; Saarela et al., 2010, 2017; Honig et al., 2015; Peterson et al., 2020, 2021; Tkach et al., 2020; Soreng et al., 2022). Many of the species of *Agrostis* that we sampled are included here for the first time in a phylogenetic study. Our core tree (Fig. 1), excluding the 48 species with incongruent plastid vs. ITS data, strongly supports the monophyly of *Agrostis* (including *Chaetopogon fasciculatus*, now recognized in *Agrostis*, and *Lachnagrostis barbuligera*, originally described as *Agrostis barbuligera*) and identifies two major clades within it: Longipaleata and Brevipaleata. Each of these clades includes three strongly supported subclades containing species with similar biogeography, indicative of multiple radiations of the genus over time in different areas, including at least two radiations into East Asia. Nevertheless, the evolutionary history of *Agrostis* is more complex than indicated in the core phylogeny. Inclusion of the many individuals with discordant ITS and plastid data in analyses (Figs. 2–5) confirms a complicated history for various lineages, sublineages, and species, likely including hybridization, introgression, and incomplete lineage sorting at different periods since the origin of the lineage.

Longipaleata (*Agrostis* subg. *Agrostis*) contains three major clades, each with a geographic tendency. Longipaleata clade L_3 contains species entirely distributed in Africa sharing a recent common ancestor with Longipaleata clade L_2, comprising a single species, *A. micrantha*, from east Asia. Longipaleata clade L_1 contains species from Europe or northwest Africa and three species of *Chaetotropis* from the western hemisphere share the same plastid type (Fig. 3).

Contrary to our placement of *Polypogon chilensis* (US voucher verified!) in the Longipaleata L_1 clade (plastid data) and the Brevipaleata B_3 clade (ITS data), a recent study using single-copy nuclear genes (Grass Phylogeny Working Group III, 2024, supplemental fig. S8) has *P. chilensis* (K voucher verified!) in a *Polypogon* clade, which, like our *Polypogon*

Fig. 3. Intersubgeneric origins of *Chaetotropis* (*C. chilensis*, *C. elongata*, *C. imberbis*), *Agrostis* (*A. bergiana*, *A. olympica*, *A. pilosula*), and *Lachnagrostis* (*L. eriantha*, *L. lachnantha*, *L. schlechteri*) with incongruent split between plastid and ITS data, and inclusion of *Bromidium* (*B. ramboi*, *B. tandilense*) within the *Agrostis* clade. Thick black branches in the phylogram indicate posterior probabilities of 0.95–1 and/or bootstrap of 95–100. Scale bar = 0.3% substitutions per site.
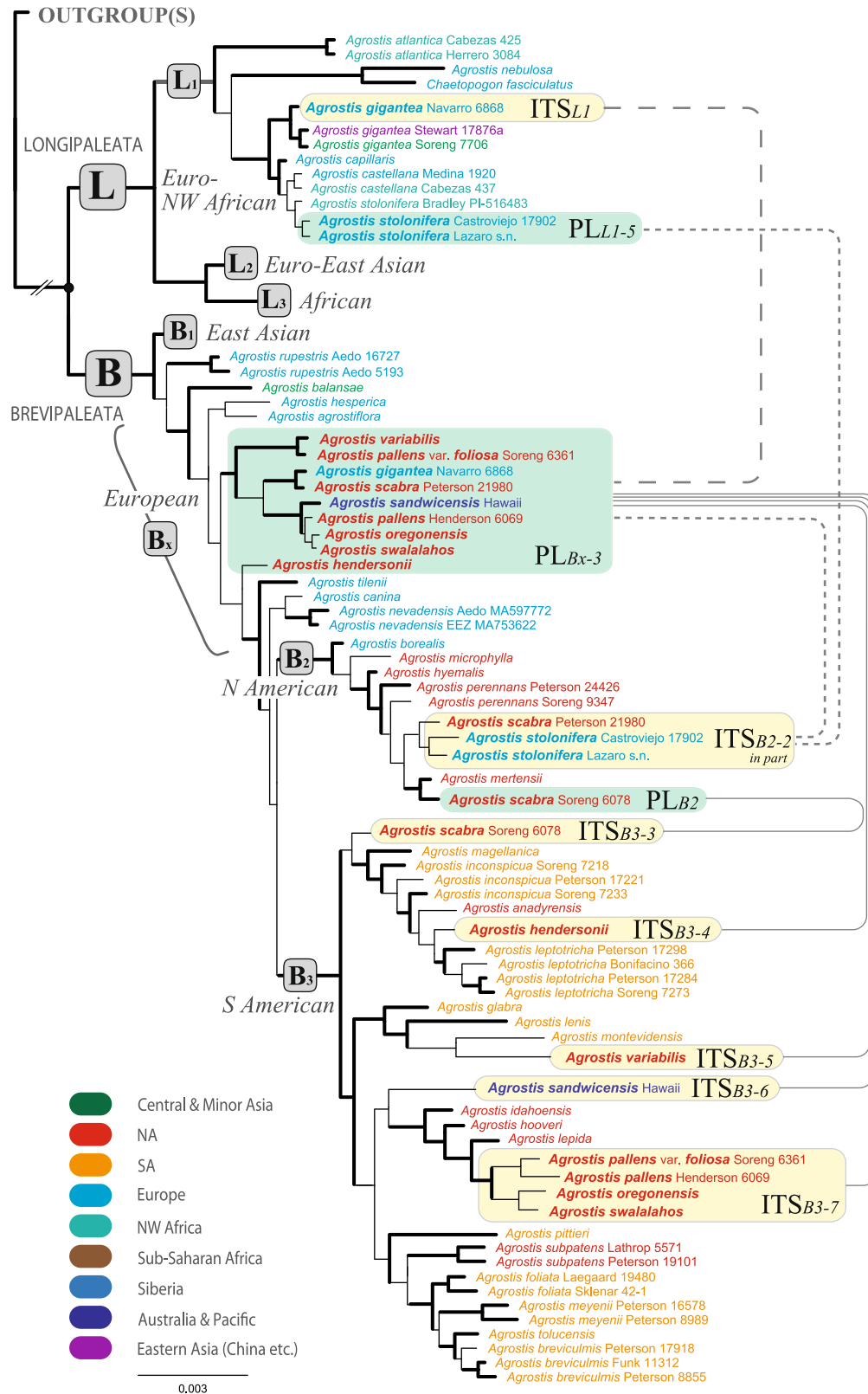
Fig. 4. Multiple inter- and intralineage origins of some species of *Agrostis* (*A. australiensis, A. dyeri, A. elliottiana, A. infirma, A. muelleriana, A. parviflora, A. pouretii, A. venusta, A. vinealis*) with Euro-Asian, East Asian, and Australian incongruent splits between plastid and ITS data all within the *Agrostis* clade. Alignment of *Linkagrostis juressi* (ITS data only) in the Longipaleata clade. Thick black branches in the phylogram indicate posterior probabilities of 0.95–1 and/or bootstrap of 95–100. Scale bar = 0.3% substitutions per site.

clade (Fig. 2), contains *P. fugax*, *P. tenellus*, and *Lachnagrostis aemula*. This hints at the fact that *P. chilensis* and perhaps other taxa formerly placed in *Chaetotropis* might have more *Polypogon* DNA than *Agrostis* DNA. Further research is needed. The few chromosome counts for *Chaetotropis* taxa are polyploid, but *C. chilensis* ploidy is unknown.

Brevipaleata (*Agrostis* subg. *Vilfa*) also consists of three major clades, two of which, Brevipaleata clades B_3 and B_2, principally contain species from the western hemisphere, the latter from South America and the former from North America. These two clades share ancestors with the B_x grade composed of species principally from Europe and *A. balansae* from central (SW Asia) Asia. Brevipaleata clade B_1 includes species principally from east Asia; although based on sharing the same plastid type, a clade of species from Australia (*A. australensis*, *A. dyeri*, *A. muelleriana*, *A. parviflora*, and *A. venusta*) and *A. infirma* are found embedded (Fig. 4). This perhaps indicates that *Agrostis* found in Australia/New Zealand arose via colonization events from East Asian ancestors.

Our results confirm some previous findings and provide new insights into the evolutionary history of *Polypogon* and *Lachnagrostis* s.l. We sampled 10 of the 22 species currently recognized in *Polypogon*—an improvement on the *Polypogon* sampling in Saarela et al. (2017)—and 10 of the 40 or so species recognized in *Lachnagrostis*. Although *Polypogon* s.l. is not monophyletic in any of our analyses, there is some geographical structuring in the relationships among the *Polypogon* species that we sampled. A close relationship between the South American species *P. australis* and *P. interruptus*, based on both ITS and plastid data, is consistent with the morphological similarity between these species (Finot et al., 2013) and consistent with trees in Saarela et al. (2017). Based on plastid data, the Chilean endemic *P. linearis* is closely related to these two species; ITS data for the species are missing in our study. South American *Polypogon* species that have not yet been included in a molecular phylogenetic study, which may be allied with species that we sampled, include *P. cachinalensis* Phil. (Chile), *P. exasperatus* (Trin.) Renvoize (Argentina, Bolivia, Chile, Peru), *P. magellanicus* (Lam.) Finot (Argentina, Chile), and *P. parvulus* Roseng., B.R. Arrill. & Izag. [syn. *Chaetotropis parvula* (Roseng., B.R. Arrill. & Izag.) Nicora] (Uruguay to northeastern Argentina). Based on ITS data, *P. australis* and *P. interruptus* are part of a clade that also includes three other *Polypogon* species that we sampled [*P. tenellus* (Australasia), *P. griquensis* (Stapf) Gibbs Russ. & L. Fish (southern Africa), *P. tenuis* (Africa)], and a subclade comprising *Lachnagrostis* species distributed in Australia and New Zealand (*L. adamsonii*, *L. aemula*, *L. billardieri*, *L. filiformis*). This topology is consistent with Saarela et al. (2017), who identified the same clade based on ITS data, but with sparser sampling (i.e., three of the four *Lachnagrostis* species sampled here, *P. australis*, and *P. interruptus*). Relationships among these taxa are less clear based on plastid data as the relevant branches are poorly supported. Three *Polypogon* species distributed broadly in the Eastern hemisphere (*P. fugax*, *P. monspeliensis*, *P. viridis*) form strongly supported clades based on plastid and ITS data, consistent with trees in Saarela et al. (2017), and these species are part of a broader clade also including *P. maritimus* and *P. viridis*. The plastid-based clade also includes *P. tenuis*

(Ascension, St. Helena, western Namibia to Cape Province), whereas in the ITS-based clade data, *P. tenuis* is part of the *Polypogon* + *Lachnagrostis* clade, suggesting a hybrid origin for this species or plastome introgression into the species, or the sample, that we sequenced. Several eastern hemisphere species of *Polypogon* remain to be included in molecular analyses, namely, *P. hissaricus* (Roshev.) Bor (Afghanistan to Xinjiang and western Himalaya), *P. ivanovae* Tzvelev (Xinjiang), *P. nilgiricus* Kabeer & V.J. Nair (southwestern India), *P. pygmeus* Tzvelev (Afghanistan), and *P. subspathaceus* Req. (Mediterranean). Similarly, several *Lachnagrostis* species from Australia and New Zealand (Cope & Gray, 2009; Jacobs & Brown, 2009; Edgar & Connor, 2010) should be included in broadly sampled phylogenetic analyses to confirm their affinities.

Additionally, based on ITS data, we find the African (southwestern Cape Province) species *Lachnagrostis polypogonoides* and the Eurasian species *A. reuteri* to be closely related to the *Polypogon* + *Lachnagrostis* s.s. clade, and the species pair *A. bourgaei* (central Mexico) + *A. exarata* (Kamchatka to Kuril Islands, Alaska to central Mexico) is embedded within it. Affinities of these four taxa differ, however, based on plastid data: *Agrostis exarata* is part of Brevipaleata clade B_2, suggesting a plastome origin from a member of this primarily North American clade; *A. bourgaei* is part of Brevipaleata clade B_3, suggesting a plastome origin from a member of this primarily Mexican/South American clade; and *L. polypogonides* is part of Longipaleata clade L_3, suggesting a plastome origin from this lineage of African species of *Agrostis* or *Lachnagrostis*. Discordance between ITS and plastid data was previously reported in *Agrostis exarata* ($2n = 28, 42, 56$) (Reichman et al., 2006; Quintanar et al., 2007; Saarela et al., 2010, 2017), and Kurchenko (2010) noted the dense, discontinuous, and compressed panicles of *A. exarata* with short, rough branches resembling those seen in *Polypogon*. In addition, *A. exarata* is one of the few species in the genus with long-awned (1 mm or more) glumes in some individuals (in others, glumes are acute, not awned); long-awned glumes represent one character used to circumscribe *Polypogon*. A similar evolutionary history may be true for the Mexican *A. bourgaei* ($2n$ = unknown; Vigosa-Mercado et al., 2023) but involving a different *Agrostis* plastome donor. Compared to most other species of *Agrostis* in Mexico, *A. bourgaei* and *A. exarata* are similar in having paleas 0.5 mm or longer, (1/5–) 1/3–3/4 the lemma length (vs. paleas absent or diminutive, up to 0.2 (–0.4) mm long and usually less than 1/5 of the lemma length). Although the introduced species *A. stolonifera*, *A. gigantea*, and *A. capillaris* also have long paleas, the only other native species in Mexico with this character state is *A. calderoniae* Acosta, known only from the western slope of the Volcan Iztaccíhuatl in the state of México (Vigosa-Mercado et al., 2023), which we did not sample. *Agrostis reuteri* (Macaronesia, western Mediterranean) also has long paleas (2/3–1 the length of an unawned lemma). The phylogenetic data do not support the circumscription of *Agrostis* subg. *Zinagrostis* according to Romero García et al. (1988a), who included two species in their subgeneric taxon: *A. reuteri* (type) and *A. truncatula*, both placed in *Neoschischkinia* by Valdes & Scholz (2006), while the latter taxon is now treated as *Agrostula truncatula* (Peterson et al., 2020). *Agrostis exarata* and *A. bourgaei* have

Fig. 5. Multiple interlineage and intralineage origins of some species of *Agrostis* (*A. gigantea, A. hendersonii, A. oregonensis, A. pallens, A. pallens* var. *foliosa, A. sandwicensis, A. scabra, A. stolonifera, A. swalalahos, A. variabilis*) with incongruent splits between plastid and ITS data. Thick black branches in the phylogram indicate posterior probabilities of 0.95–1 and/or bootstrap of 95–100. Scale bar = 0.3% substitutions per site.

rather narrow panicles, spikelets that tend to disarticulate below the glumes, and rough, scabrous glumes that are often mucronate. These are characteristics seen in some species that have been placed in *Polypogon* s.s. However, *Agrostis reuteri*, which ITS data place within the *Calamagrostis* Americana group (see Fig. 2), shares with *Polypogon* only long paleas (as opposed to that found in the species in Brevipaleata clade) and glumes with apically scabrous keels, both morphological features that have historically been used to circumscribe *Polypogon* s.s.

Based on alignment of *Chaetopogon fasiculatus* [= *Agrostis subspicata* (Willd.) Raspail] with *Polypogon, Agrostis capillaris* p.p., and *A. gigantea* p.p. in a *trnL-trnF* derived tree, Saarela et al. (2017) suggested that the species was of hybrid origin. This differs from our conclusions, which place *Chaetopogon fasiculata* in the core analysis, where there was no incongruence between combined plastid and ITS markers. In our core tree (Fig. 1), *Chaetopogon fasiculata* also aligns in the Longipaleata L_1 clade with *Agrostis capillaris, A. gigantea,* and other species. However, we did not include any incongruent species including suspected hybrids in *Polypogon* s.s. that would compromise the tree structure.

In an earlier study based on plastid and ITS markers, we found *A. reuteri* to be sister to *A. nebulosa* in the *Agrostis* clade of only 12 species (Peterson et al., 2020). The combined strength of the three plastid signals (*rpl32-trnL, rps16* intron, and *rps16-trnK*) in our combined plastid + ITS tree (Peterson et al., 2020, Fig. 1) was able to override the ITS signal that would have aligned it within the *Calamagrostis* Americana clade. At that time, we were unaware of this conflicted signal (ITS/plastid) when we chose an abbreviated selection of species to represent *Agrostis* in our tree.

Consistent with earlier studies (e.g., Saarela et al., 2017), our results support the hypothesis of either an ancient hybrid origin for the lineage comprising *Polypogon* and *Lachnagrostis* s.s. (of Australia and Pacific), including the lectotype of the latter genus (i.e., *L. filiformis*), plus *A. reuteri, A. bourgaei, A. exarata,* and *L. polypogonoides,* or introgression of the plastome from *Agrostis* into an ancestor of this lineage. Since the ITS data place these taxa in a clade that is embedded within the *Calamagrostis* Americana group—in particular, sister to a clade comprising *Calamagrostis tacomensis* and *C. howellii*, both restricted to the Pacific Northwest—an ancestor of the lineage was likely an American species of *Calamagrostis*. The plastid data, by contrast, place all these taxa, except *A. bourgaei, A. exarata,* and *L. polypogonoides,* in a clade with European-NW African *Agrostis* species, suggesting that a parent of the lineage was a member of this clade (i.e., Longipaleata clade L_1). If this putative scenario did occur, the geographical ranges of one or both hypothesized parental clades must have been broader than they are presently (as currently understood), given that the *Calamagrostis* clade that includes the lineage based on ITS data is restricted to the New World, while the *Agrostis* clade from which the plastome originated is principally restricted to the Eastern hemisphere. *Agrostis bourgaei, A. exarata,* and *L. polypogonoides* likely have experienced more recent plastome introgression from different *Agrostis* lineages (Fig. 2), given their affinities based on plastid data.

Based on our results, we suggest that the strongly supported ITS-based clade comprising *Polypogon* and *Lachnagrostis* s.s. (neither of which is resolved as mono-phyletic) plus *Agrostis bourgaei, A. exarata,* and *A. reuteri* is best recognized as a single genus of putative reticulate origin. *Polypogon* is the oldest available generic name for the lineage. An expanded *Polypogon* s.l. can be distinguished (but not easily) from *Agrostis* based on the following characters: panicles narrow and densely flowered to open and diffuse; disarticulation usually below the glumes but not always, sometimes the inflorescence completely detaching at maturity; spikelets usually 1-flowered, rarely 2-flowered and, if so, then the upper floret is reduced or sterile, sometimes with a prolonged rachilla or usually without a prolonged rachilla; and glumes often awned, upper glumes keeled and prominently scabrous along the keels, lemmas 3–5-veined, and paleas 1/2 to as long as the lemmas.

The affinities of the three species of *Chaetotropis* (= *Polypogon* sect. *Polypogonagrostis*) that we sampled are incongruent in ITS and plastid trees. Although both data partitions place the taxa within *Agrostis*, they form a poorly supported grade in Brevipaleata clade B_3 based on ITS data and a strongly supported clade in Longipaleata clade L_1 based on plastid data. These topologies are congruent with the ITS and plastid trees in Saarela et al. (2017), although they sampled only a single species of *Chaetotropis* (i.e., *Polypogon elongatus* = *Chaetotropis elongata*), including one accession that we also sampled here (*Peterson 21234*), and fewer species of *Agrostis* that are part of each of the clades in which *Chaetotropis* falls based on plastid and ITS data. In Saarela et al. (2017), based on plastid data, *P. elongatus* groups with some species of *Polypogon* (although the genus is shown to be paraphyletic in a polytomy with *Agrostis capillaris* and *A. gigantea*) that are embedded within *Agrostis*; our data show that three species of *Chaetotropis* (including *C. elongata*) form a distinct clade in either Longipaleata clade L_1 (plastid) or Brevipaleata clade B_3 (ITS) (Fig. 3). Given that continued recognition of *Chaetotropis* would render *Agrostis* paraphyletic, we propose classifying it within *Agrostis*. The species of *Chaetotropis* placement within the South American Brevipaleata clade B_3 based on ITS data is consistent with their possession of paleas 1/3–1/2 the length of the lemmas (Rúgolo, 2012; Rúgolo & Molina, 2012) and their South American biogeography, despite their discordant plastid-based affinities. Björkman (1960) initially expanded the number of species within *Chaetotropis* to four and Nicora (1978, 1993) brought it to six. These six species share several morphological features: densely scabrous glumes, paleas 1/3–1/2 the length of the lemmas, and disarticulation of the spikelets below the glumes. Accommodating these species within *Agrostis* is not necessarily prohibitive based on morphology, since they share diminutive paleas and scabrous glumes with species in Brevipaleata clade B_3. Erecting a section in the future for this clade might be necessary. However, disarticulation below the glumes is not a common feature in species of *Agrostis* and it probably led Clayton and Renvoize (1986), and Finot (2022) more recently, to place the genus as a synonym of *Polypogon*.

Our study provides new insights into the affinities of several *Lachnagrostis* and *Agrostis* species from Sub-Saharan Africa, namely, *L. eriantha, L. lachnantha, L. schlechteri,*

Agrostis bergiana, and *A. schimperina*. Affinities of these species, along with *Agrostis olympica* (Türkiye to Central Asia and Pakistan) and *A. pilosula* (Indian Subcontinent to China [W. Sichuan, Yunnan]), are with species of *Agrostis* in the Longipaleata and Brevipaleata clades based on plastid and ITS data, respectively (Fig. 3). Morphologically, the African species are similar to Longipaleata clade L_3 species, since they all possess long paleas (3/4–1 times the lemma length, Clayton, 1970) and have a similar distribution, though only two of them (*A. bergiana*, *L. eriantha*) fall within this clade and only based on plastid data. *Agrostis pilosula*, by contrast, has short paleas about 1/3 the length of the lemma, a character state aligned with species in the Brevipaleata clade B_3, of which it is part based on ITS data. *Agrostis olympica* has paleas as long as the lemma, like species within the Longipaleata clade, of which it is part based on plastid data. *Agrostis olympica* (type of *A.* sect. *Pentatherum*) is morphologically unique, having hairy lemmas with a dorsal awn and callus hairs 2/3–4/5 as long as the lemma (Tzvelev, 1983). *Agrostis olympica* appears to be closely related, possibly ancestral, to a set of African species in Longipaleata clade L_3, and some species treated as *Lachnagrostis* (Brown, 2015)—all with names in *Agrostis*—align in this African clade. These taxa in our study have more or less hairy lemmas with five veins (often excurrent), dorsal awns (sometimes absent or subapical and short), all with distinctly hairy calluses, short rachilla extensions usually present [all samples occurring in Tropical East Africa and Southern Africa were treated in *Agrostis* by Clayton (1970) and Fish et al. (2015)]. *Agrostis pilosula* (PL_{L2}/ITS_{BX}) [Himalayan] shares some of these traits. Although some of these African taxa are included in the Longipaleata clade based on both ITS and plastid data, placements of others differ in ITS and plastid trees. Some (the reticulate taxa) or all with the above trait combinations might be placed in *Agrostis* subg. *Vilfa* sect. *Pentatherum*.

We newly sampled several species from Australia and the Pacific. Among these, *Agrostis australensis* + *A. dyeri* (New Zealand) + *A. muellerina* + *A. parviflora* + *A. venusta* form a clade based on both ITS and plastid data, but relationships of the clade differ among data partitions within the Brevipaleata clade (Fig. 4). Plastid data suggest that their plastome originated from an East Asian ancestor, while ITS data suggest an origin from within the clade of North American species. Similarly, *Agrostis infirma* + *A. infirma* ssp. *remota* from Papua New Guinea and Indonesia form a clade that is part of Brevipaleata clade B_2, which otherwise includes North American species, based on ITS data and part of East Asian Brevipaleata clade B_1, which otherwise includes Eastern Asian species, based on plastid data (Fig. 4).

Affinities of *Agrostis elliottiana* are discordant between ITS and plastid data (Fig. 4). Morphologically, this North American species is similar to species that are part of the Brevipaleata clade, since they have minute or absent paleas (Harvey, 2007), consistent with their placement in this clade based on plastid data. Their affinities with species of the Longipaleata clade based on ITS data may reflect introgression from that major lineage (Fig. 4). Likewise, *Agrostis pourretii* from Europe, which has conflicting ITS and plastid signals, is morphologically similar to species of the Brevipaleata clade, since it has paleas 1/10 as long as the

lemmas (Romero García, 2021b). Plastid data place the species as sister to all other members of the Brevipaleata clade, whereas ITS data align it with other East Asian species in Longipaleata clade L_2 (ITS_{L2}). Plastid data place *Agrostis vinealis* ($PL_{Bx1,2}$), found in Europe and Siberia, in the Brevipaleata grade B_X, while ITS combines the four accessions in the East Asian Brevipaleata B_1 clade.

Affinities of some individuals of *Agrostis gigantea* (*Navarro 6868*) and *A. stolonifera* (*Castroviejo 17902* and *Lazaro s.n.*) vary among the Brevipaleata clade and Longipaleata clade L_1 based on ITS and plastid data (Fig. 5), whereas ITS and plastid markers are congruent in other accessions that we sampled of *A. gigantea* (*Soreng 7766*) and *A. stolonifera* (*Bradley s.n.*), both part of Longipaleata clade L_1. Both species generally have paleas 0.7–1.6 mm long [(1/2–) 2/3–3/4 as long as the lemma] (Romero García, 2021a), like other species of the Longipaleata clade. Intra- and intergeneric hybrids are known to occur with *Agrostis stolonifera* ($2n = 4x = 28$) as one parent, and gene flow distance via pollen for the species has been estimated at 310 km (Watrud et al., 2004; MacBryde, 2006). Members of the *A. stolonifera*/ *A. gigantea* complex are examples of allopolyploidy where repeated hybridizations have led to reticulate evolution seen in their genetic signatures and diverse morphological complexity (Rotter et al., 2010; Reichman et al., 2011). Saarela et al. (2017) similarly found intraspecific variation in some of the *Agrostis* species that they sampled (i.e., *A. mertensii*, *A. gigantea*), and they summarized earlier studies that obtained similar results. Understanding the affinities of *A. stolonifera* is important because this species is the lectotype of *Agrostis* subg. *Vilfa* (Adans.) Rouy [=*Agrostis* sect. *Vilfa* (Adans.) Roem. & Schult. = *Vilfa* Adans. = *V. stolonifera* (L.) P. Beauv. ≡ *Agrostis stolonifera* L.], the scientific name for the Longipaleata clade.

Several other species for which we sampled multiple accessions are placed in various parts of the tree (Fig. 5). Placement of one accession of *Agrostis scabra* (*Soreng 6078*, from Alaska) is part of Brevipaleata clades B_2 and B_3 based on plastid and ITS data, respectively, while another accession of the species (*Peterson 21980*, from North Carolina) is part of Brevipaleata clade B_2 based on ITS data and Brevipaleata grade B_{X-3} based on plastid data. *Agrostis scabra* ($2n = 42$) is highly variable morphologically and, in North America, can be distinguished into three groups: (1) widespread, lowland, rather weedy plants producing large panicles found in the southern USA; (2) smaller short-leaved, slow-growing plants of rocks and scree slopes found in the Rocky Mountains, Appalachians, and much of Alaska, Canada, and Greenland; and (3) luxuriant, broad-leaved plants that are found in sheltered, frost-free canyons of the southwestern USA (Harvey, 2007). Our two North American samples have characteristics of the second group.

Agrostis hendersonii and *A. microphylla* are genetically distinct and aligned in different locations in the Brevipaleata clade (Fig. 5), and these species plus *A. aristiglumis* Swallen (not included in our study), often placed as a synonym of either *A. hendersonii* or *A. microphylla*, are all thought to be closely related (Hitchcock, 1930, 1951; Swallen, 1947; Harvey, 2007; Wilson et al., 2015). These three species differ from one another in several characters: *A. aristiglumis* has paleas 1–1.2 mm long (absent in the other two species),

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A. aristiglumis and *A. hendersonii* have relatively firm and scabrous lemmas (thin and glabrous in *A. microphylla*), *A. aristiglumis* and *A. microphylla* have lemma lateral veins excurrent into 4 mucros usually less than 0.5 mm long in (lemma lateral veins excurrent into 2 mucros or short awns up to 1.5 mm long in *A. hendersonii*), and *A. aristiglumis* and *A. microphylla* have lemmas (2.5–) 3–4 mm long (1.5–2.3 mm long in *A. microphylla*) [Hitchcock, 1930, 1951; Harvey, 2007; Wilson et al., 2015; Roché et al., 2019]. Our results do not support a close relationship between *A. microphylla* and *A. hendersonii*; although the latter species is sometimes recognized as a variety of the former [*A. microphylla* var. *hendersonii* (Hitchc.) Beetle], such a circumscription is not consistent with the current phylogenetic data. The former, with congruent ITS and plastid data, is part of Brevipaleata clade B_2, whereas the latter is part of Brevipaleata clade B_3 based on ITS data and part of a grade of species sister to Brevipaleata clades $B_2 + B_3$ based on plastid data. These three species require further study, including molecular sampling from multiple accessions of each.

Our study suggests that *Agrostis oregonensis* is sister to the newly described species *A. swalalahos* from the coast range mountains in northwest Oregon (Otting & Wilson, 2023), based on both genome partitions (Fig. 5). Together, these two species are sister to *A. pallens*, a species that shares the rhizomatous habit with *A. swalalahos* (Otting & Wilson, 2023) based on ITS data, and to *A. pallens* p.p. based on plastid data. *Agrostis sandwicensis*, the only Hawaiian endemic species of *Agrostis* (O'Connor, 1990), follows the same pattern. It is part of Brevipaleata clade B_3 based on ITS data and forms a clade with *Agrostis oregonensis, A. swalalahos,* and *A. pallens* p.p. based on plastid data.

Our analyses support two major clades within *Agrostis*: Brevipaleata, which we formally recognize as *Agrostis* subg. *Vilfa*, and Longipaleata, which we recognize as *A.* subg. *Agrostis*. Historically, these two subgenera have been recognized in most subgeneric classifications within *Agrostis* (Trinius, 1820, 1824; Björkman, 1960; Widén, 1971; Tzvelev, 1976, 1983; Romero García et al., 1988a; Kurchenko, 2010; Romero García, 2021a). Additionally, both Kurchenko (2010) and Tzvelev (1976, 1983) recognized two additional sections: *A.* sect. *Trichodium* and *A.* sect. *Pseudopolypogon* in the former and *A.* sect. *Trichodium* and *A.* sect. *Pentatherum* in the latter. Although we did not include any of the five Central Asian group of species classified in *A.* sect. *Pseudopolypogon* (*A. hissarica* Roshev., *A. pamirica* Ovcz., *A. paulsenii* Hack., *A. transcaspia* Litv., and *A. subaristata* Aitch. & Hemsl.), all have been suggested to be hybrids involving species from different sections (Kurchenko, 2010). Their morphology suggests that all align within *Polypogon* s.l.

Based on ITS data, *Lachnagrostis ammobia* Edgar, *L. leptostachya* (Hook.) Zotov, and *L. uda* are part of a large *Agrostis* clade (Saarela et al., 2017, fig. 12), suggesting that they would be best placed within *Agrostis*, since we recognize *Polypogon* s.l., a genus of hybrid origin, as sharing an ITS type with *Calamagrostis*. They differ from other New Zealand species sampled that have *Polypogon*-like ITS in having awns straight or curved, versus geniculate (Edgar & Connor, 2010). Recently, Romero García (2021c) recognized

the genera *Linkagrostis* (based on *Agrostis juressi*), and *Neoschischkinia* with five species, including *Agrostis truncatula* (=*Agrostula truncatula* as treated by Peterson et al., 2020), *Agrostis nebulosa* (clade L_3), *A. pourretii*, *A. reuteri* (ITSc2/PL$_{L1-1}$, this placed here in *Polypogon*), and *A. tenerrima* (≡ *Neoschischkinia elegans*, type species). We included ITS data of *A. juressi* (unpublihed, by Acedo C, Alonso A, Llamas F. in 2014 and deposited in GenBank, and it resolved within *Agrostis* clade Longipaleata (Fig. 4).

4.2 Biogeography
4.2.1 Centers of origin of *Agrostis* based on morphology and current distribution
Although we have an incomplete sample of the species found in *Agrostis*, we can make general observations about the biogeographical history of these grasses based on their current distribution. Our phylogeny suggests that *Agrostis* originated in Europe or western Asia, since *Alpagrostis* is sister and is composed of four diploid species and one polyploid species primarily from that region (Figs. 1, 6; Peterson et al., 2020). From Europe and/or western Asia, the species of *Agrostis* radiated to Africa, the western hemisphere, and Australia.

The Agrostidinae clade has been estimated to have a mean crown age of 11.35 (9.06–13.98) mya and a stem age of 12.58 (10.16–15.14) mya (Gallaher et al., 2022). In our core tree phylogeny (Fig. 1), *Calamagrostis* is sister to all other genera of Agrostidinae and these age estimates more than likely apply to this lineage. Although Pooideae, Poeae, and Agrostidodinae are Palearctic in origins, the Calothecinae (also with a stem age of 12.58) and + Paramochloinae, a newer subtribe not considered by Gallaher et al. (2022), is distributed in the western hemisphere and is sister to the Agrostidinae, which implies that the Agrostidinae ancestral area is most likely the western hemisphere (Gallaher et al., 2022). Apparently, early in the evolutionary history of *Agrostis*, a plastid haplotype from the *Agrostis* lineage was donated to the *Calamagrostis* Americana group (receiver), where the ITS signal was assimilated, presumably via recurrent paternal backcrossing, which led to the formation of *Polypogon* s.l., a hybrid genus. This event occurred after the initial derivation of *Agrostis* in Eurasia.

There are no phylogeographical interpretations of the evolutionary history of *Agrostis*, but there are a few published theories about the distribution of species therein and centers of origin of supraspecific (sections) units (Romero García, 1988b; Kurchenko, 2010). Kurchenko (2010) includes a very good evolutionary explanation and makes the following statements: (A) species of the sections *Vilfa* and *Pseudopolypogon* represent ancestral groups due to the presence of a well-developed palea, a primitive evolutionary trait; (B) species of the sects. *Agrostis* and *Trichodium* (including *A. exarata* and *A. clavata*) represent derived groups due to the presence of a reduced palea [a secondary evolutionary reduction according to Kurchenko (2010), Philipson (1935), and Sokolovskaya (1937)]; (C) species of sect. *Vilfa* originated with the "participation" of *Calamagrostis* (i.e., via the process of intrageneric hybridization); and (D) species of the sect. *Pseudopolypogon* and *A. exarata* (from section *Trichodium*) originated with the "participation" of *Polypogon*. Conversely, Kurchenko (2010) identified four

sectional centers of origin: Western Ancient Mediterranean (Pyrenean) for sect. *Agrostis*, Central Ancient Mediterranean for sect. *Vilfa*, Central Asian for sect. *Pseudopolypogon*, and South-East Asian for sect. *Trichodium*. In addition, *Polypogon* was hypothesized to have an Afro-Brazilian origin, with two main branches: eastern (Asian) and western (American). No North or South American centers of sectional origin were suggested. Incidentally, the presence or absence of primitive or derived evolutionary traits was not associated with the relative age of the sections since Kurchenko (2010) suggested that sects. *Vilfa* and *Agrostis* originated during the Miocene–Pliocene boundary during the formation of Ancient Mediterranean flora (Popov, 1963), while sect. *Pseudopolypogon* originated during the Pleistocene with the formation of mountain massifs of Central Asia (Malyshev, 1976).

4.2.2 Phylogeography of *Agrostis* and associated genera

The core phylogenetic analysis of *Agrostis* (Fig. 1) represents an ordered geographic pattern. It suggests that the formation of two major groups, Longipaleata (L) and Brevipaleata (B), occurred rather simultaneously somewhere in Europe (i.e., the western part of Ancient Mediterranean) (Fig. 6). This assumption is supported by our current phylogeny (Figs. 1–5), which places the European groups (L_1 and B_x) at the base of both corresponding major clades (L and B), and by the earlier studies based on the contemporary distribution of the species of *Agrostis*, their morphology, cytology, and past biogeoclimatic events (Popov, 1963; Tateoka, 1971; Widén, 1971; Probatova, 1974; Malyshev, 1976; Tzvelev, 1976; Romero García et al., 1988a; Kurchenko, 2010). Romero García et al. (1988a) placed the origin of *Agrostis* in Southwestern Europe based on the high ratio of diploid species (7 out of 18) that occur in the region. Additional evidence for the European origin of *Agrostis* is the sister, *Alpagrostis* (Peterson et al., 2020), species that were formerly treated within *Agrostis*. According to the core phylogeny, the primary, presumably European split between Longipaleata (L) and Brevipaleata (B) is followed by a separation of African L lineage, Asian L and B lineages, North American B lineage, and South American B lineage. However, after application of the taxon duplication approach for the specimens with incongruent plastid and ITS sequences (Figs. 2–5), we were able to detect "missing" complementary, putatively hybrid African B, North American L, and South American L lineages. Based on this similarity of phylogeographic events, we were able to establish a general phylogeographic pattern of *Agrostis* (Fig. 6) that is characterized by having a main European to South American vector of distribution of the lineages, including a sequence of five distributional phases developing along this vector. We identified these five phases to describe similar phylogeographic events found for both major groups. We also identified a sixth phase, which is placed in reverse to the main vector of distribution to represent the history of *Polypogon, Lachnagrostis* group, Australian *Agrostis*, and European and African polypogonoids. Finally, we accepted the sequence of the phases I–VI as a relative chronology, which is used to elucidate the role of *Calamagrostis* in the formation of *Polypogon*, and to identify correlated

events in the evolutionary history of *Calamagrostis* and *Agrostis* (Fig. 6).

4.2.3 Phases of phylogeographic distribution in *Agrostis*

Phase I (European) represents the origin and primary distribution of Longipaleata (L, *A.* subg. *Vilfa*) and Brevipaleata (B, *A.* subg. *Agrostis*) in Europe.

Phase II (African) includes the following: (A) separation and distribution of the European L_1 lineage of Longipaleata, separation of the common L_2–L_3 lineage in Eastern Europe–Western Asia, separation and migration of L_3 lineage into Africa [probably via Levant (eastern Mediterranean environs], and origin, speciation, and distribution of African Longipaleata and (B) separation and distribution of multiple small European B_x lineages of Brevipaleata, migration of some of the B_x lineages (probably via the Iberian Peninsula) into Northwestern Africa, or further south, hybridization with African Longipaleata (L_3), and origin and speciation of African lachnagrostoids carrying the plastid DNA type of African Longipaleata and the nrDNA ITS type of European Brevipaleata (Fig. 3). Many researchers placed the origin of European Brevipaleata (approximately corresponding to sect. *Agrostis* sensu Kurchenko, 2010) in the Alpine or Pyrenean area in Western Europe (Romero García et al., 1988a). The shortest migration route from the Pyrenean area into Africa lies through the Iberian Peninsula. We hypothesize that the migration of B_x lineages into Africa happened later than the migration of L_3, since they hybridized with the already established African Longipaleata. The hybridization and subsequent speciation resulted in the formation of lachnagrostoid species (*L. schlechteri, L. eriantha, L. lachnantha,* and *A. bergiana*), bearing some features characteristic in genus *Lachnagrostis* (former, as treated below), such as hairy lemmas but only distantly related to the type *L. filiformis*. We can putatively locate the origin of this hybrid lineage in the current area of the Sahara, which has been periodically, and up until prehistoric times, transformed into a grassland, followed each time by desertification (Boos & Korty, 2016; Swann et al., 2014). This process can account for the disappearance of one of the progenitors (species of B_x lineage) and independent subsequent speciation of the African lachnagrostoids.

Phase III (Asian) represents (A) separation and distribution of the Asian monotypic L_2 lineage of Longipaleata, currently including only *A. micrantha*, a taxon showing great genetic variability; (B) separation and distribution of the Asian B_1 lineage of Brevipaleata; (C) hybridization of some representatives of European B_x lineages and established Asian B_1 lineage; and D) speciation and distribution of *A. vinealis* carrying plastid DNA type of European Brevipaleata and the nrDNA ITS type of Asian Brevipaleata (Fig. 4). The widespread species, *A. clavata*, is commonly associated (Tzvelev, 1976; Kurchenko, 2010; Tzvelev & Probatova, 2019) with sect. *Trichodium* (type = *A. scabra*). However, in our analysis, *A. clavata* is aligned with a tight group of East Asian endemics (B_1 as abbreviated in Fig. 5), which phylogenetically is only one of the sister groups to the distinct American (B_2) group containing *A. scabra*. It is difficult to determine whether the remaining species of the East Asian group are derivatives of *A. clavata* (possibly its ancestral form with lower ploidy level) or if the species originated within East
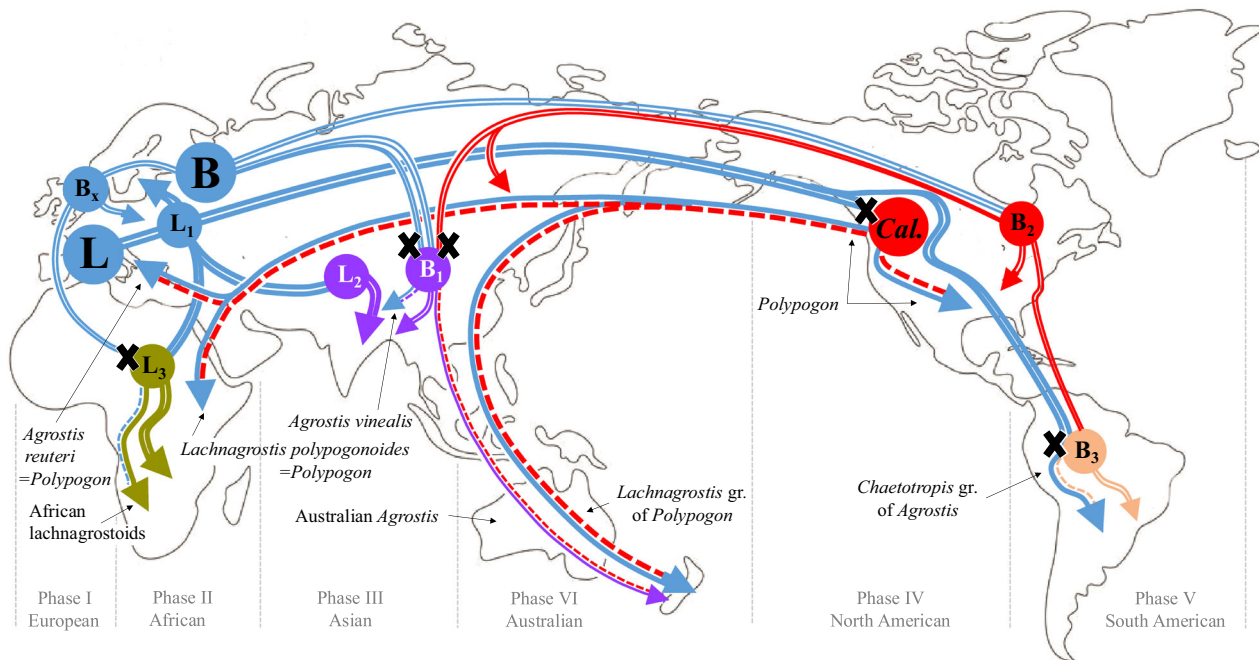
Fig. 6. *Agrostis* phylogeography based on phylogenetic inference and correlation between plastid and ITS (nrDNA) lineages. Circles correspond to major putative speciation centers (B, Brevipaleata; Cal., *Calamagrostis* Americana group; L, Longipaleata) identified in Figs. 1–5. Solid thick double lines represent the distribution of congruent plastid and ITS lineages in Longipaleata (L); solid thin double lines represent the distribution of congruent plastid and ITS lineages in Brevipaleata (B); thick dashed lines represent the distribution of incongruent ITS lineages that originated within *Calamagrostis* (Cal.); and thin dashed lines represent the distribution of incongruent ITS lineages that originated in Brevipaleata (B). The color of arrowheads corresponds to plastid lineages. Phases I–VI demarcate the stages of development of the phylogeographic pattern within *Agrostis*.

Asian group and only later achieved a wide distribution. Some evidence can be drawn from the evolutionary history of another widespread species, *A. vinealis*. In our study, *A. vinealis* is represented by four specimens (collected in Europe and Siberia) sharing two somewhat different plastid types of presumably European origin, and the singular nrDNA ITS type of presumably East Asian origin (Fig. 4). Since the distribution of *A. vinealis* could have happened only after its hybrid speciation in East Asia, we can identify the out-of-East Asia wide distribution pattern, probably characteristic for other species of *Agrostis*, such as *A. clavata*.

Phase IV (North American) represents (A) distribution of the European L_1 lineage of Longipaleata into North America, hybridization of representatives of this lineage with the Americana group of *Calamagrostis*, formation and distribution of *Polypogon*, carrying the plastid DNA type of the Longipaleata group of European *Agrostis* and the nrDNA ITS type of American *Calamagrostis* and (B) separation and distribution of the North American B_2 lineage of Brevipaleata (Fig. 2). The widespread species *A. mertensii* is commonly associated with sect. *Agraulus* = *Agrostis* (Tzvelev, 1976) or sect. *Agrostis* (Kurchenko, 2010; Tzvelev & Probatova, 2019); both sections have *A. canina* as the type. However, Hultén (1942) indicated close relationships between *A. mertensii* and *A. hyemalis*, belonging to the sect. *Trichodium*. Kurchenko (2010) placed *A. mertensii* in group II of sect. *Agrostis*, which is characterized by small anthers, a

trait that is rather common among species of the sect. *Trichodium* (represented here by North American B_2 lineage), is in congruence with our findings. Along with *A. scabra*, *A. mertensii* is a widespread species, occurring mainly in North America, but also in northwestern South America, Asian Far East, and northern Europe. Tateoka (1971), Widén (1971), and Tzvelev (1976) advocate the circumboreal dispersal of *A. mertensii*, probably in the Pleistocene, with its range later being interrupted, following by the formation of *A. borealis* in northern Europe. We tend to agree with this. Nevertheless, we place the origin of *A. mertensii*, *A. scabra*, and the entire B_2 lineage in North America.

Phase V (South American) represents (A) distribution of the North American B_2 lineage of Brevipaleata into South America, and the separation and distribution of the South American B_3 lineage of Brevipaleata and (B) distribution of the European L_1 lineage of Longipaleata into South America, the hybridization of representatives of this lineage with some species of South American Brevipaleata, and the formation of the *Chaetotropis* group in *Agrostis*.

Phase VI (Australian) represents (A) putative circumboreal distribution of the North American B_2 lineage of Brevipaleata, the hybridization of representatives of this lineage with Asian B_1 lineage, the formation and distribution into Australia and New Zealand of the hybridogenic group of *Agrostis* carrying plastid DNA type of the Asian B_1 lineage and the nrDNA ITS

type of the North American B$_2$ lineage of Brevipaleata (Fig. 4) and (B) out-of-North America expansion of intergeneric hybrid genus *Polypogon*, the separation and distribution of the European and African monotypic branches of *Polypogon* (*Agrostis reuteri* and *Lachnagrostis polypogonoides*, respectively), the distribution of *Polypogon* into Australia and New Zealand, and the development of a morphologically distinct *Lachnagrostis* group (formerly treated as an independent genus) of Australian *Polypogon*. This is the most complex phase that probably occurred after the colonization of Australia by hybridogenic lineages of Brevipaleata (resulting from putative intersectional hybridization within *Agrostis*) and Longipaleata (resulting from intergeneric hybridization of this lineage with *Calamagrostis*). In our earlier work on the phylogeny of *Calamagrostis* (Peterson et al., 2021), we hypothesized that the origin of *Calamagrostis* took place somewhere in North America, followed by a separation of South American and North American lineages (Meridionalis and Americana groups, respectively). The third split in the phylogeny of *Calamagrostis* led to the formation of proto-Eurasian lineages, followed by its migration via Beringia and subsequent diversification on Eurasian continent. Using the sequence phylogeographical phases as the relative chronology, we assume that *Agrostis* arose much earlier than *Calamagrostis*. Based on our phylogenetic evidence, by the time an ancestor of *Agrostis* hybridized with North American *Calamagrostis*, the genus (*Agrostis*) had already undergone the formation of most of its major groups, that is, the core phylogenetic pattern was fully established. The are several studies emphasizing the asynchronous or asymmetrical character of Beringian Interchange (Jiang et al., 2019). It is possible that the phylogeography of *Agrostis* and *Calamagrostis* reflects one such asynchronous distribution event through Beringia, where the first event included the distribution of congruent European lineages (i.e., carrying congruent plastid and nrDNA types) of Longipaleata and Brevipaleata from Eurasia into North America, following a forward vector of distribution for *Agrostis*, while the second event included the distribution of hybridogenic genus *Polypogon*, a congruent lineage of American Brevipaleata, and congruent proto-Eurasian lineages of *Calamagrostis* from North America into Eurasia, following a reverse vector of distribution for *Agrostis* and a forward vector of distribution for *Calamagrostis*. We consider the separation of monotypic European and African branches of *Polypogon* as well as the formation and distribution of Australian *Agrostis* being co-phasal events. In addition, we anticipate the expansion of *Polypogon* by inclusion of the Central Asian group of species attributed by Kurchenko (2010) to the section *Pseudopolypogon* Kurcz. The presence of prominent morphological features in these Central Asian species, such as the separation of the spikelet with a stipe, suggests that it is quite possible.

4.2.4 Basal lineages or solitary migrants
We detected two puzzling basal plastid lineages belonging to North American *Agrostis elliottiana* and European *Agrostis pourretii* (Fig. 4). The acceptance of *A. elliottiana* as a basal lineage and an indicator of the place of origin of entire Brevipaleata would require interpretation of much bigger number of phylogeographic events and an additional number of distribution reversals. It is possible that one of the basal lineages of Brevipaleata hybridized with representatives of

basal lineages of European Longipaleata and then migrated into North America during Phase IV. Similarly, *A. pourretii* could have hybridized with an Asian representative of Longipaleata, which subsequently recolonized Europe. Alternatively, a hybridization with some ancestral form of *A. tenerrima* could have occurred in Europe. Romero García et al. (1988a) considered them to be closely related and placed them in the sect. *Vilfa*. Incidentally, all three species probably acquired their annual habit independently as an adaptation to harsh environmental conditions.

The representative of the former South American genus *Bromidium* Nees & Meyen appears out of place among Eurasian Longipaleata (Figs. 1, 4). It is characterized by reduced palea, annual or perennial habit, congruent plastid and nrDNA types, and geographical isolation from phylogenetically cognate taxa. It is possible that the reduced palea represents a secondary reduction and morphological convergence with Brevipaleata.

5 Conclusion

Based on our analyses, we find no molecular support for recognizing the genera *Bromidium*, *Chaetopogon*, *Chaetotropis*, *Linkagrostis*, or *Neoschischkinia*, since they appear to be nested in *Agrostis*. However, we recognize *Polypogon* s.l. as a hybrid genus with a greatly expanded circumscription, and a reduced number of key characteristics, such as distinctly keeled upper glumes that are scabrous (often strongly so), paleas 2/3 to as long as the lemma, and with glumes that are often awned. If all species of *Polypogon* are lumped within *Agrostis*, as recently proposed by Röser and Tkach (2024), *Calamagrostis* would be paraphyletic, and all genera and species allied with *Agrostis* in our core phylogeny, i.e., *Alpagrostis, Podagrostis, Gastridium, Triplachne*, and *Calamagrostis* would need to be accommodated within *Agrostis*. We feel that this approach would destabilize taxonomy, ultimately reducing phylogenetic information that these generic names contain. Intergeneric reticulation is common in grasses (Tkach et al, 2020), with more than 80 named nothogenera, and increasingly more genera of reticulate origin are being detected by genetic methods (more than 30 genera and larger groups are noted as "reticulate" in Soreng et al., 2022, appendix 1). Within Poeae, beyond Agrostidinae and other tribes within the grass family, notably Andropogoneae Dumort., Bambuseae Kunth ex Dumort., Triticeae Dumort., have similar problems in generic delimitation but we do not advocate collapsing these into one or a few genera.

Further study is needed to ascertain all lineages that exist within *Agrostis*. Our present inquiry is only a preliminary glimpse at the evolutionary history in this large genus and related species, and we implore other systematists to continue the investigative crusade by adding more species and additional molecular tools, such as whole genomes and low-copy nuclear genes.

6 Taxonomy

Based on our DNA-derived phylogenies, we are proposing to retain *Polypogon* with an expanded circumscription as a

genus of reticulate origin, since many species share the ITS type derived from within the Americana group of *Calamagrostis*. Therefore, we are making nine new combinations in *Polypogon* for species that we sampled. In addition, we are recognizing former species in *Bromidium*, *Chaetotropis*, *Chaetopogon*, *Lachnagrostis*, and *Polypogon* in *Agrostis*, even though some show incongruent placement within our phylogenies, but all align within *Agrostis*. In many instances, names are available in the genera which we recognize here or in the above-mentioned taxa, as summarized below. Where they are not, we propose here the necessary combinations. We also propose lectotypes for several existing combinations.

6.1 Agrostis

Agrostis austroamericana Röser & Tkach, Schlechtendalia 41: 65. 2024. *nom. nov.* Basionym: *Chaetotropis chilensis* Kunth, Révis. Gramin. 1: 271, t. 47. 1829, *non Agrostis chilensis* Trin., 1836. Type: Chile, Chilensi, Jan 1823–1825, *d'Urville s.n.* (lectotype, **designated here**: P02644429 [image!]; isolectotypes: BAA Typus 3499!, P02644425 [image!]) ≡ *Polypogon chilensis* (Kunth) Pilg., Repert. Spec. Nov. Regni Veg. 16: 386. 1920.

= *Agrostis muricata* (J. Presl) Kunth, Enum Pl. 1: 219. 1833. Basionym: *Vilfa muricata* J. Presl, Reliq. Haenk 1(4–5): 240. 1830. Type: Peru, *T.P.X. Haenke s.n.* (lectotype, **designated here**: PRC450952 [image!]).

Agrostis barbuligera Stapf, Fl. Cap. 7: 548–549. 1899. Type: South Africa, Mt. Boschberg, Somerset Division, 4300 ft, *P. MacOwan 2189* (lectotype, **designated here**: K000367420 [image!]) ≡ *Lachnagrostis barbuligera* (Stapf) Rúgolo & A.M. Molina, Bot. Nuevo Milenio 28. 2002.

Agrostis elongatiligulata Röser & Tkach, Schlechtendalia 41: 65. 2024. *nom. nov.* Basionym: *Polypogon elongatus* Kunth, Nov. Gen. Sp. (quarto ed.) 1: 134–135. 1815 [1816], *non Agrostis elongata* Lam., 1791, *nom. illeg. superfl.* Type: Ecuador, Chillo Quitensium 3., *A.J.A. Bonpland s.n.* (lectotype, **designated here**: P00135063 [image!]; isolectotypes: B-W-1559, P-00669393 [image!]) ≡ *Chaetotropis elongata* (Kunth) Björkman, Symb. Bot. Upsal. 17(1): 14. 1960.

= *Polypogon inaequalis* Trin., Gram. Panic. 24. 1826. Type: Brazil, *Langsdorff s.n.* (lectotype, **designated here**: LE-TRIN-1565.07a!; isolectotype: US-999294! fragm. ex LE-TRIN).

Agrostis eriantha Hack., Vierteljahrsschr. Naturf. Ges. Zürich 49: 172. 1904. Type: South Africa, in humidis pr. Pretoria, 4700 ft, 6 Dec 1894, *R. Schlecter 4144* (lectotype, **designated here**: W19160036234 [image!]; isolectotypes: BM000922815 [image!], FR0030125 [image!], K000367406 [image!], MPU027097 [image!], PRE0592110-0 [image!], US-75384! fragm. ex W) ≡ *Lachnagrostis eriantha* (Hack.) A.J. Br., Muelleria 34: 40. 2015.

Agrostis lachnantha Nees, Index Seminum, quae pro mutua commutatione offert Hortus Botanticus. Wratislaviensis, p. 1 (name), p. 3 (description and one location) (Ind. Sem. Hort. Bot. Wratislav.) 1834. Type: South Africa, Cape Province,wet, stony places in the bed of the Zwartkopsrivier [= Swartkops River], 1st height, *cf. Ecklon & J.F. Drège 4492* (lectotype, **designated here**: W-RCHB0276289 [image!]; isolectotypes: K (probable), W0075422 [image!]) ≡ *Podosemum lachnanthum* (Nees) Nees, Fl. Afr. Austral. Ill. 1: 148. 1841. ≡ *Lachnagrostis*

lachnantha (Nees) Rúgolo & A.M. Molina, Bot. Nuevo Milenio 29. 2002.

Note: Nees (1836) cited "Index Seminum, quae pro mutua commutatione offert Hortus Botanticus. Wratislaviensis 1834" for the place of publication, and the one location cited there matches that of the *Ecklon & Drège* specimen cited under *Podosemum lachnantum* (Nees, 1841).

Agrostis lyallii Hook. f., Fl. Nov.-Zel. 1: 297. 1853. Type: New Zealand, Milford Sound, *Lyall s.n.* (holotype: K000838246 [image!]) ≡ *Deyeuxia forsteri* var. *lyallii* (Hook. f.) Hack., Man. New Zealand Fl. 869. 1906. ≡ *Deyeuxia filiformis* var. *lyallii* (Hook. f.) Hack., Subantarctic Isl. 2: 474. 1909 ≡ *Deyeuxia filiformis* var. *lyallii* (Hook. f.) Zotov, Trans. Roy. Soc. New Zealand 73: 235. 1943 ≡ *Lachnagrostis lyallii* (Hook. f.) Zotov, Rec. Domin. Mus. 5: 142. 1965.

Agrostis nowodworskyi Röser & Tkach, Schlechtendalia 41: 65. 2024. Basionym: *Nowodworskya imberbis* Phil., Anales Univ. Chile 43: 562. 1873 (*non Agrostis imberbis* Phil. 1896). Type: Chile, Juan Fernandez Islands, a orillas del mar en el puerto del Ingles, *Philippi s.n.* (holotype: SGO-PHIL-63114; isotypes: BAA, US-95294! fragm. ex W, SGO-63114). ≡ *Polypogon imberbis* (Phil.) Johow, Estud. H. Juan Fernandez 36. 1896 ≡ *Chaetotropis imberbis* (Phil.) Björkman, Symb. Bot. Upsal. 17(1): 14. 1960.

= *Agrostis tehuelcha* Speg., Anales Mus. Nac. Hist. Nat. Buenos Aires Ser. 3, 7: 186. 1902. Type: Argentina, Santa Cruz, in uliginosis secus Río Santa Cruz, Feb 1882, *C. Spegazzini 2546* (lectotype, designated by V.L. Finot et al., J. Bot. Res. Inst. Texas 7(1): 184. 2013: LP-5370; isolectotype: US-1818806! ex LP).

Agrostis schlechteri Rendle, J. Bot. 37(441): 380. 1899. Type: South Africa: French Hook, 2800 ft, 11 Feb 1897, *R. Schlechter 10274*; (holotype: BM000922821 [image!]; isotypes: BOL139285 [image!], G00015730 [image!], G00015731 [image!], GRA0000154-0 [image!], K000367422 [image!]) ≡ *Lachnagrostis schlechteri* (Rendle) Rúgolo & A.M. Molina, Bot. Nuevo Milenio 29. 2002.

Agrostis subspicata (Willd.) Raspail, Ann. Sci. Nat. (Paris) 5: 449. 1825. Basionym: *Polypogon subspicatus* Willd., Neue Schriften Ges. Naturf. Freunde Berlin 3: 443–444. 1801. Type: Spain, auf trocken Aekern in Estremadura, *Schousboe s.n.* (lectotype, **designated here**: B-W01560-010 [image!]; isolectotype: C10016833 [p.p. 2, image!]).

= *Chaetopogon fasciculatus* (Link) Hayek, Repert. Spec. Nov. Regni Veg. Beih. 30(3): 335. 1932 ≡ *Chaeturus fasciculatus* Link, J. Bot. (Schrader) ii. 313. 1799, *non Agrostis fasciculata* (Kunth) Roem. & Schult., 1817 ≡ *Agrostis linkii* Banfi, Galasso & Bartolucci, Nat. Hist. Sci. 5(1): 54–55. 2018.

6.2 Polypogon

Polypogon adamsonii (Vickery) P.M. Peterson, Soreng & Romasch., **comb. nov.** Basionym: *Agrostis adamsonii* Vickery, Contr. New South Wales Natl. Herb. 1: 107, 108. 1941 ≡ *Lachnagrostis adamsonii* (Vickery) S.W.L. Jacobs, Telopea 9(3): 445. 2001. Type: Australia, Victoria, Melbourne, 12 Nov 1853, *F.M. Adamson 226* (holotype, K000838268 [image!]).

Polypogon aemulus (R. Br.) P.M. Peterson, Soreng & Romasch., **comb. nov.** Basionym: *Agrostis aemula* R. Br., Prodr. 72. 1810 ≡ *Vilfa aemula* (R. Br.) P. Beauv., Ess. Agrostogr. 16: 146, 181. 1812 ≡ *Lachnagrostis aemula* (R. Br.)

Trin., Fund. Agrost. 128. 1820 ≡ *Deyeuxia aemula* (R. Br.) Kunth, Révis. Gramin. 1: 77. 1829 ≡ *Calamagrostis aemula* (R. Br.) Steud., Nomencl. Bot. 2nd ed. 1: 249. 1840 ≡ *Deyeuxia filiformis* var. *aemula* (R. Br.) Domin, Biblioth. Bot. 20(85): 352. 1915. Type: Australia, New South Wales, Port Jackson and Port Dalrymple (Tasmania), *R. Brown 6219* [plant on left side of sheet] (lectotype, designated by J.W. Vickery, Contr, New South Wales Natl. Herb. 1: 115. 1941: BM000573965 [image!; Vickery excluded the plant on the right with filiform leaf blades]; isolectotype: K00083255, left half of sheet).

Polypogon billardierei (R. Br.) P.M. Peterson, Soreng & Romasch., **comb. nov.** Basionym: *Agrostis billardierei* R. Br., Prodr. 171. 1810 ≡ *Vilfa billardierei* (R. Br.) P. Beauv., Ess. Agrostogr. 16: 147. 1812 ≡ *Lachnagrostis billardieri* (R. Br.) Trin., Fund. Agrost. 128, t. 10. 1820 ≡ *Deyeuxia billardierei* (R. Br.) Kunth, Révis. Gramin. 1: 77. 1829 ≡ *Calamagrostis billardierei* (R. Br.) Steud., Nomencl. Bot. 2nd ed. 1: 249. 1840 ≡ *Calamagrostis aemula* var. *billardierei* (R. Br.) Maiden & Betche, Census New South Wales Pl. 21. 1916. Type: Australia, New South Whales, Port Jackson, *R. Brown 6218* (lectotype, designated by J.W. Vickery, Contr. New South Wales Natl. Herb. 1: 109. 1941: BM000573963 [image! Vickery excluded the plant on left but included the two on the right]; isolectotypes: BM013767106, K000838267 [image! annotated by J.W. Vickery]).

Note: Orthographic variant; *billardieri*, corrected to *billardierei*.

Polypogon bourgaei (E. Fourn.) P.M. Peterson, Soreng & Romasch., **comb. nov.** Basionym: *Agrostis bourgaei* E. Fourn., Mexic. Pl. 2: 95. 1886. Type: Mexico, Estado Mexico, Pedrégal près Tizapan, vallée de Mexico, 2 Aug 1865, *E. Bourgeau 682* (lectotype, **designated here**: P00740531 [image!]; isolectotypes: P00166464 [image!], US-556238! fragm. ex P).

Polypogon exaratus (Trin.) P.M. Peterson, Soreng & Romasch., **comb. nov.** Basionym: *Agrostis exarata* Trin., Gram. Unifl. Sesquifl. 207. 1824. Type: U.S.A., Alaska, Unalaschka, 1829, campis a se lectam comm. cl. Eschholz, *Eschcsholtz s.n.* (lectotype, **designated here**: LE-TRIN-1606.06 a!, excluding the left hand sample collected by *Kastalsky*; isolectotype: LE-A/423-C6!). Note: Tzvelev & Probatova (2019) on p. 252 cite Tzvelev (1976) on p. 339, as designating a lectotype at LE, but there is more than on sheet at LE (other syntypes are noted from BR and K).

Polypogon filiformis (G. Forst.) P.M. Peterson, Soreng & Romasch., **comb. nov.** Basionym: *Avena filiformis* G. Forst., Fl. Ins. Austr. 9. 1786 ≡ *Agrostis avenacea* J.F. Gmel., Syst. Nat., ed. 13[bis] 2(1): 171. 1791, *nom. nov.*, non *Agrostis filiformis* Vill. 1787 ≡ *Lachnagrostis filiformis* (G. Forst.) Trin., Fund. Agrost. 128, pl. 10. 1820. Type: New Zealand, Insula Paschatis (Easter Island), 1779, *J.R. Forster s.n.* (lectotype, designated by E. Edgar, New Zealand J. Bot. 33: 19. 1995: B-W-2208; isolectotype: W0026518 [image!]).

Polypogon littoralis (Hack.) P.M. Peterson, Soreng & Romasch., **comb. nov.** Basionym: *Deyeuxia forsteri* var. *littoralis* Hack., New Zealand J. Bot. 33(1): 23–26. 1995 ≡ *Lachnagrostis littoralis* (Hack.) Edgar, New Zealand J. Bot. 33(1): 23–26. 1995. Type: New Zealand, Kermadec Islands, NE from New Zealand, *R.H. Shakespear* [*Cheeseman 1136*] (lectotype, designated by E. Edgar, New Zealand J. Bot. 33: 23. 1995: "W-7916", W19040007916 [image!]; isolectotypes: BAB00000180 [image!], BAB00000181 [image!], BAB00000182 [image!], WELT-76589).

Polypogon polypogonoides (Stapf) P.M. Peterson, Soreng & Romasch., **comb. nov.** Basionym: *Agrostis polypogonoides*

Stapf, Fl. Cap. 7: 549. 1899 ≡ *Lachnagrostis polypogonoides* (Stapf) A.J. Br., Muelleria 34: 40. 2015. Type: South Africa, Coast Region, Cape Peninsula, Muizenburg Vlei, *W. Dod 2349* (lectotype, **designated here**: K000367375 [image!]; isolectotypes: BM000922820 [image!], BOL139282 [image!], BOL139283 [image!], BOL139284 [image!]).

Polypogon reuteri (Boiss.) P.M. Peterson, Soreng & Romasch., **comb. nov.** Basionym: *Agrostis reuteri* Boiss., Voy. Bot. Espagne 2: 645. 1845. Type: Spain, in herbosis et arenosis regionis calidae et montanae, in provincia Malacitana Prolongo, prope Estepona Haenseler, *G.F. Reuter s.n.* (lectotype, designated by H.M. Burdet & A. Charpin, Candollea 36: 555. 1981: G00195317 [image!]; isolectotype: G00195320 [image!]) ≡ *Neoschischkinia reuteri* (Boiss.) Valdés & H. Scholz, Willdenowia 36(2): 663. 2006.

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Supplementary Material

The following supplementary material is available online for this article at http://onlinelibrary.wiley.com/doi/10.1111/jse.13175/suppinfo:

Appendix S1. Taxon voucher (collector, number, and where the specimen is housed), country of origin, and GenBank accession for DNA sequences of *rps16–trnK, rps16 intron, rpl32–trnL,* and ITS regions; bold indicates new accession; a dash (–) indicates missing data; *sequence obtained from GenBank.

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