

Genome origin and phylogenetic relationships of *Campeiostrachys* (Triticeae: Poaceae) based on nuclear and chloroplast DNA regions

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Abstract

Background and aims – *Campeiostrachys* is an allohexaploid perennial genus of the Triticeae tribe (Poaceae). The allopolyploids of Triticeae are produced by interspecific hybridization of different genera. In this study, we investigate the genome origin of *Campeiostrachys* and the relationships of some species based on phylogenetic analyses.

Material and methods – Two nuclear (*Acc1* and *DMC1*) and two chloroplast (*matK* and *rps16*) DNA regions of the species of *Campeiostrachys* and its related genera were used for phylogenetic analyses.

Key results – The *Acc1* and *DMC1* sequences revealed that the genome composition of all *Campeiostrachys* species in our study is StYH, suggesting that *Campeiostrachys* may have originated by the natural hybridization between species with StY and H genomes, as no species with Y or HY genomes have been found in the wild. The results from the chloroplast regions indicated that the maternal donor of the *Campeiostrachys* species contains the St subgenome. In addition, phylogenetic analysis of the nuclear sequences showed that *C. purpuraristata* always groups with the species of the *C. dahurica* complex in the St, Y, or H clade, distinct from other species in the genus. Also, *C. calcicola*, *C. kamoji*, and *C. tsukushiensis* var. *transiens* are distinct yet closely related species.

Conclusion – *Campeiostrachys* species originated from the natural hybridization of the tetraploid species of *Roegneria* (StY) with the diploid species of *Hordeum* (H), with *Roegneria* (StY) acting as the maternal donor. *Campeiostrachys purpuraristata* should be classified into the *C. dahurica* complex and treated as *C. dahurica* var. *purpuraristata*.

Keywords

allohexaploid, *Campeiostrachys*, genome constitution, maternal donor, natural hybridization, phylogeny

INTRODUCTION

Hybridization and polyploidization play a key role in plant evolution and speciation (Stebbins 1950; Soltis and Soltis 2000; Otto and Whitton 2000). Polyploids formed by intraspecific genome replication or hybridization

of different genotypes are autopolyploids, while those formed by interspecific hybridization are allopolyploids (Stebbins 1947; Grant 1981; Liu et al. 2006; Brassac and Blattner 2015). The tribe Triticeae, an important gene pool for the genetic improvement of wheat, barley, and

other Triticeae crops (Dewey 1984; Lu 1993), includes many polyploid taxa (Yen et al. 2005; Baum et al. 2011). Among these, the allopolyploids of Triticeae are produced by intergeneric hybridization of the genera with different genome composition (Sears 1954; Kimber and Alonso 1981; Dewey 1984; Heslop-Harrison 1992; Petersen et al. 2011). Based on the genomic system of classification in Triticeae, the species with the same genome or genome combinations were classified into one genus (Löve 1984; Yen et al. 2005; Baum et al. 2011; Lucía et al. 2019). Thus, these allopolyploid species are classified into different polyploid genera based on their genome composition (Cai 1997; Yen et al. 2005; Barkworth et al. 2009; Baum et al. 2011; Yen and Yang 2013; Lucía et al. 2019).

The genus *Campeiostrachys* Drobow was established by Drobow (1941), and currently holds 15 species and 13 varieties (Baum et al. 2011; Yen and Yang 2013; Yang et al. 2015, 2016; Tan et al. 2024). Cytogenetic analyses have revealed that all *Campeiostrachys* species are hexaploid and contain three subgenomes (**St**, **Y**, and **H**) (Baum et al. 2011; Yen and Yang 2013). The **St** and **H** subgenomes are supposed to have been donated by the diploid *Pseudoroegneria* (Nevski) Á.Löve and by *Hordeum* L., respectively (Mason-Gamer 2004; Sun et al. 2008; Sha et al. 2017; Tang et al. 2017). However, the origin of the **Y** subgenome remains unknown (Jensen 1990; Kellogg et al. 1996; Adderley and Sun 2014). As an allopolyploid genus, *Campeiostrachys* originated from natural hybridization between related genera in the Triticeae, but its parents cannot be identified (Baum et al. 2011; Petersen et al. 2011; Lei et al. 2022).

The relationship between some species within *Campeiostrachys* remains unclear. For example, the taxa included in the *Campeiostrachys dahurica* (Turcz. ex Griseb.) B.R.Baum, J.L.Yang & C.Yen (= *Elymus dahuricus* Turcz. ex Griseb.) complex have been debated. Because the morphological difference is small, Lu (1993) included *Elymus dahuricus*, *E. excelsus* Turcz. ex Griseb., *E. tangutorum* (Nevski) Hand.-Mazz., *Elymus dahuricus* var. *cylindricus* Franch., *E. purpuraristatus* C.P.Wang & X.L.Yang, and *E. villifer* C.P.Wang & X.L.Yang in the *E. dahuricus* complex. In the Flora of China, *E. purpuraristatus* is treated as an independent species (Chen and Zhu 2006). Combined morphological data and genome composition determined that *E. excelsus*, *E. tangutorum*, and *E. dahuricus* var. *cylindricus* were to be classified into the genus *Campeiostrachys*, and included in the *C. dahurica* complex as varieties (Baum et al. 2011; Yen and Yang 2013). Genome in situ hybridization (GISH) results showed that the genome composition of *E. purpuraristatus* is **StYH** and the species should be classified into *Campeiostrachys* (Tan et al. 2021). At present, the relationship between *C. purpuraristata* (C.P.Wang & X.L.Yang) Y.H.Zhou, H.Q.Zhang & Wei Huan Chen and the *C. dahurica* complex is unclear. Based on morphological and molecular data, the relationship between *Campeiostrachys kamoji* (Ohwi) B.R.Baum, J.L.Yang & C.Yen, *Campeiostrachys tsukushiensis* var.

transiens (Hack.) C.Yen & J.L.Yang, and *C. calcicola* (Keng) Y.H.Zhou, H.Q.Zhang & M.Q.Deng is also uncertain (Kuo 1987; Lu et al. 1990; Yen and Yang 2013).

Phylogenetic analyses have been proven as a fast and effective way for identifying genome composition, species relationships, and progenitor species of allopolyploid taxa, revealing the origin and evolutionary history of polyploid plants (Fortune et al. 2007; Blattner 2009; Fan et al. 2013; Bieniek et al. 2015; Baum et al. 2015). When the DNA sequences of diploid donors and allopolyploids in Triticeae correspond, this allows for the determination of the genome composition of the allopolyploid (Petersen et al. 2006; Wang et al. 2019). Single-copy nuclear genes are biparentally inherited and less susceptible to concerted evolution, making them ideal markers for identifying parental donors and evolutionary relationships of polyploid taxa (Soltis et al. 2004; McMillan and Sun 2004; Rauscher et al. 2004; Liu et al. 2006). In contrast, chloroplast markers are maternally inherited (Hodge et al. 2010; Middleton et al. 2014; Sha et al. 2017), and these sequences have therefore been widely used to identify the maternal donor of allopolyploid species or genera in Triticeae (Dong et al. 2015; Lei et al. 2018).

In this context, the objectives of this study on 15 *Campeiostrachys* polyploids and the diploid and polyploids of related genera are: (1) to elucidate the genome origin of *Campeiostrachys*; (2) to investigate the maternal donor of *Campeiostrachys* species; (3) to explore the phylogenetic relationships among *Campeiostrachys* species.

MATERIAL AND METHODS

Plant material

Most of the material was collected by the authors' research team, except for material of *Campeiostrachys drobovii* (Nevski) B.R.Baum, J.L.Yang, & C.Yen (PI 314203), *C. tsukushiensis* var. *transiens* (PI 276396), and *Bromus inermis* Leyss. (PI 618974), which was kindly provided by the USDA National Plant Germplasm System (<https://www.ars-grin.gov>). Specimens of the material listed in Table 1 are kept at the Herbarium of Triticeae Research Institute of Sichuan Agricultural University, China (SAUTI).

In addition to the material mentioned in Table 1, we also downloaded the *Acc1*, *DMC1*, *matK*, and *rps16* sequences of closely related species (*Roegneria* K.Koch **StY**, *Elymus* L. **StH**, *Stenostachys* Turcz. **HW**, *Campeiostrachys* **StYH**, *Kengyilia* C.Yen & J.L.Yang **StYP**, *Anthosachne* Steud. **StYW**, *Pascopyrum* Á.Löve **StYHW**, *Connorochloa* Barkworth, S.W.L.Jacobs & H.Q.Zhang **StHNsXm**, and some diploid species of the Triticeae) from GenBank. Detailed information is provided in Suppl. materials 1–3.

DNA amplification and sequencing

The total genomic DNA was extracted from fresh leaves using the CTAB method (Doyle and Doyle 1990).

Table 1. The materials used for sequencing in this study.

Species	Genome	Accession No.	Origin
<i>Campeiostrachys aristiglumis</i>	StYH	Y 0614	Xinjiang
<i>Campeiostrachys calcicola</i>	StYH	ZY 1005	Sichuan
<i>Campeiostrachys drobovii</i>	StYH	PI 314203	Russian
<i>Campeiostrachys dahurica</i>	StYH	ZY 11033	Inner Mongolia
<i>Campeiostrachys dahurica</i> var. <i>cylindrica</i>	StYH	Y 0750	Xinjiang
<i>Campeiostrachys dahurica</i> var. <i>excelsis</i>	StYH	ZY 11034	Inner Mongolia
<i>Campeiostrachys dahurica</i> var. <i>tangutorum</i>	StYH	Y 2092	Sichuan
<i>Campeiostrachys kamoji</i>	StYH	ZY 1007	Sichuan
<i>Campeiostrachys nutans</i>	StYH	Y 2235	-
<i>Campeiostrachys purpuraristata</i>	StYH	ZY 11075	Inner Mongolia
<i>Campeiostrachys schrenkiana</i>	StYH	Y 2426	-
<i>Campeiostrachys tsukushiensis</i> var. <i>transiens</i>	StYH	PI 276396	Sweden
<i>Elymus atratus</i>	StYH	ZY 15005	Sichuan
<i>Elymus breviaristatus</i>	StYH	ZY 17008	Sichuan
<i>Elymus sinosubmuticus</i>	StYH	ZY 17004	Sichuan
<i>Hordeum bogdanii</i>	H	ZY 11066	Inner Mongolia
<i>Bromus inermis</i> subsp. <i>inermis</i>	-	PI 618974	Xinjiang

Table 2. Primers and PCR profiles used in this study.

Gene	Primer	Sequence of primer (5'-3')	PCR profiles
<i>Acc1</i>	F	CCCAATATTTATCATGAGACTTGCA	1 cycle: 5 min 95°C; 35 cycles: 30 s 95°C, 30 s 56°C, 2 min 30 s 68°C;
	R	CAACATTTGAATGAATHCTCCACG	1 cycle: 10 min 68°C
<i>DMC1</i>	F	TGCCAATTGCTGAGAGATTTG	1 cycle: 4 min 95°C; 35 cycles: 1 min 95°C, 1 min 52°C, 1 min 72°C;
	R	AGCCACCTGTTGTAATCTGG	1 cycle: 10 min 72°C
<i>matK</i>	F	CGATCTATTCATTCAATATTTTC	1 cycle: 4 min 95°C; 35 cycles: 1 min 95°C, 1 min 50°C, 1 min 30 s
	R	TCTAGCACACGAAAGTCGAAAGT	72°C; 1 cycle: 10 min 72°C
<i>rps16</i>	F	AAACGATGTGGTAGAAAGCAAC	1 cycle: 4 min 95°C; 35 cycles: 1 min 95°C, 1 min 53°C, 1 min 72°C;
	R	AAACGATGTGGTAGAAAGCAAC	1 cycle: 10 min 72°C

The *Acc1*, *DMC1*, *matK*, and *rps16* sequences were amplified with primers and PCR cycles shown in Table 2. Clone using pClone007 Versatile Simple Vector Kit (TSINGKE Biological Technology, Beijing, China), and 20–30 independent clones were randomly selected for sequencing by Sangon Biological Engineering and Technology Service Ltd. (Shanghai, China).

Phylogenetic analyses

DNA sequences were confirmed through BLAST (Boratyn et al. 2012) on the NCBI database. The sequences were aligned using MAFFT v.7.313 (Kato et al. 2002), and jModelTest v.3.0 (Posada and Crandall 1998) was used to determine the best-fit DNA substitution models and gamma rate heterogeneity for subsequent analyses. Phylogenetic analyses for each marker alone were conducted using the maximum-likelihood (ML) method in PhyML 3.0 (Guindon et al. 2009) and Bayesian inference (BI) in MrBayes v.3.1.2 (Huelsenbeck and

Ronquist 2001). *Bromus inermis* was used as the outgroup. Statistical support for the nodes in the ML analysis was estimated by using 1000 fast bootstrap replicates. For the combined dataset (*Acc1* + *DMC1* and *rps16* + *matK*), tandem sequences were processed using PhyloSuite v.1.2.2 (Zhang et al. 2020), and ML and BI were performed using raxmlGui v.2.0 (Edler et al. 2021) and MrBayes v.3.1.2, respectively.

RESULTS

Phylogenetic analyses based on nuclear markers

Acc1 sequences

The length of the *Acc1* sequences of the *Campeiostrachys* species ranges from 1423 to 1448 bp. The data matrix contains 1827 characters, of which 288 are parsimony uninformative and 134 are parsimony informative. The *Acc1* data matrix of 88 sequences was analysed with ML

using the TIM1+I+G model (-Ln likelihood = 8078.0741). The assumed nucleotide frequencies were A = 0.2546, C = 0.1827, G = 0.2161, T = 0.3467. The tree topology generated by the BI analysis is similar to that inferred by the ML analysis. The ML tree with bootstrap support values (BS, above the branches) and Bayesian posterior probability (PP, below the branches) is displayed in Fig. 1.

All *Campeioestachys* species have three copies of the *Acc1* sequence, which are grouped in the **St**, **Y**, and **H** clades (Fig. 1). The **St** clade (BS = 93%, PP = 1.00) comprises the diploid species of *Pseudoroegneria* (**St** genome donor), the tetraploid species of *Elymus* (**StH**), the tetraploid species of *Roegneria* (**StY**), and *Campeioestachys* species (**StYH**). Within this clade, *Campeioestachys tsukushiensis* var. *transiens*, *C. kamoji*, and *C. calcicola* cluster together (BS = 82%, PP = 0.99). In addition, *Campeioestachys dahurica*, *C. dahurica* var. *cylindrica* (Franch.) B.R.Baum, J.L.Yang & C.Yen, *C. dahurica* var. *tangutorum* (Nevski) B.R.Baum, J.L.Yang & C.Yen, and *C. purpuraristata* form a group (BS = 50%, PP = 0.92). The **Y** clade (BS = 90%, PP = 1.00) includes the species of *Dasyphyrum* (Coss. & Durieu) Maire (**V**), *Peridictyon* Seberg, Fred. & Baden (**Xp**), *Roegneria* (**StY**), and *Campeioestachys* (**StYH**). Within this clade, species of *Campeioestachys* group with *Roegneria grandis* Keng and *R. pendulina* Nevski (BS = 94%, PP = 1.00); and *C. kamoji*, *C. calcicola*, and *C. tsukushiensis* var. *transiens* cluster in a subclade (BS = 98%, PP = 1.00). Furthermore, *C. dahurica*, *C. dahurica* var. *tangutorum*, *C. dahurica* var. *excelsis* (Turcz. ex Griseb.) B.R.Baum, J.L.Yang & C.Yen, *C. dahurica* var. *cylindrica*, and *C. purpuraristata* form a paraphyletic clade (BS = 62%, PP = 0.92). Finally, the **H** clade (BS = 100%, PP = 1.00) contains *Hordeum* species (**H** genome donor), *Elymus* species (**StH**), and *Campeioestachys* species (**StYH**). Among them, *C. dahurica*, *C. dahurica* var. *cylindrica*, *C. dahurica* var. *excelsis*, and *C. purpuraristata* group together (BS = 86%, PP = 1.00), while *C. kamoji*, *C. calcicola*, *C. tsukushiensis* var. *transiens*, and *C. drobovii* group together (BS = 99%, PP = 1.00).

DMC1 sequences

The length of the *DMC1* sequences of the *Campeioestachys* species ranges from 1013 to 1087 bp. The data matrix contains 1266 characters, of which 249 are parsimony uninformative and 103 are parsimony informative. The *DMC1* data matrix was analysed with ML using the TIM3+G model (-Ln likelihood = 5162.2108). The assumed nucleotide frequencies were A = 0.3219, C = 0.2140, G = 0.2088, T = 0.2553. The phylogenetic analysis of 103 *DMC1* sequences was performed using *Bromus inermis* as the outgroup (Fig. 2). The tree topology generated by the BI analysis is similar to that inferred by the ML analysis.

Three *DMC1* sequence copies of the *Campeioestachys* species are divided into three well-supported clades, which are named the **St**, **Y**, and **H** clades (Fig. 2). In the

St clade (BS = 99%, PP = 1.00), *Campeioestachys* species are grouped with *Pseudoroegneria* species (**St**), *Roegneria* species (**StY**), and *Elymus* species (**StH**). Within this clade, *C. kamoji*, *C. calcicola*, and *C. tsukushiensis* var. *transiens* are grouped (BS = 69%, PP = 0.96). In addition, *C. purpuraristata* is closely associated with *Pseudoroegneria spicata* (Pursh) Á.Löve, *Roegneria semicostata* (Steud.) Kitag., and *C. dahurica* var. *tangutorum*. Also, *Campeioestachys dahurica*, *C. dahurica* var. *cylindrica*, and *C. dahurica* var. *excelsis* are closely related. However, none of them fall into a distinct clade. The **Y** clade (BS = 93%, PP = 1.00) only includes the species of *Roegneria* (**StY**) and *Campeioestachys* (**StYH**). Of which, *C. dahurica* groups with *C. dahurica* var. *cylindrica*, *C. dahurica* var. *excelsis*, *C. dahurica* var. *tangutorum*, *C. purpuraristata*, *Roegneria anthosachnoides* Keng, and *R. gmelinii* (Griseb.) Kitag. (BS = 51%, PP = 0.90). *Campeioestachys kamoji*, *C. calcicola*, and *C. tsukushiensis* var. *transiens* cluster into a subclade (BS = 62%, PP = 0.98). Finally, the **H** clade (BS = 100%, PP = 1.00) includes the species of *Hordeum* (**H**), *Elymus* (**StH**), and *Campeioestachys* (**StYH**). Among them, *C. kamoji*, *C. calcicola*, and *C. tsukushiensis* var. *transiens* are grouped with *Hordeum brachyantherum* Nevski (BS = 61%, PP = 0.97).

Acc1+DMC1 sequences

The phylogenetic tree constructed by combining *Acc1* and *DMC1* sequences is consistent with the one constructed by the single regions. All *Campeioestachys* species are divided into three clades (Fig. 3). In the **St** clade, *Campeioestachys* species cluster with the species of *Pseudoroegneria*, *Roegneria*, and *Elymus* with strong support (BS = 100%, PP = 1.00). Among them, *C. kamoji*, *C. calcicola*, and *C. tsukushiensis* var. *transiens* are clustered together (BS = 90%, PP = 1.00). *Campeioestachys dahurica*, *C. dahurica* var. *cylindrica*, *C. dahurica* var. *excelsis*, *C. dahurica* var. *tangutorum*, and *C. purpuraristata* form a group (BS = 54%, PP = 0.94). The **Y** clade (BS = 92%, PP = 0.99) includes not only the species of *Roegneria* and *Campeioestachys* but also the *Dasyphyrum* species (**V**) and *Peridictyon* species (**Xp**).

In the **Y** clade, the *Campeioestachys* species are clustered together (BS = 93%, PP = 1.00). Of which, *C. dahurica*, *C. dahurica* var. *cylindrica*, *C. dahurica* var. *excelsis*, *C. dahurica* var. *tangutorum*, *C. purpuraristata* cluster together (BS = 80%, PP = 0.99). Besides, *C. kamoji*, *C. calcicola*, and *C. tsukushiensis* var. *transiens* cluster into one group (BS = 99%, PP = 1.00). The **H** clade (BS = 100%, PP = 1.00) includes the species of *Hordeum* (**H**), *Elymus* (**StH**), and *Campeioestachys* (**StYH**). Among them, *C. kamoji*, *C. calcicola*, and *C. tsukushiensis* var. *transiens* are grouped together (BS = 100%, PP = 1.00). Besides, *C. dahurica*, *C. dahurica* var. *cylindrica*, *C. dahurica* var. *excelsis*, and *C. purpuraristata* cluster together (BS = 94%, PP = 1.00).

Phylogenetic analyses based on chloroplast markers

matK sequences

The *matK* matrix contains 60 taxa and 844 characters, including 99 variable information loci and 38 parsimony informative loci. The phylogenetic analysis was based on maximum likelihood (ML) using GTR+I+G as the best-fit model (-Ln likelihood = 2142.3028). The assumed nucleotide frequencies were A = 0.3094, C = 0.1808, G

= 0.1523, T = 0.3575. Both ML and BI trees show the *matK* sequences of *Campeiostachys* species divided into the St+V+E clade (BS = 51%) (Fig. 4A). This clade not only includes the diploid species of *Pseudoroegneria* (St), *Lophopyrum* Á.Löve (E^c), *Thinopyrum* Á.Löve (E^b), and *Dasyphyrum* (V), but also the polyploid species of *Elymus* (StH), *Roegneria* (StY), *Campeiostachys* (StYH), *Kengyilia* (StYP), *Pascopyrum* (StHNsXm), and *Connorochloa* (StYHW). Within this clade, *C. calcicola*, *C. tsukushiensis* var. *transiens*, and *C. kamoji* are grouped together (BS

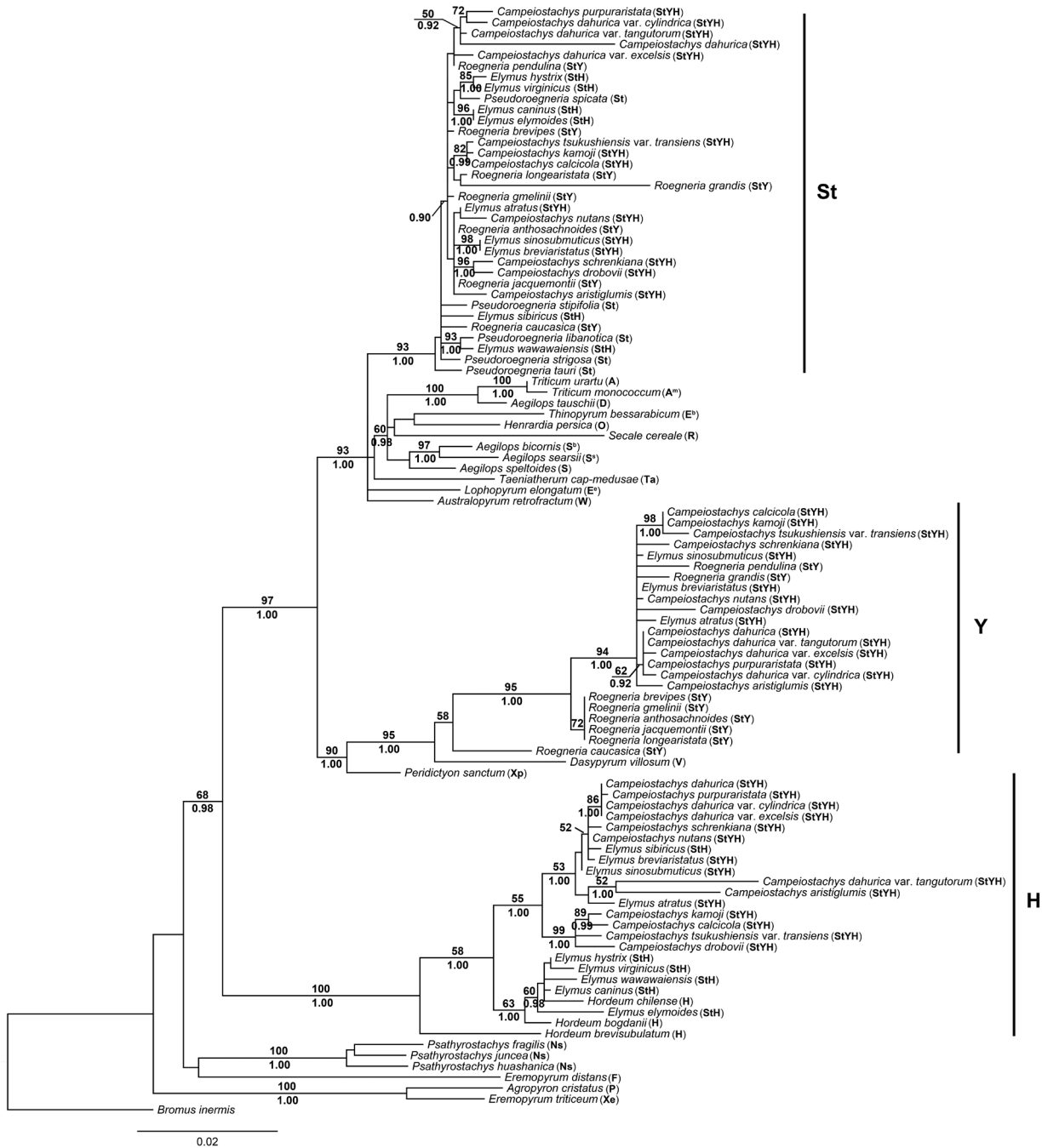


Figure 1. Maximum likelihood tree derived from *Acc1* sequences of *Campeiostachys* and related species. The capital letters in brackets after the species name indicate the genome composition of the species. The numbers above and below the branches indicate bootstrap values > 50% and Bayesian posterior probability values > 0.90, respectively.

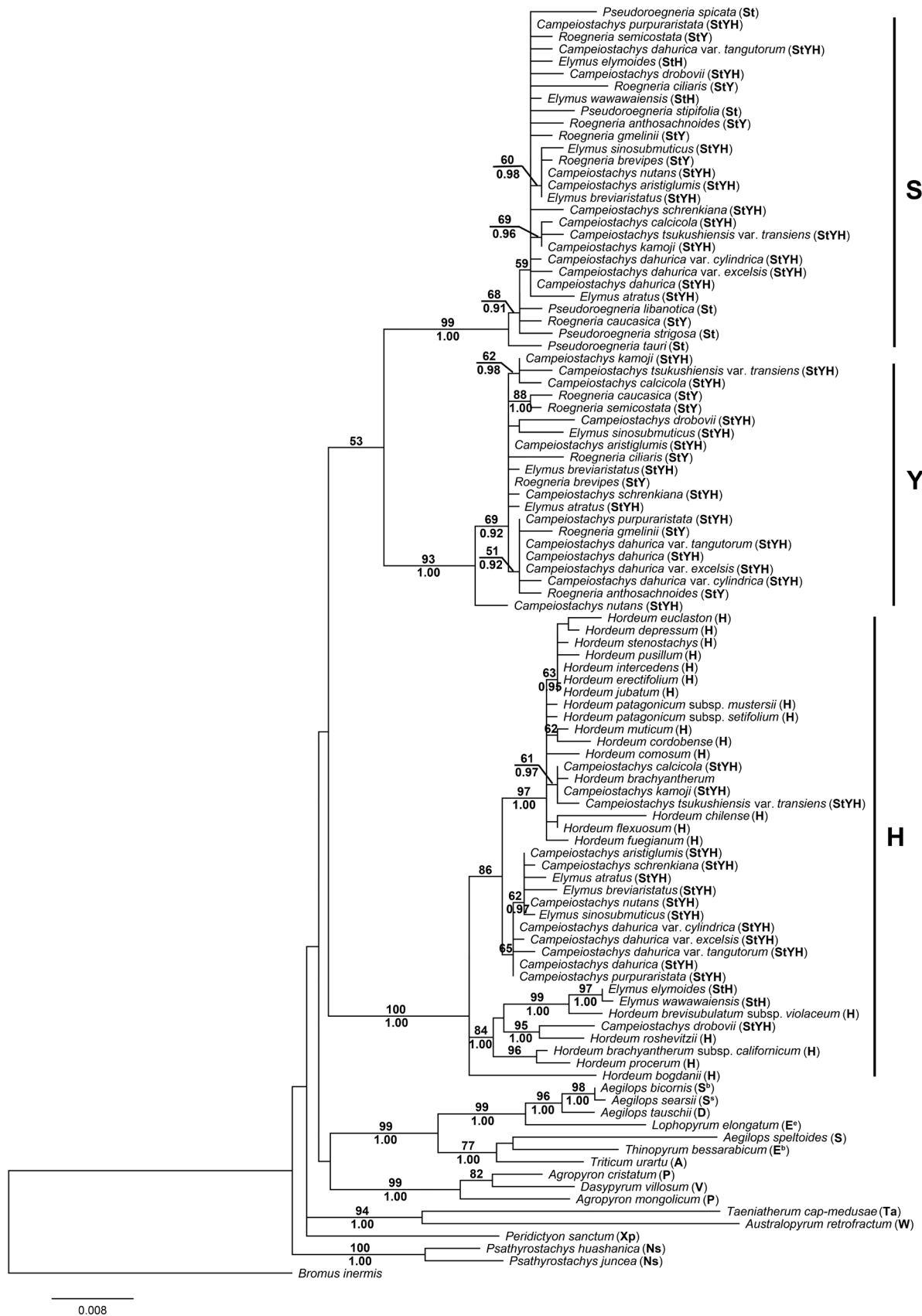


Figure 2. Maximum likelihood tree derived from *DMC1* sequences of *Campeiostrachys* and related species. The capital letters in brackets after the species name indicate the genome composition of the species. The numbers above and below the branches indicate bootstrap values > 50% and Bayesian posterior probability values > 0.90, respectively.

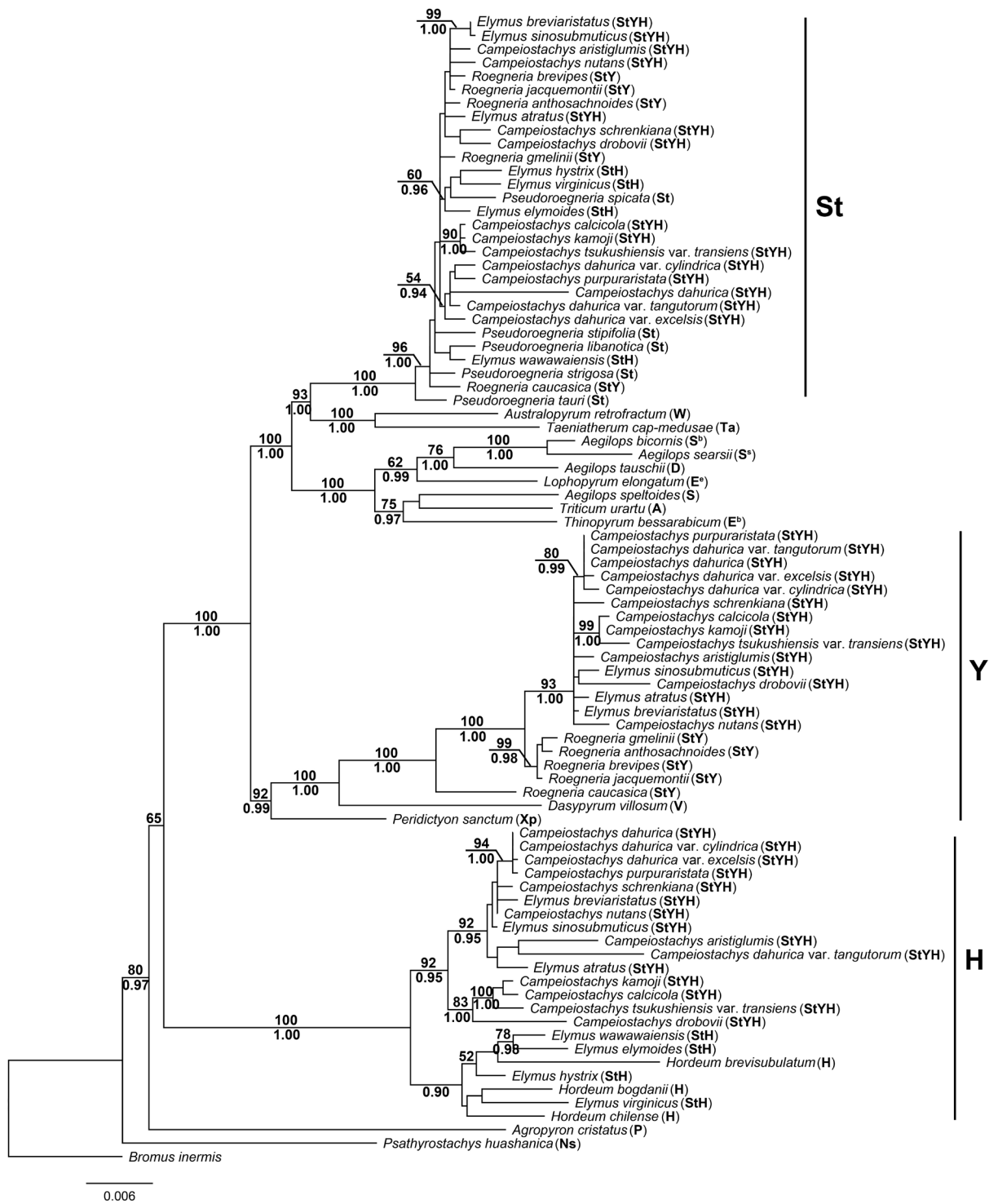


Figure 3. Maximum likelihood tree derived from *Acc1+DMC1* sequences of *Campeioestachys* and related species. The capital letters in brackets after the species name indicate the genome composition of the species. The numbers above and below the branches indicate bootstrap values > 50% and Bayesian posterior probability values > 0.90, respectively.

= 63%, PP = 0.97). All species of *Campeioestachys* are clustered in the **St+V+E** clade instead of the **H** clade.

rps16 sequences

A total of 53 *rps16* sequences were used for ML analysis. The *rps16* sequences matrix contains 706 characters, of which 47 informative loci and 22 parsimony informative loci. The phylogenetic analysis based on the *rps16* sequences was conducted using TIM1+G, which was identified as the best-fit model (-Ln likelihood = 1688.6674). The assumed nucleotide frequencies were A = 0.2991, C = 0.1925, G = 0.1478, T = 0.3606. In addition to *Campeioestachys* species, the **St+V+E** clade (BS = 50%) also included the diploid species of *Pseudoroegneria* (**St**), *Lophopyrum* (**E^c**), *Thinopyrum* (**E^b**), and *Dasyphyrum* (**V**) (Fig. 4B). In addition, polyploid species which contain the **St** subgenome also cluster in this clade, including the species of *Elymus* (**StH**), *Roegneria* (**StY**), *Kengyilia* (**StYP**), *Pascopyrum* (**StHNSXm**), and *Connorochloa* (**StYHW**).

matK + rps16 sequences

The BI tree and ML tree based on concatenated gene sequences exhibit highly similar topologies. All *Campeioestachys* species cluster in the same clade, named the **St+V+E** clade (BS = 58%, PP = 0.91) (Fig. 4C). This

subclade also includes the species of *Pseudoroegneria* (**St**), *Lophopyrum* (**E^c**), *Thinopyrum* (**E^b**), *Dasyphyrum* (**V**), *Elymus* (**StH**), *Roegneria* (**StY**), *Kengyilia* (**StYP**), *Pascopyrum* (**StHNSXm**), and *Connorochloa* (**StYHW**). Among them, *C. calcicola*, *C. tsukushiensis* var. *transiens*, and *C. kamoji* cluster together (BS = 67%, PP = 0.90). *Hordeum* species and *Stenostachys narduroides* Turcz. (**HW**) cluster together in a single subclade (BS = 100%, PP = 1.00).

DISCUSSION

The origin of the genus *Campeioestachys*

Traditionally, the species in Triticeae with the same genome or genome combination have been classified into the same genus (Löve 1982; Yen et al. 2005; Zhang and Zhou 2007; Baum et al. 2011; Yen and Yang 2011). The correspondence between the DNA sequences of diploid donors and allopolyploids in Triticeae allows the determination of the genome composition of these species through phylogenetic analyses (Petersen et al. 2006; Sun and Komatsuda 2010; Gao et al. 2014; Lei et al. 2022). Cytologically, the genome composition of *Pseudoroegneria* species is **St**, *Hordeum* species is **H**,

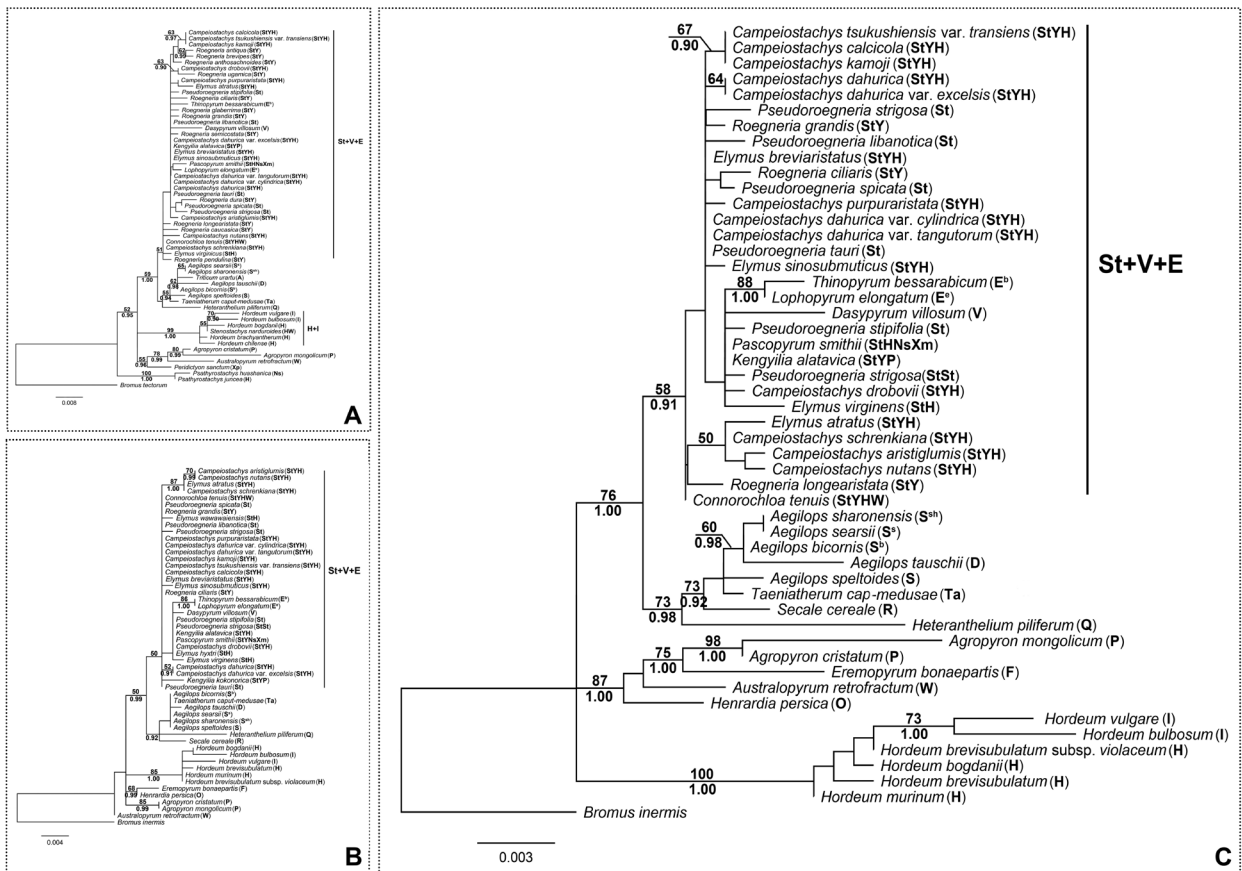


Figure 4. Maximum likelihood tree derived from chloroplast regions of *Campeioestachys* and related species. **A.** *matK*. **B.** *rps16*. **C.** *matK+rps16*. The capital letters in brackets after the species name indicate the genome composition of the species. The numbers above and below the branches indicate bootstrap values > 50% and Bayesian posterior probability values > 0.90, respectively.

Elymus species is **StH**, *Roegneria* species is **StY**, and *Campeioestachys* species is **StYH** (Dewey 1984; Yen et al. 2005; Wang et al. 2019). In the present study, the sequences from *Campeioestachys* species with separated into three distinct clades. The one-copy sequence from each *Pseudoroegneria* species (**St**), *Elymus* species (**StH**), *Roegneria* species (**StY**), and *Campeioestachys* species (**StYH**) formed a group. Therefore, this clade was named the **St** clade using the genomic symbol of the diploid species. One copy sequence from each *Hordeum* species (**H**), *Elymus* species (**StH**), and *Campeioestachys* species grouped into one clade, named the **H** clade using the genomic symbol of the diploid species. The remaining copy sequence from each *Campeioestachys* species grouped with the other copy sequences from *Roegneria* species (**StY**). This indicates that the remaining copy of the *Acc1* and *DMC1* sequence from these species should have been amplified from the **Y** genome. Therefore, this clade was named the **Y** clade. The results of the phylogenetic analyses based on *Acc1* and *DMC1* revealed that the *Roegneria* species contain **St** and **Y** copies, *Elymus* species contain **St** and **H** copies, and all *Campeioestachys* species contain **St**, **Y**, and **H** copies (Fig. 1). This indicates distinct genome compositions among these three genera, despite their indistinguishable morphological characteristics. Besides, the diverse genome compositions of *Roegneria*, *Elymus*, and *Campeioestachys* suggest different evolutionary origins.

Allopolyploids in Triticeae arise by interspecific hybridization involving different genera with different genome compositions (Sears 1954; Kimber and Alonso 1981; Dewey 1984; Heslop-Harrison 1992; Petersen et al. 2011; Yen and Yang 2011). Based on its genome composition, the possible origins of *Campeioestachys* are as follows: **St** × **HY**, **Y** × **StH**, or **H** × **StY**. Genera known to possess the **Y** genome within Triticeae include *Roegneria* (**StY**), *Campeioestachys* (**StYH**), *Kengyilia* (**StYP**), *Anthosachne* (**StYW**), and *Connorochloa* (**StYWH**), with no species containing **Y** or **HY** genomes found in the wild (Yen and Yang 1990; Torabinejad and Mueller 1993; Barkworth et al. 2009; Baum et al. 2011; Yen and Yang 2011, 2013; Gao et al. 2014). The phylogenetic analyses based on *trnL-F*, *ndhF*, and *trnH-psbA* chloroplast markers all indicated that the *Campeioestachys* species are more closely related to the *Roegneria* species (**StY**) than to *Elymus* (**StH**) (Liu et al. 2006; Lei et al. 2018). The analysis results of genome resequencing revealed that *Hordeum roshevitzii* Bowden (**H**) exhibits the highest homology with the **H** subgenome of *E. nutans* Griseb. (**StYH**) (= *Campeioestachys nutans* (Griseb.) B.R.Baum, J.L.Yang & C.Yen), while *E. burchan-buddae* (Nevski) Tzvelev (**StY**) exhibits the highest homology with the **St** and **Y** subgenomes of *E. nutans* (Xiong et al. 2025). The analysis results based on the chloroplast genome also indicate that the maternal donor of *Campeioestachys* species is more likely to be the genus *Roegneria* (**StY**) (Sha et al. 2025). Overall, we are more inclined to assume

that *Campeioestachys* originated by natural hybridization involving Triticeae species with both **StY** and **H** genomes.

The maternal donor of *Campeioestachys*

The cpDNA is maternally inherited in grasses (Middleton et al. 2014; Lei et al. 2018; Wang et al. 2019). Most studies suggest that *Pseudoroegneria* (**St**) serves as the maternal donor of most species containing the **St** subgenome in Triticeae (Mason-Gamer et al. 2002; McMillan and Sun 2004; Sha et al. 2010; Luo et al. 2012; Chen et al. 2021). This may occur from the increased success of hybridization when the species containing the **St** subgenome acts as the maternal parent, especially in intergeneric hybridization scenarios (Redinbaugh et al. 2000). However, some studies have shown that species with **StY** and **P** genomes both contributed to the origin of the species with **StYP** as maternal donors (Luo et al. 2012; Chen et al. 2021). Based on phylogenetic analyses of the chloroplast sequences *ndhF* and *trnH-psbA*, Lei et al. (2018) suggested that *Pseudoroegneria* (**St**) or *Roegneria* (**StY**) might be the maternal donors of the five *Campeioestachys* species. In the present study, the results of phylogenetic analyses based on *matK* and *rps16* sequences revealed that the 15 *Campeioestachys* species formed a clade with the species containing **St** subgenome (whether diploid or polyploid) and diploids with **V**, **E** genome, but not with *Hordeum* (the **H** diploid donor) (Fig. 2). Nuclear gene data confirmed that the species of *Campeioestachys* do not contain **E** and **V** genomes, also supported by cytological results (Yen and Yang 2013; Yang et al. 2017; Tan et al. 2021, 2022, 2024). Therefore, the maternal donor of *Campeioestachys* species contains the **St** subgenome.

Based on the analysis of the single-copy nuclear gene and cpDNA sequences (Figs 1–4), we propose that *Campeioestachys* may have originated from a natural cross between a tetraploid species of *Roegneria* (**StY**) as the maternal donor and a diploid species of *Hordeum* (**H**) as the paternal donor.

Phylogenetic relationships of some species in *Campeioestachys*

Campeioestachys purpuraristata and the *C. dahurica* complex

Elymus purpuraristatus (= *Campeioestachys purpuraristata*) is a perennial grass, mainly distributed in Inner Mongolia (Kuo 1987). Based on its morphological characteristics, it was classified into the genus *Elymus* (Kuo 1987; Yen and Yang 2013). Subsequently, the results of genomic in situ hybridization and phylogenetic analyses confirmed its genome composition as **StYH**, leading to its taxonomic revision to *C. purpuraristata* (Tan et al. 2021). Morphologically, *C. purpuraristata* is similar to the species of the *C. dahurica* complex, for example, the leaves are curled inward, the spikes erect or slightly curved, and spikelets densely arranged (Kuo 1987; Agafonov et al. 2001; Yen and Yang 2013). Cytogenetic analyses revealed that the

average *c*-value of the hexaploid hybrid *E. purpuraristatus* × *C. dahurica* var. *tangutorum* (StYH) was 0.79 with an average of 19.11 bivalents, and the percentage of stained pollen grains and seed set of the hybrids was 86.00% and 62.69%, respectively (Tan et al. 2021). In the present study, it is noteworthy that *C. purpuraristata* is always grouped with the species of the *C. dahurica* complex in the St, Y, or H clade, as observed from both *Acc1* and *DMC1* sequence data (Figs 1, 2). Based on our molecular analyses in conjunction with previous studies (Yen and Yang 2013; Tan et al. 2021), we propose that the relationship between *C. purpuraristata* and *C. dahurica* var. *tangutorum* is infraspecific rather than interspecific. Consequently, it would be more appropriate to classify *C. purpuraristata* as a member of the *C. dahurica* complex. Thus, we suggest that *C. purpuraristata* should be reclassified.

Campeiostrachys dahurica* var. *purpuraristata

(C.P.Wang & X.L.Yang) Y.H.Zhou, H.Q.Zhang, W.H.Chen & L.Tan, **stat. nov.**

urn:lsid:ipni.org:names:77368636-1

Elymus purpuraristatus C.P.Wang & H.L.Yang, Bulletin of Botanical Research Harbin 4(4): 83. 1984. (Yang and Wang 1984)

Campeiostrachys purpuraristata (C.P.Wang & X.L.Yang) Y.H.Zhou, H.Q.Zhang & Wei Huan Chen (Tan et al. 2021: 252)

Type. CHINA • Inner Mongolia, Daqing Mountains; 6 Aug. 1965; C.P. Wang 278; holotype: NMAC!

Campeiostrachys calcicola* and *C. kamoji

Roegneria calcicola Keng (= *Campeiostrachys calcicola*) and *Roegneria kamoji* (Ohwi) Ohwi ex Keng (= *C. kamoji*) are perennial herbs within Triticeae (Kuo 1987). In the present study, phylogenetic analyses demonstrated that *Campeiostrachys calcicola* is closely related to *C. kamoji* (Figs 1–4). The distribution of *C. calcicola* and *C. kamoji* overlaps: *C. kamoji* is mainly distributed across most parts of China and the Korean Peninsula, while *C. calcicola* is restricted to calcareous hillside meadows and riversides in Southwest China (Kuo 1987). Morphologically, *C. calcicola* closely resembles *C. kamoji*: the leaf blade flat, the leaf sheaths glabrous, each rachis node bearing a single green or greyish green spikelet, and the spikelets are sparse. The biggest difference between the two species is that in *C. calcicola* the palea is longer than the lemma, whereas the palea is shorter than the lemma in *C. kamoji* (Kuo 1987; Yen and Yang 2013). However, the hybrids of *C. calcicola* × *C. kamoji* exhibited a low percentage of stained pollen grains and seed set (Tan et al. 2021), indicating significant reproductive isolation between them. In conclusion, based on molecular and morphological results, we assert that *C. calcicola* and *C. kamoji* are distinct yet closely related species.

Campeiostrachys kamoji* and *C. tsukushiensis* var. *transiens

Lu et al. (1990) compared the morphological characteristics of *Roegneria kamoji* (= *Campeiostrachys kamoji*) from China and *Agropyron semicostatum* var. *transiens* Hack. (= *C. tsukushiensis* var. *transiens*) from Japan, as well as the chromosome pairing of their hybrids. They suggested that the genomes of both species had high homology and should belong to the same taxonomic taxon. Thus, they were combined and named *Roegneria tsukushiensis* (Hack.) B.Rong Lu, Yen & J.L.Yang and *R. tsukushiensis* var. *transiens* (Hack.) B.Rong Lu, Yen & J.L.Yang, respectively. Then, according to the morphological characteristics and genome composition, the species were revised as *Campeiostrachys kamoji* and *C. tsukushiensis* var. *transiens*, respectively (Baum et al. 2011; Yen and Yang 2013). In terms of distribution, there is no overlap in their geographical distribution, as *Campeiostrachys kamoji* is mainly distributed in China (except Xinjiang, Tibet, and Qinghai) and the Korean Peninsula, while *C. tsukushiensis* var. *transiens* is mainly distributed in Japan (Baum et al. 2011; Yen and Yang 2013). In addition, there are a few morphological differences between *Campeiostrachys tsukushiensis* var. *transiens* and *C. kamoji*. Compared to *Campeiostrachys kamoji*, *C. tsukushiensis* var. *transiens* is a taller plant, and has longer spikes and longer lemma awn (Lu et al. 1990; Yen and Yang 2013). Also, there is only one spikelet on each rachis node in *Campeiostrachys kamoji*, while there are 2–3 spikelets on each node in *C. tsukushiensis* var. *transiens* (Baum et al. 2011; Yen and Yang 2013). The spikelet number at each node is one of the important morphological indicators for classifying species in the Triticeae. In this study, the analysis results of *Acc1* and *DMC1* sequences showed that *Campeiostrachys kamoji* was closely related to *C. tsukushiensis* var. *transiens* (Figs 1, 2). The F₁ hybrids of *Campeiostrachys kamoji* and *C. tsukushiensis* var. *transiens* exhibit a high frequency of bivalents (17–21) during meiosis metaphase I. However, the lower pollen staining rate and setting rate of their F₁ hybrid indicates that these two species share the same chromosome composition, although their reproductive isolation degree is high (Lu et al. 1990). Based on the results of cytogenetic and molecular analyses, combined with morphological characteristics and geographical distribution, we conclude that *Campeiostrachys kamoji* and *C. tsukushiensis* var. *transiens* represent distinct taxa.

CONCLUSION

Campeiostrachys species originated from natural hybridization between the tetraploid species of *Roegneria* (StY) and the diploid species of *Hordeum* (H), with *Roegneria* (StY) acting as the maternal donor. *Campeiostrachys purpuraristata* should be classified into the *Campeiostrachys dahurica* complex and treated as *Campeiostrachys dahurica* var. *purpuraristata* (C.P.Wang & H.L.Yang) Y.H.Zhou, H.Q.Zhang, W.H.Chen & L.Tan.

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SUPPLEMENTARY MATERIALS

Supplementary material 1

The *Acc1* sequences used in the phylogenetic analyses.

<https://doi.org/10.5091/plecevo.153974.suppl1>

Supplementary material 2

The *DMC1* sequences used in the phylogenetic analyses.

<https://doi.org/10.5091/plecevo.153974.suppl2>

Supplementary material 3

The *matK* and *rps16* sequences used in the phylogenetic analyses.

<https://doi.org/10.5091/plecevo.153974.suppl3>