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Phylogenetic relationships of *Triticum* and *Aegilops* and evidence for the origin of the **A**, **B**, and **D** genomes of common wheat (*Triticum aestivum*)

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Abstract

Common wheat (*Triticum aestivum*) has for decades been a textbook example of the evolution of a major crop species by allopolyploidization. Using a sophisticated extension of the PCR technique, we have successfully isolated two single-copy nuclear genes, DMC1 and EF–G, from each of the three genomes found in hexaploid wheat (BA^uD) and from the two genomes of the tetraploid progenitor *Triticum turgidum* (BA^u). By subjecting these sequences to phylogenetic analysis together with sequences from representatives of all the diploid Triticeae genera we are able for the first time to provide simultaneous and strongly supported evidence for the D genome being derived from *Aegilops tauschii*, the A^u genome being derived from *Triticum urartu*, and the hitherto enigmatic B genome being derived from *Aegilops speltoides*. Previous problems of identifying the B genome donor may be associated with a higher diversification rate of the B genome compared to the A^u genome in the polyploid wheats. The phylogenetic hypothesis further suggests that neither *Triticum*, *Aegilops*, nor *Triticum* plus *Aegilops* are monophyletic.

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1. Introduction

Common wheat (*Triticum aestivum*) has since the pioneering studies by Kihara (1924) been the textbook example of the evolution of a major crop species by allopolyploidization. According to generally accepted interpretations (Cox, 1998) common wheat is an allohexaploid (genomic constitution **BBA**^uA^uDD) derived through hybridization between a domesticated form of tetraploid, wild emmer, *Triticum turgidum* ssp. *dicoccoides* (genomic constitution **BBA**^uA^u), and the diploid *Aegilops tauschii* (genomic constitution **DD**). Wild emmer itself is supposed to be an allotetraploid derived through hybridization between two wild diploids: *Triticum urartu* contributing the

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A^u genome and possibly *Aegilops speltoides* contributing the **B** genome. However, despite decades of intensive research the origin of the **B** genome has remained controversial (e.g., Huang et al., 2002a) and accordingly the genome of *Ae. speltoides* is usually not designated **B** but **S** (Cox, 1998; Huang et al., 2002a,b; Wang et al., 1996). Generally, the **S** genome is shared by a group of species (*Aegilops* L. section *Sitopsis* (Jaub. & Spach) Zhuk.), which in addition to *Ae. speltoides* (**S**) includes *Ae. bicornis* (**S**^b), *Ae. longissima* (**S**^l), *Ae. searsii* (**S**^s), and *Ae. sharonensis* (**S**^l) (Slageren, 1994).

The origin of *T. aestivum* and other polyploid wheat species has been subject of numerous studies and the above scenario is the accepted consensus based on all evidence. The literature on the subject is immense, but only papers using an explicit phylogenetic method will be cited here. This includes papers using parsimony, maximum

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likelihood, and Bayesian inference, but not neighbor joining, UPGMA, or other phenetic approaches, which are poor estimators of phylogeny (e.g., Farris, 1983). An unfortunate large proportion of papers are based on neighbour joining and/or UPGMA analyses (e.g., Büren, 2001; Galili et al., 2000; Giorgi et al., 2002; Goryunova et al., 2004; Ishii et al., 2001; Provan et al., 2004; Sasanuma et al., 2004; Sourdille et al., 2001; Ünlü and Sümer, 2005; Vakhitov et al., 2003; C. Wang et al., 2000; G.-Z. Wang et al., 2000; Wang et al., 2000b). Most of the published phylogenetic analyses suffer from a limited, biased taxon sampling, either including polyploid wheat and its *a priori* assumed progenitors (Buchner et al., 2004) or only a few additional Aegilops and/or Triticum L. species (Blake et al., 1999; Huang et al., 2002a,b; Zhang et al., 2002). Rarely are all diploid species of Aegilops and Triticum included (Sallares and Brown, 2004) and few include more than one or a few other Triticeae species—often Hordeum vulgare L. and/or Secale cereale L.as outgroups. This becomes a problem as two of the many areas of disagreement among recent Triticeae phylogenies are the potential monophyly of Triticum plus Aegilops and monophyly of Aegilops itself (Helfgott and Mason-Gamer, 2004; Hsiao et al., 1995; Kellogg and Appels, 1995; Kellogg et al., 1996; Mason-Gamer, 2001, 2005; Mason-Gamer and Kellogg, 1996; Mason-Gamer et al., 1998, 2002; Petersen and Seberg, 1997, 2000, 2002; Seberg and Frederiksen, 2001; Seberg and Petersen, in press). Present phylogenetic analyses all show that Hordeum L. and Secale L. are poor choices of outgroups. Hence, the taxon sampling in the majority of studies of Triticum/Aegilops phylogeny inevitable restricts results to the expected.

The present study intends to remedy this restricted taxon sampling primarily in an attempt to elucidate the origin of tetraploid and hexaploid wheats. Sequences from plastid and nuclear genes obtained from both tetraploid and hexaploid wheats are included in phylogenetic analyses together with sequences from all diploid species of Aegilops and Triticum (Slageren, 1994) and representatives of all genomes traditionally recognized in diploid Triticeae (Wang et al., 1996). This broad taxon sampling simultaneous provides new evidence about the phylogeny of Aegilops. We use partial nucleotide sequences from two singlecopy nuclear genes, DMC1 (disrupted meiotic cDNA) and EF-G (translation elongation factor G), and one plastid gene, ndhF (NADH dehydrogenase subunit F). Allotetraploid and allohexaploid species ideally have two or three copies of each nuclear gene (disregarding potential allelic variation that could produce four or six copies) each received from the diploid ancestors. To pick them up successfully from the genome, we consider an experimental approach employing copy-specific PCR primers to be the most appropriate, because recombination among PCRgenerated sequence fragments is negligible (Cronn et al., 2002). The nuclear genes were chosen because they have been used previously for phylogenetic reconstruction of the diploid Triticeae genera (Aagesen et al., 2005; Petersen and Seberg, 2000, 2002; Seberg and Petersen, in press) and successfully elucidated the origin of two tetraploid species of *Hordeum* (Petersen and Seberg, 2004). Previous phylogenetic analyses of the diploid Triticeae genera include the plastid genes *rbcL* and *rpoA* (Aagesen et al., 2005; Petersen and Seberg, 1997; Seberg and Petersen, in press), but here we have chosen *ndh*F because of its higher variability. Preliminary results from the present study have been published as proceedings from the 5th International Triticeae Symposium (Petersen and Seberg, 2005).

2. Materials and methods

Taxon sampling was based on previous phylogenetic analyses of the diploid Triticeae (Aagesen et al., 2005; Petersen and Seberg, 1997, 2000, 2002; Seberg and Petersen, in press), but in addition 12 accessions of diploid species of *Aegilops/Triticum*, five accessions of tetraploid *T. turgidum*, and one accession of hexaploid, common wheat, *T. aestivum* cv. Kadet, were included. For a complete taxon list, incl. GenBank accession numbers, see Table 1. With a single exception (see Table 1), voucher specimens are deposited at C. Genomic designations follow Wang et al. (1996).

PCR and sequencing of *ndh*F were performed using the primers ndhF1318 and ndhF2110R (Olmstead and Sweere, 1994). PCR was performed under standard conditions using standard *Taq* polymerase (Amersham Bioscience) and the products were purified using the QIAquick PCR purification kit (Qiagen) according to the manufacturer's instructions. Cycle sequencing was performed using the ABI PRISM BigDye Terminator Cycle Sequencing Ready Reaction Kit with AmpliTaq DNA Polymerase, FS (Applied Biosystems), and the products were purified using the DyeEX Spin kit (Qiagen) according to the manufacturer's instructions. DNA fragments were separated on an ABI 377 (Applied Biosystems) automated sequencer, and sequence editing was conducted using Sequencher 4.2.2.

In the diploid species PCR and sequencing of the nuclear genes, DMC1 and EF-G, were performed as described by Petersen and Seberg (2000, 2003). Amplification and isolation of each of the gene copies of EF-G and DMC1 from the polyploid species largely followed the procedure described by Petersen and Seberg (2004) except that cloning was entirely avoided. Initially, PCR and sequencing were performed using the same primers as for the diploid species but under less stringent conditions, resulting in sequences showing clear signs of polymorphisms. Inspection of these sequences allowed the construction of genome specific primers. These primers were designed following the MAMA technique (Cha et al., 1992) (mismatch amplification mutation assay), which deliberately incorporates a mismatching nucleotide at the ultimate or penultimate 3' position of the primer. Mismatch at both the ultimate and the penultimate 3' positions effectively prevent amplification of the undesired sequences. The technique makes cloning superfluous and avoids PCR artefacts such as chimeric products, which by their potential abundance may otherwise obscure interpretation of results completely

Table 1

S	Specimens and	GenBan	k accession	numbers	of the	Triticeae	plus two	species of	f Bromus	used as o	utgroups
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C618 Branus arenta L. DQ24783 DQ24783 DQ24783 DQ24784 A73264 A7386187 M6062 Acglops hoursis (Forsk). Jaub. & Spach; Egypt, Singeren et al. 19-04-1989, ICARDD DQ24781 DQ24782 DQ247853 DQ247853 DQ247810 DQ247853 DQ247853 DQ247853 DQ247854 A7386198 M6673 Acglops consols Turkey, Intry, Linty: California Riverside G1300 DQ24780 DQ247850 DQ247854	Accession No.	Species; voucher information ^a	ndhF	DMC1	EF-G
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H6771 Australopyrum rectinizum (Labill) Å. Löve DQ247877 AF277252 AY836190 H6723 Australopyrum rectorjacum (Vickery) Å. Löve AF267662 AP277253 AY836192 H6724 Australopyrum rectorjacum (Nees) B.K. Simon — AF267662 AP277253 AY836192 H4200 Australopyrum reluinum DQ247887 AP277254 AY836191 H5551 Crithopsis delikeun (Schut), Roshev. DQ247881 AP277238 AY836196 H5552 Eremopyrum tiliosum (M. Bieb) Maire DQ247881 AP277254 AY836196 H5555 Hermardia persice (Boits), C.E. Hubb. Nevski DQ247885 AP277254 AY836198 H5556 Hermardia persice (Boits), C.E. Hubb. Spach DQ247886 AP277250 AY836200 H1942 Hordeam brachyamherun Newki ssp. californicum Covas & Stebbins) Bothmer, N. Jacobsen & R.B. Jørg. DQ247887 AP277260 AY836201 H1150 Hordeam marium Huds, ssp. gusoneaum (Pa1, Thell. DQ247880 AP277254 AY836204 H277254 HY83620 DQ47889 AP277254 AY836204	H5572	Amblyopyrum muticum Eig	DQ247876	AF277243	AY836189
H6723 Austrolopyrum velutium (Ness) B.K.Simon $-$ APE3765 APE37251 AY836191 H4200 Austrolopyrum velutium (Ness) B.K.Simon DQ247885 $-$ - -	H6771	Australopyrum pectinatum (Labill.) Á. Löve	DQ247877	AF277252	AY836190
H6724 Australopyrum vielatiuum (Nees) B.K. Simon — AV836192 H4200 Australopyrum vielatiuum DQ24788 AF277253 AV836195 H5551 Darypyrum villosum (M. Bieb, Maire DQ24788 AF277236 AV836195 H5552 Erenopyrum villosum (M. Bieb, Maire DQ24788 AF277236 AV836196 H5553 Erenopyrum villosum (Gaerta), Nevski DQ24788 AF277237 AV836198 H5555 Heterandeling nifferum Hockst, ex Jaub, & Spach DQ24788 AF277238 AV836198 H5556 Hererandeling nifferum Hockst, ex Jaub, & Spach DQ247886 AF277257 AV836200 H1942 Hordeum brachyantherum Nevski sp. callfornicum Covas & Stebbins) Bothmer, N. Jacobsen & Seberg DQ247880 AF277257 AV836203 H1150 Hordeum marinum L uss, gaucant (Steud), Tzvelev DQ247880 AF277257 AV836204 H219 Hordeum nutinum L uss, sp. gausancem (ParL), Thell. DQ24789 AF277264 AV836204 H313 Hordeum vulgare L, sp. spontaneum (C. Koch) Thell. DQ24789 AF2772764 AV836204 H575 Peridicyon sanctun Quarka, Sberg, fredil & Baden DQ24789 AF277264	H6723	Australopyrum retrofractum (Vickery) Á. Löve	AF267662	AF277251	AY836191
H4200 Austradopyrum velatium DQ247878 $$ $-$ H5558 Crithopsis delizana (Schul), Roshev. DQ247851 AF277240 AY83609 H5551 Dasypyrum villosum (M. Bieb.) Maire DQ247881 AF277238 AY836195 H5552 Eremopyrum villosum (M. Bieb.) Maire DQ247881 AF277237 AY836197 H5551 Decargates are pentini (C.E. Hubb.) Melderis DQ247884 AF277237 AY836197 H6511 Festucopsis serpentini (C.E. Hubb.) Melderis DQ247884 AF277255 AY836199 H5557 Heteranthelium piliferum Hochst, ex Jaub & Spach DQ247886 AF277250 AY836202 H1942 Hordeum excitpolium Bothmer, N. Jacobsen & R.B. Jorg. DQ247886 AF277257 AY836203 H1150 Hordeum murium Huds, ssp. gassonearum (Parl, Thell. DQ247880 AF277261 AY836204 H299 Hordeum murium Los Sp. gaussonearum (Parl, Thell. DQ247890 AF277261 AY836203 H5575 Peridicitora scattomateum (C. Koch) Thell. DQ247890 AF277261 AY836204 H692 Lophopyrum elongatum (Host) Å. Löve DQ247897 AF277261 AY836208	H6724	Australopyrum velutinum (Nees) B.K. Simon		AF277253	AY836192
H5558 Crithopsis delifean (Schult), Roshev. DQ247895 AF277240 AYX36209 H5551 Davgpyrum villsum (M. Bieb, Maire DQ247881 AF277238 AYX36195 H5552 Eremopyrum villsum (M. Bieb, Maire DQ247882 AF277236 AYX36196 H5553 Eremopyrum villsum (M. Bieb, Maire DQ247883 AF277237 AYX36198 H5556 Heurandia persica (Bois), C.E. Hubb, DQ247885 AF277238 AYX36198 H5557 Heterandheim pilferum Hochst, ex Jaub, & Spach DQ247886 AF277257 AYX36200 H1942 Hordeum mainum Huds, ssp. gassoneanum (Parl) Thell. DQ247888 AF277257 AYX36204 H1959 Hordeum mainum Luss, sp. gassoneanum (Parl) Thell. DQ247890 AF277258 AYX36208 H5575 Peridicyon sanctum (Janka) Seberg, Fred, & Baden DQ247890 AF277264 AYX36208 H5375 Peridicyon sanctum (Janka) Seberg, Fred, & Baden DQ247890 AF277264 AYX36208 H5375 Peridicyon sanctum (Janka) Seberg, Fred, & Baden DQ247897 AF277264 AYX36208 H977 Psathyrostachys fr	H4200	Australopyrum velutinum	DQ247878		_
H5561 Dasypyrum tillosum (M. Bieb.) Maire DQ247881 AF277238 AY836195 H5552 Eremopyrum ditams (K. Koch) Nevski DQ247883 AF277237 AY836196 H5553 Eremopyrum triticeum (Gaetta.) Nevski DQ247884 AF277237 AY836196 H5555 Henaradia perisca (Boiss.) C.E. Hubb. DQ247884 AF277237 AY836198 H5557 Heteranthelium pildjerum Hochst. ex Jaub. & Spach DQ247886 AF277238 AY836200 H1942 Hordeum marinum Huds. Sep. gasoneamum (Pat.) Thell. DQ247887 AF277250 AY836202 H1150 Hordeum marinum Huds. Sep. gasoneamum (Pat.) Thell. DQ247888 AF277257 AY836204 H2199 Hordeum marinum Huds. Sep. gasoneamum (Pat.) Thell. DQ247890 AF277254 AY836204 H3139 Hordeum marinum Huds. Sep. gasoneamum (Pat.) Thell. DQ247890 AF277246 AY836208 H5757 Peridictyon sanctum (Ianka) Seberg. Fred. & Baden DQ247890 AF277246 AY836208 H577 Perathyrostachys fragiff. (Bois). Nevskis ap., fragiffs DQ247897 AF277244 AY836216 H577 </td <td>H5558</td> <td>Crithopsis delileana (Schult.) Roshev.</td> <td>DQ247895</td> <td>AF277240</td> <td>AY836209</td>	H5558	Crithopsis delileana (Schult.) Roshev.	DQ247895	AF277240	AY836209
H5552 Eremopyrum distans (K. Koch) Nevski DQ247882 AF277236 AY836196 H5553 Eremopyrum distans (K. Koch) Nevski DQ247884 AF277237 AY836197 H6511 Festucopsis serpentini (C.E. Hubb.) Melderis DQ247884 AF277237 AY836198 H5556 Heraratheim pilferum Hochst. et. Jub. & Spach DQ247886 AF277236 AY836209 H1942 Hordeum brachyantherum Nevski sp. californicum Covas & Stebbins) Bothmer, N. Jacobsen & Seberg DQ247887 AF277256 AY836202 H1150 Hordeum marinum L. ssp. gaucann (Steud) Tytelv DQ247889 AF277258 AY836202 H299 Hordeum nurinum L. ssp. gaucann (Steud) Tytelv DQ247890 AF277258 AY836203 H3131 Hordeum nuinum L. ssp. gaucann (Steud) Tytelv DQ247890 AF277254 AY836205 H6692 Lophopyrum elongarun (Choch) Å Löve DQ247890 AF277264 AY836205 H5757 Peridictyon sanctum (Janka) Seberg, Fred. & Baden DQ247890 AF277264 AY836210 H4372 Psathyrostachys fragilis so; liðus in Baden DQ247898 AF277246 AY836211	H5561	Dasypyrum villosum (M. Bieb.) Maire	DQ247881	AF277238	AY836195
H5553 Eremopyrum triticeum (Gaetta), Nevski DQ247883 AF277237 AY836197 H6511 Festucopsis serpentinii (C.E. Hubb.) DQ247884 AF277237 AY836198 H5556 Henrardiu persite (Boiss, C.E. Hubb. DQ247884 AF277235 AY83609 H5557 Heteranthelian piliferum Hochst. ex Jaub. & Spach DQ247886 AF277236 AY83600 H1942 Hordeum brachyantheram Nevski ssp. culjornicum Covas & Stebbins) Bothmer, N. Jacobsen & R.B. Jorg. DQ247889 AF277257 AY836201 H1150 Hordeum marinum Buths, ssp. gussoneanum (Parl) Thell. DQ247890 AF277257 AY836204 H299 Hordeum marinum L. ssp. glaucum (Steud) Tzvelev DQ247890 AF277254 AY836204 H5575 Peridictyon sanctam (C. Koch) Thell. DQ247890 AF277264 AY836208 H917 Psathyrostachys fragilf (Bois). Nevski sp. fragilfs DQ247896 AF277264 AY836214 H432 Psathyrostachys fragilf (Bois). Nevski sp. fragilfs DQ247897 AF277264 AY836214 H9182 Psathyrostachys fragilf (Bois). Nevski sp. fragilfs DQ247900 AF277248	H5552	Eremopyrum distans (K. Koch) Nevski	DQ247882	AF277236	AY836196
H6511 Festucopsis serpentini (C.E. Hubb.) Melderis DQ47884 AF277247 AY836198 H5556 Henrardia persica (Boiss). C.E. Hubb. DQ247885 AF277255 AY836199 H1557 Heteranthelium piliferum Hockst. ex Jaub. & Spach DQ247885 AF277256 AY836200 H1942 Hordeam brachyantherum Nevski sep. californicum DQ247886 AF277257 AY836202 H1150 Hordeam marinum Huds. sep. gusoneanum (Parl) Thell. DQ247888 AF277257 AY836204 H299 Hordeam marinum Luss. palacum (Steucul) Txvelev DQ247889 AF277257 AY836204 H313 Hordeam varinum Huds. sep. gusoneanum (Parl) Thell. DQ247891 AF277262 AY836206 H5555 Peridictyon sanctum (Lanka) Seberg. Fred. & Baden DQ247896 AF277261 AY836208 H917 Psathyrostachys fragilis (Boiss.) Nevski sep. fragilis DQ247896 AF277261 AY836208 H917 Psathyrostachys fragilis Nevski sep. fragilis DQ247896 AF277247 AY836208 H917 Psathyrostachys fragilis Nevski sep. fragilis DQ247896 AF277261 AY836218 H918 Psathyrostachys fragilis Resp. sillowus Baden DQ247898	H5553	Eremopyrum triticeum (Gaertn.) Nevski	DQ247883	AF277237	AY836197
H5556 Henrardia persica (Boiss.) C.E. Hubb. DQ47885 AF277255 AY836199 H5557 Heteranthelium piliferum Hochst, ex Jaub. & Spach DQ47886 AF277238 AY836200 H942 Hordeum brachyantherum Nevski ssp. californicum DQ47887 AF277260 AY836201 H150 Hordeum merinum Huds. ssp. gussoneanum (Parl.) Thell. DQ47888 AF277257 AY836202 H299 Hordeum marinum L. ssp. glaucum (Steud.) Txvelev DQ247880 AF277258 AY836206 H602 Lophopyrum elongatum (Host) Å. Löve DQ247880 AF277264 AY836208 H602 Lophopyrum elongatum (Host) Å. Löve DQ247890 AF277264 AY836208 H917 Psathyrostachys fragilis (Boiss.) Nevski ssp. fragilis DQ247897 AF277263 AY836210 H4322 Psathyrostachys forgilis ssp. villosus Baden DQ247896 AF277264 AY836212 H9182 Psathyrostachys stolonifyromis Baden DQ247890 AF277245 AY836213 H0822 Pseudoroegneria spicata (Pursh) Å. Löve DQ247890 AF277245 AY836213 H0254 Taenintherum ca	H6511	Festucopsis serpentinii (C.E. Hubb.) Melderis	DQ247884	AF277247	AY836198
H5557 Heteranthelium piliferum Hochst. ex Jaub. & Spach DQ247886 AF277238 AY836200 H1942 Hordeum brachyantherum Nevski sp. californicum DQ247887 AF277260 AY836201 H1150 Hordeum erectifolium Bothmer, N. Jacobsen & Seberg DQ247888 AF277259 AY836202 H299 Hordeum marinum Huds. ssp. gussonemum (Parl.) Thell. DQ247880 AF277258 AY836203 H801 Hordeum nurinum L. ssp. glaucum (Steud.) Txvelev DQ247890 AF277264 AY836204 H3139 Hordeum nurinum L. ssp. glaucum (Steud.) Txvelev DQ247890 AF277246 AY836206 H4557 Peridictyon sanctum (Janka) Seberg, Fred. & Baden DQ247890 AF27724 AY836210 H917 Psathyrostachys fragilis (Boiss). Nevski ssp. fragilis DQ247890 AF27724 AY836211 H9182 Psathyrostachys fragilis sp. villouss Baden DQ247899 AF277244 AY836213 H0252 Pseudoroegneria spicata (Pursh) Å. Löve DQ247890 AF277244 AY836213 H0254 Taeniatherum caput-medusae (L.) Nevski DQ247807 AF277244 AY836213	H5556	Henrardia persica (Boiss.) C.E. Hubb.	DQ247885	AF277255	AY836199
H1942 Hordeum brachyantherum Nevski ssp. californicam (Covas & Stebbins) Bothmer, N. Jacobsen & R.B. Jørg. DQ247887 A F277260 A Y836202 H1150 Hordeum mercitifolium Bothmer, N. Jacobsen & R.B. Jørg. DQ247889 A F277257 A Y836202 H299 Hordeum marinum Huds. ssp. giassoneanum (Patl) Thell. DQ247889 A F277257 A Y836203 H801 Hordeum marinum L. ssp. glaucum (Steud,) Tzvelev DQ247890 A F277262 A Y836205 H602 Lophopyrum elongatum (Host) Å. Löve DQ247891 A F277264 A Y836208 H917 Psathyrostachys fragilis (Boiss), Nevski ssp. fragilis Sp. eillosus Baden DQ247894 A F277261 A Y836210 H4332 Psathyrostachys fragilis sp. eillosus Baden DQ247890 A F277264 A Y836214 H382 Psathyrostachys stoloniformis Baden DQ247890 A F277244 A Y836214 H4342 Secale strictum (C. Presh) C. Presl DQ247890 A F277244 A Y836214 H4342 Secale strictum (C. Presh) C. Presl DQ247890 A F277244 A Y836216 H0254 Thinopyrum bessarabicum DQ247800 A F277245 <td< td=""><td>H5557</td><td>Heteranthelium piliferum Hochst. ex Jaub. & Spach</td><td>DQ247886</td><td>AF277238</td><td>AY836200</td></td<>	H5557	Heteranthelium piliferum Hochst. ex Jaub. & Spach	DQ247886	AF277238	AY836200
(Covas & Stebbins) Bothmer, N. Jacobsen & Seberg DQ247887 AF277250 AY836201 H1150 Hordeum mercitiofium Bothmer, N. Jacobsen & R.B. Jorg. DQ247888 AF277257 AY836202 H299 Hordeum marinum Huds. ssp. gusoneanun (Parl.) Thell. DQ247880 AF277257 AY836203 H801 Hordeum murinum L. ssp. glaucum (Steud, Tzvelev DQ247890 AF277254 AY836205 H6692 Lophopyrum elongatum (Host) Å. Löve DQ247891 AF277244 AY836208 H5757 Peridictyon sanctum (Janka) Seberg, Fred. & Baden DQ247896 AF277261 AY836211 H917 Psathyrostachys fragilis (Boiss.) Nevski ssp. fragilis DQ247896 AF277246 AY836211 H9182 Psathyrostachys fragilis ssp. villosus Baden DQ247896 AF277246 AY836212 H9822 Pseudorogeneria spicat (Pursh) Å. Löve DQ247890 AF277244 AY836213 H0524 Taeniatherum caput-medusae (L). Nevski DQ247890 AF277244 AY836216 H6725 Thinopyrum bessarabicum Ms24. Löve — AF277254 AY836216 H6725 Thino	H1942	Hordeum brachyantherum Nevski ssp. californicum			
H1150 Hordeum erectifolium Bothmer, N. Jacobsen & R. B. Jørg. DQ247888 AF277259 AY836202 H299 Hordeum marinum Huds. ssp. guasoneamum (Parl.) Thell. DQ247890 AF277258 AY836203 H301 Hordeum murinum L. ssp. glaucum (Steud.) Tzvelev DQ247890 AF277258 AY836204 H3139 Hordeum nurinum L. ssp. glaucum (Steud.) Tzvelev DQ247890 AF277254 AY836205 H6692 Lophopyrum elongatum (Host) Å. Löve DQ247894 AF277244 AY836206 H5575 Peridictyon sanctum (Janka) Seberg, Fred. & Baden DQ247896 AF277264 AY836210 H4372 Psathyrostachys fragilis (Boiss.) Nevski ssp. fragilis DQ247897 AF277264 AY836211 H9182 Pseudoroegneria spicata (Pursh) Å. Löve DQ247899 AF277248 AY836213 H0254 Taeniatherum caput-medusate (L.) Nevski DQ247890 AF277254 AY836213 H0255 Thinopyrum bessarabicum (Saývul. & Rayss) Å. Löve — AF277254 AY836217 H0254 Taeniatherum caput-medusate (L.) Nevski DQ247800 AF277254 AY836213 H0254<		(Covas & Stebbins) Bothmer, N. Jacobsen & Seberg	DQ247887	AF277260	AY836201
H299 Hordeum marinum Huds. ssp. gussoneanum (Parl.) Thell. DQ247889 AF277257 AY836203 H801 Hordeum murinum L. ssp. glaucum (Steud.) Tzvelev DQ247890 AF277258 AY836204 H801 Hordeum murinum L. ssp. glaucum (Steud.) Tzvelev DQ247891 AF277258 AY836205 H6692 Lophopyrum elongatum (Host) Å. Löve DQ247892 AF277264 AY836206 H5575 Peridictyon sanctum (Janka) Seberg, Fred. & Baden DQ247890 AF277264 AY836210 H4372 Psathyrostachys fragilis (Boiss), Nevski ssp. fragilis DQ247897 AF277264 AY836212 H982 Pseudoroegneria spicata (Pursh) Å. Löve DQ247890 AF277254 AY836213 H10254 Taeniatherum caput-medusae (L.) Nevski DQ247890 AF277254 AY836217 H6725 Thinopyrum bessarabicum DQ247800 AF277254 AY836217 H6725 Thinopyrum bessarabicum DQ247800 AF277250 AY836217 H6725 Thinopyrum bessarabicum DQ247800 AF277250 AY836217 H6729 Thinopyrum bessarabicum DQ247816 <td>H1150</td> <td>Hordeum erectifolium Bothmer, N. Jacobsen & R.B. Jørg.</td> <td>DQ247888</td> <td>AF277259</td> <td>AY836202</td>	H1150	Hordeum erectifolium Bothmer, N. Jacobsen & R.B. Jørg.	DQ247888	AF277259	AY836202
H801 Hordeum murium L. ssp. glaucum (Steud.) Tzvelev DQ247890 AF277258 AY836204 H3139 Hordeum vulgare L. ssp. spontaneum (C. Koch) Thell. DQ247891 AF277262 AY836205 H6692 Lophopyrum elongatum (Host) A. Löve DQ247894 AF277246 AY836208 H5575 Peridictyon sanctum (Janka) Seberg, Fred. & Baden DQ247894 AF277261 AY836208 H917 Psathyrostachys fragilis Ssp. ilbious Baden DQ247896 AF277264 AY836212 H9182 Psathyrostachys fragilis Ssp. ilbious Baden DQ247898 AF277264 AY836212 H9082 Pseudoroegneria spicata (Pursh) Å. Löve DQ247898 AF277246 AY836213 H0054 Taeniatherum caput-medusae (L.) Nevski DQ247890 AF277248 AY836216 H0725 Thinopyrum bessarabicum DQ247890 AF277254 AY836217 H6724 Triticium aesticum L. cv. Kadet DQ247800 AF277254 AY836217 H6725 Thinopyrum bessarabicum DQ247802 AF277250 AY836194 Triticum turgidum L. ssp. dicoccoides; Turkey, B. Johnson, GRIN PI 428051	H299	Hordeum marinum Huds. ssp. gussoneanum (Parl.) Thell.	DQ247889	AF277257	AY836203
H3139 Hordeum vulgare L. ssp. spontaneum (C. Koch) Thell. DQ247891 AF277262 AY836205 H6692 Lophopyrum elongatum (Host) Å. Löve DQ247892 AF277244 AY836206 H5775 Peridictyron sanctum (Ianka) Sbeterg, Fred. & Baden DQ247896 AF277244 AY836208 H917 Psathyrostachys fragilis (Boiss.) Nevski ssp. fragilis DQ247896 AF277261 AY836210 H4372 Psathyrostachys stoloniformis Baden DQ247897 AF277264 AY836212 H9082 Pseudoroegneria spicata (Pursh) Å. Löve DQ247899 AF277244 AY836214 H4324 Secale strictum (C. Presl) C. Presl DQ247899 AF277244 AY836214 H4324 Secale strictum (C. Presl) C. Presl DQ247890 AF277244 AY836214 H4324 Secale strictum (C. Presl) C. Presl DQ247890 AF277244 AY836217 H6725 Thinopyrum bessarabicum (Saÿvul. & Rayss) Á. Löve — AF277254 AY83617 H6725 Thinopyrum bessarabicum DQ247803 — — — H4547 Triticum maestivum L. cv. Kadet	H801	Hordeum murinum L. ssp. glaucum (Steud.) Tzvelev	DQ247890	AF277258	AY836204
H6692 Lophopyrum elongatum (Host) Å. Löve DQ247892 AF277246 AY836206 H5575 Peridictyon sanctum (Janka) Seberg, Fred. & Baden DQ247894 AF277261 AY836208 H917 Psathyrostachys fragilis Sps. villosus Baden DQ247897 AF277261 AY836211 H9182 Psathyrostachys fragilis sps. villosus Baden DQ247890 AF277246 AY836212 H9082 Pseudoroegneria spicata (Pursh) Å. Löve DQ247890 AF277248 AY836214 H4342 Sceale strictum (C. Presl) C. Presl DQ247800 AF277248 AY836216 H6725 Thinopyrum bessarabicum Sayatis DQ247900 AF277254 AY836217 H6729 Thinopyrum bessarabicum Sayatis DQ247903 - - H4547 Triticum monococcum L., Turkey, Petersen & Ørgaard 31-08-1991 DQ247880 AF277250 AY836217 H6729 Thinopyrum L. ev. Kadet n.a. DQ247846 (D) DQ247872 (D) H6840 Triticum turgidum L. ssp. dicoccoides; Turkey, B. Johnson, GRIN PI 428051 DQ247846 (D) DQ247862 (A) H6841 Triticum tur	H3139	Hordeum vulgare L. ssp. spontaneum (C. Koch) Thell.	DQ247891	AF277262	AY836205
H5575 Peridictyon sanctum (Janka) Seberg, Fred. & Baden DQ247894 AF277244 AY836208 H917 Psathyrostachys fragilis (Boiss.) Nevski ssp. fragilis DQ247897 AF277261 AY836210 H917 Psathyrostachys fragilis (Boiss.) Nevski ssp. fragilis DQ247897 AF277261 AY836211 H9182 Psathyrostachys stoloniformis Baden DQ247898 AF277264 AY836212 H9082 Pseudoroegneria spicata (Pursh) Å. Löve DQ247890 AF277248 AY836213 H10254 Taeniatherum caput-medusae (L.) Nevski DQ247900 AF277248 AY836213 H10254 Taeniatherum caput-medusae (L.) Nevski DQ247900 AF277254 AY836216 H6725 Thinopyrum bessarabicum (Saÿvul. & Rayss) Å. Löve — AF277250 AY836194 H6729 Thinopyrum bessarabicum DQ247800 F72750 AY836194 Triticum aestivum L. ev. Kadet na. DQ247840 DQ247871 (A) na. DQ247844 (A) DQ247867 (A) H6840 Triticum turgidum L. ssp. dicoccoides; Turkey, B. Johnson, GRIN PI 470944 DQ247817 (A) DQ247845 (A)	H6692	Lophopyrum elongatum (Host) Á. Löve	DQ247892	AF277246	AY836206
H917 Psathyrostachys fragilis (Boiss.) Nevski ssp. fragilis DQ247896 AF277261 AY836210 H4372 Psathyrostachys fragilis ssp. villosus Baden DQ247897 AF277263 AY836211 H9182 Psathyrostachys stoliniformis Baden DQ247898 AF277245 AY836212 H9082 Pseudoroegneria spicata (Pursh) A. Löve DQ247890 AF277245 AY836213 H4342 Secale strictum (C. Presl) C. Presl DQ247900 AF277248 AY836213 H10254 Taeniatherum caput-medusae (L.) Nevski DQ247902 AF277254 AY836217 H6725 Thinopyrum besscarabicum DQ247903	H5575	Peridictyon sanctum (Janka) Seberg, Fred. & Baden	DQ247894	AF277244	AY836208
H4372 Psathyrostachys fragilis ssp. villosus Baden DQ247897 AF277263 AY836211 H9182 Psathyrostachys stoloniformis Baden DQ247898 AF277264 AY836212 H9082 Pseudoroegneria spicata (Pursh) Á. Löve DQ247890 AF277245 AY836213 H9082 Secade strictum (C. Presl) C. Presl DQ247890 AF277248 AY836213 H10254 Taeniatherum caput-medusae (L.) Nevski DQ247890 AF277254 AY836216 H6725 Thinopyrum bessarabicum (Saÿvul. & Rayss) Á. Löve — AF277254 AY836217 H6729 Thinopyrum bessarabicum (Saÿvul. & Rayss) Á. Löve — AF277254 AY836194 JTriticum aestivum L. cv. Kadet DQ247800 — — — H6840 Triticum turgidum L. ssp. dicoccoides; Turkey, B. Johnson, GRIN PI 428051 DQ247846 DQ247866 DQ247867 A) H6841 Triticum turgidum ssp. durum (Desf.) Husn.; Jordan, S. Kohli, GRIN PI 371823 DQ247837 B) DQ247866 A)	H917	Psathyrostachys fragilis (Boiss.) Nevski ssp. fragilis	DQ247896	AF277261	AY836210
H9182 Psathyrostachys stoloniformis Baden DQ247898 AF277264 AY836212 H9082 Pseudoroegneria spicata (Pursh) Å. Löve DQ247890 AF277245 AY836213 H4342 Secale strictum (C. Presl) C. Presl DQ247899 AF277248 AY836213 H10254 Taeniatherum caput-medusae (L.) Nevski DQ247909 AF277248 AY836216 H6725 Thinopyrum bessarabicum (Saÿvul. & Rayss) Å. Löve — AF277254 AY836217 H6729 Thinopyrum bessarabicum DQ247800 AF277254 AY836217 H4547 Triticum monococcum L., Turkey, Petersen & Ørgaard 31-08-1991 DQ247880 AF277250 AY836194 DQ247801 DQ247880 AF277250 AY836194 DQ2478070 (B) n.a. DQ247880 AF277250 AY836216 M6840 Triticum turgidum L. sv. Kadet DQ2478071 (B) DQ247870 (B) n.a. DQ247844 (B) DQ247872 (D) DQ247827 (D) H6841 Triticum turgidum ssp. dicoccoides; Turkey, B. Johnson, GRIN PI 428051 DQ247814 (A) DQ247863 (B) H6838 Triticum turgid	H4372	Psathyrostachys fragilis ssp. villosus Baden	DQ247897	AF277263	AY836211
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H10254Taeniatherum caput-medusae (L.) NevskiDQ247902AF277249AY836216H6725Thinopyrum bessarabicum (Saÿvul. & Rayss) Á. Löve—AF277254AY836217H6729Thinopyrum bessarabicumDQ247903———H4547Triticium monococcum L., Turkey, Petersen & Ørgaard 31-08-1991DQ247880AF277254AY836194DQ247821DQ247880AF277254AY836194DQ247820DQ247880AF2772754AY836194H6840Triticum aestivum L. ev. KadetDQ247880AF277210DQ247844 (B)DQ247870 (B)n.a.DQ247886 (D)DQ247827 (D)DQ247827 (D)H6841Triticum turgidum L. ssp. dicoccoides; Turkey, B. Johnson, GRIN PI 428051DQ247918DQ247866 (B)DQ247862 (B)n.a.DQ247814 (A)DQ247866 (B)DQ247866 (B)DQ247866 (A)H6841Triticum turgidum ssp. dicoccoides; Israel, E. Nevo, GRIN PI 470944DQ247916DQ247837 (B)DQ247866 (B)n.a.DQ247886DQ247866 (B)n.a.DQ247884 (B)DQ247866 (A)H6838Triticum turgidum ssp. durum (Desf.) Husn.; Jordan, S. Kohli, GRIN PI 371823DQ247916DQ247838 (B)DQ247866 (A)h6842Triticum turgidum ssp. durum; Iran, H. Springfield, GRIN PI 208908DQ247920DQ247838 (B)DQ247866 (A)n.a.DQ247864 (A)DQ247866 (A)n.a.DQ247866 (A)DQ247866 (A)h6664Triticum urartu Tumanian ex Gandilyan; Iran, Univ. California Riverside G1545DQ247908DQ247865DQ247866 (A)h6665Tr	H4342	Secale strictum (C. Presl) C. Presl	DQ247899	AF277248	AY836213
H6725Thinopyrum bessarabicum (Saÿvul. & Rayss) Á. Löve—AF277254AY836217H6729Thinopyrum bessarabicumDQ247903——…##	H10254	Taeniatherum caput-medusae (L.) Nevski	DQ247902	AF277249	AY836216
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H4547Triticium monococcum L., Turkey, Petersen & Ørgaard 31-08-1991DQ247880AF277250AY836194Triticum aestivum L. ev. KadetDQ247844 (B)DQ247870 (B)n.a.DQ247845 (A)DQ247871 (A)n.a.DQ247846 (D)DQ247827 (D)H6840Triticum turgidum L. ssp. dicoccoides; Turkey, B. Johnson, GRIN PI 428051DQ247918DQ247836 (B)DQ247867 (A)H6841Triticum turgidum ssp. dicoccoides; Israel, E. Nevo, GRIN PI 428051DQ247919DQ247837 (B)DQ247867 (A)H6841Triticum turgidum ssp. dicoccoides; Israel, E. Nevo, GRIN PI 470944DQ247919DQ247837 (B)DQ247863 (B)H6838Triticum turgidum ssp. durum (Desf.) Husn.; Jordan, S. Kohli, GRIN PI 371823n.a.DQ247842 (A)DQ247868 (A)H6842Triticum turgidum ssp. durum; Iran, H. Springfield, GRIN PI 208908DQ247910DQ247838 (B)DQ247869 (A)H6839Triticum turgidum ssp. turgidum; Iran, C. Qualset, GRIN PI 624727DQ247917DQ247835 (B)DQ247866 (A)H6664Triticum urartuTumanian ex Gandilyan; Iran, Univ. California Riverside G1545DQ247908DQ247826DQ247852H6665Triticum urartu; Turkey, Univ. California Riverside G1956DQ247809DQ247827DQ247853	H6729	Thinopyrum bessarabicum	DQ247903	_	
Triticum aestivum L. cv. Kadet $DQ247821$ $DQ247844$ (B) $DQ247870$ (B)n.a. $DQ247845$ (A) $DQ247871$ (A)n.a. $DQ247845$ (D) $DQ247872$ (D)H6840Triticum turgidum L. ssp. dicoccoides; Turkey, B. Johnson, GRIN PI 428051 $DQ247816$ (B) $DQ247866$ (B)(Körn. ex Asch. & Graebn.) Thell. $DQ247811$ $DQ247847$ (A) $DQ247867$ (A)H6841Triticum turgidum ssp. dicoccoides; Israel, E. Nevo, GRIN PI 470944 $DQ247919$ $DQ247837$ (B) $DQ247863$ (B)H6838Triticum turgidum ssp. durum (Desf.) Husn.; Jordan, S. Kohli, GRIN PI 371823 $DQ247916$ $DQ247834$ (B) $DQ247860$ (A)H6842Triticum turgidum ssp. durum; Iran, H. Springfield, GRIN PI 208908 $DQ247834$ (B) $DQ247865$ (A)H6839Triticum turgidum ssp. turgidum; Iran, C. Qualset, GRIN PI 624727 $DQ247917$ $DQ247835$ (B) $DQ247860$ (A)H6664Triticum urartuTumanian ex Gandilyan; Iran, Univ. California Riverside G1545 $DQ247908$ $DQ247826$ $DQ247852$ H6665Triticum urartu; Turkey, Univ. California Riverside G1545 $DQ247807$ $DQ247827$ $DQ247857$	H4547	Triticium monococcum L., Turkey, Petersen & Ørgaard 31-08-1991	DQ247880	AF277250	AY836194
n.a. DQ247845 (A) DQ247817 (A) n.a. DQ247846 (D) DQ247872 (D) H6840 Triticum turgidum L. ssp. dicoccoides; Turkey, B. Johnson, GRIN PI 428051 DQ247918 DQ247836 (B) DQ247862 (B) (Körn. ex Asch. & Graebn.) Thell. n.a. DQ247811 (A) DQ247826 (B) DQ247826 (B) H6841 Triticum turgidum ssp. dicoccoides; Israel, E. Nevo, GRIN PI 470944 DQ247919 DQ247837 (B) DQ247863 (B) H6838 Triticum turgidum ssp. durum (Desf.) Husn.; Jordan, S. Kohli, GRIN PI 371823 DQ247916 DQ247834 (B) DQ247860 (B) n.a. DQ247839 (A) DQ247865 (A) H6842 Triticum turgidum ssp. durum; Iran, H. Springfield, GRIN PI 208908 DQ247920 DQ247838 (B) DQ247864 (B) n.a. DQ247843 (A) DQ247869 (A) H6839 Triticum turgidum ssp. turgidum; Iran, C. Qualset, GRIN PI 624727 DQ247917 DQ247835 (B) DQ247861 (B) n.a. DQ247840 (A) DQ247866 (A) H6664 Triticum urartu Tumanian ex Gandilyan; Iran, Univ. California Riverside G1545 DQ247908 DQ247826 DQ247852 H6665 Triticum urartu; Turkey, Univ. California Riverside G1956 DQ247909 DQ247827		Triticum aestivum L. cv. Kadet	DQ247921	DQ247844 (B)	DQ247870 (B)
 n.a. DQ247846 (D) DQ247872 (D) H6840 Triticum turgidum L. ssp. dicoccoides; Turkey, B. Johnson, GRIN PI 428051 (Körn. ex Asch. & Graebn.) Thell. H6841 Triticum turgidum ssp. dicoccoides; Israel, E. Nevo, GRIN PI 470944 H6838 Triticum turgidum ssp. durum (Desf.) Husn.; Jordan, S. Kohli, GRIN PI 371823 H6842 Triticum turgidum ssp. durum; Iran, H. Springfield, GRIN PI 208908 H6842 Triticum turgidum ssp. durum; Iran, C. Qualset, GRIN PI 624727 H6664 Triticum urartu Tumanian ex Gandilyan; Iran, Univ. California Riverside G1545 H6665 Triticum urartu; Turkey, Univ. California Riverside G1956 n.a. DQ24780 (D) DQ247827 (D) DQ247827 (D) DQ247827 (D) DQ247827 (D) DQ247827 (D) DQ247827 (D) DQ247827 (D) DQ247837 (B) DQ247868 (A) DQ247868 (A) DQ247869 (A) DQ247869 (A) DQ247869 (A) DQ247860 (B) n.a. DQ247840 (A) DQ247869 (A) DQ247840 (A) DQ247866 (A) DQ247840 (A) DQ247866 (A) DQ247840 (A) DQ247866 (A) DQ247840 (A) DQ247852 DQ247909 DQ247827 DQ247853 			n.a.	DQ247845 (A)	DQ247871 (A)
H6840Triticum turgidum L. ssp. dicoccoides; Turkey, B. Johnson, GRIN PI 428051 (Körn. ex Asch. & Graebn.) Thell.DQ247918 n.a.DQ247836 (B) DQ247811 (A)DQ247862 (B) 			n.a.	DQ247846 (D)	DQ247872 (D)
(Körn. ex Asch. & Graebn.) Thell.n.a.DQ247841 (A)DQ247867 (A)H6841Triticum turgidum ssp. dicoccoides; Israel, E. Nevo, GRIN PI 470944DQ247919DQ247837 (B)DQ247863 (B)H6838Triticum turgidum ssp. durum (Desf.) Husn.; Jordan, S. Kohli, GRIN PI 371823DQ247916DQ247834 (B)DQ247868 (A)H6842Triticum turgidum ssp. durum; Iran, H. Springfield, GRIN PI 208908DQ247920DQ247838 (B)DQ247865 (A)H6839Triticum turgidum ssp. turgidum; Iran, C. Qualset, GRIN PI 624727DQ247917DQ247835 (B)DQ247869 (A)H6664Triticum urartuTumanian ex Gandilyan; Iran, Univ. California Riverside G1545DQ247908DQ247826DQ247852H6665Triticum urartu;, Turkey, Univ. California Riverside G1956DQ247909DQ247827DQ247853	H6840	Triticum turgidum L. ssp. dicoccoides; Turkey, B. Johnson, GRIN PI 428051	DQ247918	DQ247836 (B)	DQ247862 (B)
H6841Triticum turgidum ssp. dicoccoides; Israel, E. Nevo, GRIN PI 470944DQ247919DQ247837 (B)DQ247836 (B)H6838Triticum turgidum ssp. durum (Desf.) Husn.; Jordan, S. Kohli, GRIN PI 371823DQ247916DQ247834 (B)DQ247860 (B)H6842Triticum turgidum ssp. durum; Iran, H. Springfield, GRIN PI 208908DQ247920DQ247838 (B)DQ247865 (A)H6839Triticum turgidum ssp. turgidum; Iran, C. Qualset, GRIN PI 624727DQ247917DQ247835 (B)DQ247869 (A)H6664Triticum urartuTumanian ex Gandilyan; Iran, Univ. California Riverside G1545DQ247908DQ247826DQ247852H6665Triticum urartu;, Turkey, Univ. California Riverside G1956DQ247909DQ247827DQ247853		(Körn. ex Asch. & Graebn.) Thell.	n.a.	DQ247841 (A)	DQ247867 (A)
 n.a. DQ247842 (A) DQ247868 (A) DQ247816 (B) DQ247834 (B) DQ247860 (B) n.a. DQ247839 (A) DQ247843 (A) DQ247865 (A) H6839 Triticum turgidum ssp. turgidum; Iran, C. Qualset, GRIN PI 624727 DQ247917 DQ247835 (B) DQ247869 (A) H6664 Triticum urartu Tumanian ex Gandilyan; Iran, Univ. California Riverside G1545 DQ247908 DQ247826 DQ247852 H6665 Triticum urartu; Turkey, Univ. California Riverside G1956 	H6841	Triticum turgidum ssp. dicoccoides; Israel, E. Nevo, GRIN PI 470944	DQ247919	DQ247837 (B)	DQ247863 (B)
H6838Triticum turgidum ssp. durum (Desf.) Husn.; Jordan, S. Kohli, GRIN PI 371823DQ247916DQ247834 (B)DQ247860 (B)n.a.DQ247839 (A)DQ247865 (A)H6842Triticum turgidum ssp. durum; Iran, H. Springfield, GRIN PI 208908DQ247920DQ247838 (B)DQ247866 (A)H6839Triticum turgidum ssp. turgidum; Iran, C. Qualset, GRIN PI 624727DQ247917DQ247835 (B)DQ247869 (A)H6664Triticum urartuTumanian ex Gandilyan; Iran, Univ. California Riverside G1545DQ247908DQ247826DQ247852H6665Triticum urartu; Turkey, Univ. California Riverside G1956DQ247909DQ247827DQ247853			n.a.	DQ247842 (A)	DQ247868 (A)
https://dots.org/10.1001/1001/1001/1001/1001/1001/1001/	H6838	Triticum turgidum ssp. durum (Desf.) Husn.; Jordan, S. Kohli, GRIN PI 371823	DQ247916	DQ247834 (B)	DQ247860 (B)
H6842Triticum turgidum ssp. durum; Iran, H. Springfield, GRIN PI 208908DQ247920DQ247838 (B)DQ247864 (B)H6839Triticum turgidum ssp. turgidum; Iran, C. Qualset, GRIN PI 624727DQ247917DQ247835 (B)DQ247869 (A)H6664Triticum urartuTumanian ex Gandilyan; Iran, Univ. California Riverside G1545DQ247908DQ247826DQ247852H6665Triticum urartu; Turkey, Univ. California Riverside G1565DQ247909DQ247827DQ247853			n.a.	DQ247839 (A)	DQ247865 (A)
n.a.DQ247843 (A)DQ247869 (A)H6839Triticum turgidum ssp. turgidum; Iran, C. Qualset, GRIN PI 624727DQ247917DQ247835 (B)DQ247861 (B)n.a.DQ247840 (A)DQ247866 (A)H6664Triticum urartuTumanian ex Gandilyan; Iran, Univ. California Riverside G1545DQ247908DQ247826DQ247852H6665Triticum urartu; Turkey, Univ. California Riverside G1956DQ247809DQ247827DQ247853	H6842	Triticum turgidum ssp. durum; Iran, H. Springfield, GRIN PI 208908	DQ247920	DQ247838 (B)	DQ247864 (B)
H6839Triticum turgidum ssp. turgidum; Iran, C. Qualset, GRIN PI 624727DQ247917DQ247835 (B)DQ247861 (B)H6664Triticum urartu Tumanian ex Gandilyan; Iran, Univ. California Riverside G1545DQ247804 (A)DQ247866 (A)H6665Triticum urartu; Turkey, Univ. California Riverside G1956DQ247908DQ247826DQ247852DQ247807DQ247827DQ247853		- ·	n.a.	DQ247843 (A)	DQ247869 (A)
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H6664Triticum urartuTumanian ex Gandilyan; Iran, Univ. California Riverside G1545DQ247908DQ247826DQ247852H6665Triticum urartu; Turkey, Univ. California Riverside G1956DQ247909DQ247827DQ247853			n.a.	DQ247840 (A)	DQ247866 (A)
H6665Triticum urartu; Turkey, Univ. California Riverside G1956DQ247909DQ247827DQ247853	H6664	Triticum urartu Tumanian ex Gandilyan; Iran, Univ. California Riverside G1545	DQ247908	DQ247826	DQ247852
	H6665	Triticum urartu; Turkey, Univ. California Riverside G1956	DQ247909	DQ247827	DQ247853

GenBank Accession Nos. DQ247821–DQ247921 are new submissions. n.a., not applicable.

^a Voucher information is only included if not previously published (Petersen and Seberg, 1997, 2000). Vouchers are deposited at C unless indicated otherwise.

(Cronn et al., 2002). A list of the primers used can be found in Table 2, but future studies may benefit from the now existing sequences enabling design of additional genome specific primers. All sequences were aligned manually. Alignment of *ndh*F sequences was trivial, and introduction of new DMC1 and EF–G sequences into existing matrices for the Triticeae (Petersen and Seberg, 2000; Seberg and Petersen, in press) was unproblematic as well. The matrix is available at TreeBASE (study Accession No. SN2595).

Phylogenetic analyses were made for each of the three individual genes and on a combined matrix including all sequences. The gene trees constructed from the separate analyses of DMC1 and EF-G sequences were used to infer homology of the two or three copies of each of the genes found in the polyploids. Hence, in the combined analysis the individual copies of each nuclear gene of the polyploids were matched in accordance with inferred homology. E.g., when a copy of DMC1 from T. aestivum was found to have the same sister group relationships as a copy of EF-G, the two sequences were considered derived from the same progenitor and matched accordingly. Similarly, the position of the polyploid taxa on the *ndh*F gene tree was used to determine which of the nuclear gene sequences to combine with each ndhF sequence, on the assumption that the ndhF sequence from a polyploid groups with its maternal progenitor. Nuclear sequences inferred to have been donated by the paternal parent would not be matched by any *ndh*F sequence, and were accompanied by missing data in the ndhF character set. The DMC1 sequences include a small number of MITEs (Petersen and Seberg, 2000), which were excluded from the analyses. Analyses were performed using both PAUP*, version 4.0b8 (Swofford, 2001) and WinClada, version 1.00.08 (Nixon, 2002), spawning the matrix to NONA version 2.0 (Goloboff, 1993). PAUP*, version 4.0b8 has been preferred to the most recent version 10, as the latter version under some circumstances outputs erroneous tree lengths and an excessive number of tree islands. Uninformative sites were excluded, and informative characters were equally weighted and treated as unordered. Gaps were treated as ambiguous data (?). Initial attempts to code the gaps following the procedure of Simmons and Ochoterena (2000) only increased incongruence among the data partitions and we choose not to apply gap coding. Branches

Table 2 Primers used for PCR and sequencing of DMC1 and EE-G were collapsed when their minimum length were zero (amb-). Analyses performed in PAUP* were using heuristic search, 100 random addition sequences, holding five trees at each step, TBR swapping, and Steepest Descent. In WinClada the matrices were executed using the heuristic search options hold100, mult*100, max*, and hold/10. Support for individual clades was calculated as jackknife values in WinClada running 1.000 replicates, each with the options mult*100, max*, hold/10, and keeping max. 1.000 trees.

The number of character changes occurring within the A^u genome clade and the **B** genome clade on each of the nuclear gene trees was calculated using PAUP^{*} under both ACCTRAN and DELTRAN optimization.

3. Results

In all polyploid wheats, we successfully amplified the expected two or three copies of each nuclear gene. Sequences obtained using the genome specific primers did not contain polymorphic sites, so we conclude that each of the sequence copies has no allelic variation.

The DMC1 matrix includes 1497 aligned positions of which 168 are phylogenetically informative. Phylogenetic analysis resulted in 12 equally parsimonious trees of length 331 (ci = 0.67, ri = 0.87). One of the 12 trees is shown as Fig. 1. Within the A^{u} genome clade only two character changes occur; both within the subclade including sequences extracted from the polyploid taxa. In the **B** genome clade 11 or 12 character changes occur in the subclade including the diploid specimens of *Ae. speltoides*, and seven (ACCTRAN optimization) or eight (DEL-TRAN optimization) changes occur in the subclade including including sequences extracted from the polyploid taxa.

The EF-G matrix includes 916 aligned positions of which 175 are phylogenetically informative. Phylogenetic analysis resulted in four equally parsimonious trees of length 313 (ci=0.68, ri=0.90). One of the four trees is shown as Fig. 2. Within the A^{u} genome clade six character changes occur; four within the subclade including sequences extracted from the polyploid taxa, two within the subclade including the two specimens of *T. urartu*. In the **B** genome clade 13 or 14 character changes occur depending

I finitelo used for I eft d	he sequencing of Differ and Er G				
DMC1:		EFG:			
TDMC1E13	CTGGCACAAATGCTGTCCCG	cMWG699T3-3	CTGCTGACATACTGGAACATCTCGG		
TDMC15R	AGCCACCTGTTGTAATCTGG	cMWG699T7-3	TTTGGGTGATGTTATTGGTGACTTG		
TDMC1E10R	TGGTTGGTGATGTACACTGCA	cMWG699T3-2	AACTGTTTTCTCATTTGTGA		
TDMC1E10	TGCCAATTGCTGAGAGATTTG	cMWG699T7-2	AAGTGTCCTTGCCTTCCAAA		
tritDMC1CGF	TTCCGTGTTGATTTCAGTGGCG	EFGT1A	TTAAGCAGTACTCCTTTATGA		
tritDMC1TGF	TTCCGTGTTGATTTCAGTGGTG	EFGT2TR	CTACACTCAGAATTAGTACATCT		
tritDMC1AGR	GCAATCTTTGTAAGGCGGGAAG	TEFGDR	CAGACAGCAGATCCTGGC		
tritDMC1CGR	GCAATCTTTGTAAGGCGGGACG	TEFG417BF	GCCGAGCATCTGTAATTTAGTC		
TDMC1GGF	GATCTCAACTGTGCTCATGTGG	TEFG530AR	GCAAAGCAAGTTCAATTCTCCG		
TDMC1A409CR	AATGCAAGCATTCGACTACAC	TEFG530AF	CTGCTGTCTGAAATATTTCTGC		
TDMC1D409CR	GCAAGCAGCATTCGACTACTC				



— 5 changes

Fig. 1. One of 12 equally parsimonious gene trees (length 331, ci = 0.67, ri = 0.87) derived from phylogenetic analysis of sequence data from the nuclear gene DMC1. Branches that collapse in the strict consensus tree are marked with an *. Numbers above or below branches are jackknife proportions.

on optimization procedure. Eight changes occur in the subclade including sequences extracted from the polyploid taxa, and five (ACCTRAN optimization) or six (DEL-TRAN optimization) changes occur in the subclade including the diploid specimens of *Ae. speltoides*.

The *ndh*F matrix includes 777 positions of which 49 are phylogenetically informative. Phylogenetic analysis resulted in three equally parsimonious trees of length 65 (ci = 0.83, ri = 0.94). One of the trees is shown in Fig. 3.

Though the individual gene trees are incongruent they show exactly the same sister group relationships of the sequences from tetraploid and hexaploid wheats. Hence, combining the sequences in a total evidence analysis was unproblematic. Combined analysis of all data sets resulted in eight equally parsimonious trees of length 783 (ci = 0.63, ri = 0.85). The strict consensus tree is shown in Fig. 4. WinClada and PAUP* consistently gave the same results.



Fig. 2. One of four equally parsimonious gene trees (length 313, ci = 0.68, ri = 0.90) derived from phylogenetic analysis of sequence data from the nuclear gene EF–G. Branches that collapse in the strict consensus tree are marked with an *. Numbers above or below branches are jackknife proportions.

4. Discussion

The total evidence analysis presented here provides new evidence about Triticeae phylogeny. However, the phylogeny of the entire tribe has already been discussed in numerous papers (e.g., Hsiao et al., 1995; Kellogg and Appels, 1995; Kellogg et al., 1996; Mason-Gamer, 2005; Mason-Gamer and Kellogg, 1996; Mason-Gamer et al., 1998; Petersen and Seberg, 1997, 2000, 2002; Seberg and Frederiksen, 2001; Seberg and Petersen, in press) and is subject to ongoing research. Hence, the following discussion will concentrate on the phylogenetic relationships within and between *Aegilops* and *Triticum*. In the discussion reference will be made to other published phylogenetic analyses. However, interpretation of the results is often hampered by the limited taxon sampling (see above).

4.1. Is Aegilops plus Triticum monophyletic?

Aegilops and Triticum are occasionally considered congeneric (e.g., Bowden, 1959; Dvořák and Zhang, 1992; Yen et al., 2005), and monophyly of the group would conveniently solve the nomenclatural problems caused by the presence of allopolyploid species making one of the



Fig. 3. One of three equally parsimonious gene trees (length 65, ci = 0.83, ri = 0.94) derived from phylogenetic analysis of sequence data from the plastid gene *ndh*F. Branches that collapse in the strict consensus tree are marked with an *. Numbers above or below branches are jackknife proportion.

genera paraphyletic. However, the present phylogenetic hypothesis refutes monophyly of *Aegilops* plus *Triticum* (Fig. 4) in agreement with most other phylogenetic analysis of the Triticeae. In our analysis monophyly is severely violated by the position of *Ae. speltoides* and the **B** genome copies of polyploid wheats in a basal trifurcation within the Triticeae. Even if this is ignored a monophyletic group including *Aegilops* and *Triticum* would still

have to include *Amblyopyrum* (Jaub. & Spach) Eig, *Thinopyrum* Á. Löve, *Lophopyrum* Á. Löve, and *Crithopsis* Jaub. & Spach. Monophyly of *Aegilops* plus *Triticum* has been refuted by many other molecular data (Kellogg and Appels, 1995; Mason-Gamer, 2001, 2004, 2005; Petersen and Seberg, 1997; Sallares and Brown, 2004; Seberg and Petersen, in press) and by morphological data (Seberg and Frederiksen, 2001).



Fig. 4. Strict consensus tree based on eight equally parsimonious trees (length 783, ci = 0.63, ri = 0.85) derived from combined analysis from two nuclear genes, DMC1 and EF–G, and one plastid gene, *ndh*F. Numbers above branches are jackknife proportions.

However, some molecular data do show a monophyletic *Aegilops* plus *Triticum* clade. Hsiao et al. (1995) analysing ITS sequence data found the group monophyletic, but did not include *Amblyopyrum* in their analysis, and only recovered the group after weighting of the data—reanalysis of the unweighted data refuted monophyly (Kellogg et al., 1996). Kellogg and Appels (1995) analysing short spacers of 5S RNA genes also found the group monophyletic, but

Amblyopyrum and Ae. speltoides were not included. Mason-Gamer and Kellogg (1996) and Mason-Gamer et al. (1998, 2002) analysing plastid RFLP data, nucleotide sequences from the granule-bound starch synthase gene, and three different plastid data sets, respectively, recovered the group as monophyletic or potentially monophyletic, but Amblyo-pyrum was still not included in any of the analyses and Crithopsis was not included in the latter two. Addition of

other Triticeae taxa to the granule-bound starch synthase gene data set made the group non-monophyletic (Mason-Gamer, 2004). Hence, to various degrees the results from these analyses are not conclusive.

4.2. Is Aegilops monophyletic?

Given the basal position of *Ae. speltoides* within the Triticeae the genus *Aegilops* is not monophyletic in the present analysis (Fig. 4). Monophyly is also violated by the position of the **D** genome of *T. aestivum* within a weakly supported *Aegilops* clade containing all species of *Aegilops* except *Ae. speltoides.* The special problems related to the allopolyploid wheats will be dealt with in further detail below and are not discussed further here.

Previously published phylogenetic analyses based on other molecular data also mostly refute monophyly of Aegilops. Plastid and nuclear RFLP data showed diploid species of Triticum embedded within Aegilops (Dvořák and Zhang, 1992; Mason-Gamer and Kellogg, 1996). Plastid rpoA and rbcL sequence data showed that Aegilops as a minimum would have to include Triticum and Amblyopyrum, too, though monophyly potentially could be restored by the exclusion of Ae. speltoides (Petersen and Seberg, 1997; Seberg and Petersen, in press). Combined analysis of three plastid data sets (rpoA, three tRNA gene spacers, RFLPs) supported inclusion of Triticum (Amblyopyrum is not sampled) and Ae. speltoides as the sister to the Triticum-Aegilops clade (Mason-Gamer et al., 2002), whereas combined analysis of only two of the data sets (rpoA, three tRNA gene spacers) showed Ae. speltoides plus Taeniatherum Nevski as the sister group to the remaining species of Aegilops (Mason-Gamer, 2004). However, in the latter analysis neither Amblyopyrum nor Triticum were included.

Whereas plastid data consistently refutes monophyly of Aegilops, other nuclear sequences not included in the present study give different results. Data from the long spacer units of 5S RNA genes excluded Ae. speltoides from a monophyletic group of four other species of Aegilops, but the short spacer units of the 5S RNA genes did show a monophyletic Aegilops (Kellogg and Appels, 1995). However, the latter analysis did not include Ae. speltoides. The analysis of ITS data by Hsiao et al. (1995) resulted in a monophyletic Aegilops, but only two species (Ae. speltoides and Ae. tauschii) were included and Amblyopyrum was not sampled. In another analysis of ITS sequence data including more species of Aegilops, but only Triticum and Amblyopyrum as representatives of other Triticeae genera, Amblyopyrum was grouped within Aegilops (Wang et al., 2000a). Granule-bound starch synthase gene sequences supported Aegilops (incl. Ae. speltoides) as monophyletic, but Amblyopyrum and Taeniatherum were not sampled (Mason-Gamer et al., 1998). Addition of Taeniatherum plus many more taxa from the Triticeae made Aegilops nonmonophyletic, with the four species included being located in two groups (Ae. speltoides, Ae. caudata and Ae. tauschii, Ae. uniaristata) which together can only be made monophyletic by inclusion of *Triticum*, *Dasypyrum* (Coss. & Durieu) T. Durand, *Lophypyrum*, and *Thinopyrum*. Recent data from β -amylase genes confirmed non-monophyly of *Aegilops*, but the phylogenetic relationships suggested by the data may be strongly influenced by a varying number of paralogs found in different species included in the study (Mason-Gamer, 2005). Not even morphological data used in the circumscription of the genus *Aegilops* clearly support monophyly of *Aegilops*, which is included in an unresolved clade together with *Amblyopyrum* (Seberg and Frederiksen, 2001). Morphology, however, leaves no doubt about the inclusion of *Ae. speltoides* in the clade.

Hence, the majority of evidence seems to suggest that *Aegilops* is not monophyletic. However, it is possible that monophyly can be restored just by the exclusion of *Ae. speltoides*. To maintain only monophyletic higher level taxa *Ae. speltoides* would have to be removed from *Aegilops* and transferred to the genus *Sitopsis* (Jaub & Spach) Á. Löve. *Sitopsis* was originally formed to comprise all members of *Ae.* section *Sitopsis* (Löve, 1982, 1984), but in the proposed circumscription the genus would be monotypic.

Within Aegilops Slageren (1994) recognized five sections all of which include diploid species. Three sections include only one diploid species (Ae. umbellulata (U) in section Aegilops; Ae. caudata (C) in section Cylindropyrum (Jaub. & Spach) Zhuk.; Ae. tauschii (D) in section Vertebrata Zhuk. emend. Kihara) together with one or more polyploid species. The remaining sections only include diploid species: Ae. comosa (M) and Ae. uniaristata (N) belong to section Comopyrum (Jaub. & Spach) Zhuk. and Ae. speltoides (S), Ae. bicornis (S^b), Ae. longissima (S^l), Ae. searsii (S^s), and Ae. sharonensis (S¹) belong to section Sitopsis. Whereas section Comopyrum is strongly supported (98% jackknife) as monophyletic by the present analysis section Sitopsis is not (Fig. 4). In the latter section the position of *Ae. speltoides* as dealt with above violates monophyly, but the remaining species do form a strongly supported monophyletic group (99% jackknife). Hence, it seems appropriate to maintain S as the genomic designation for species of section Sitopsis, whereas we agree with Sallares and Brown (2004) that the genome of Ae. speltoides should be designated B rather than S. However, the study by Huang et al. (2002a) showed that some, but not all specimens of Ae. speltoides, formed a monophyletic group together with other species of section Sitopsis, suggesting that further studies are needed to clarify the relationships of Ae. speltoides. Apart from Ae. caudata section Cylindropyrum comprises only one tetraploid species, Aegilops cylindrica Host with the genomic composition CD. As Ae. caudata and Ae. tauschii are not sister taxa section Cylindropyrum is non-monophyletic. Section Vertebrata including Ae. tauschii comprises tetraploid and hexaploid species also including the N, the U, and some "unknown" genomes (Wang et al., 1996). The present analysis shows section Sitopsis (excl. Ae. speltoides) as the sister to Ae. tauschii (and the D genome of T. aestivum), hence, section Vertebrata is also non-monophyletic. The same is true for section Aegilops, where the tetraploid and hexaploid species combine the U genome with the genomes M, N, C, and S.

Few other phylogenetic analyses have included a sufficient number of species to bear evidence on Aegilops phylogeny. However, Mason-Gamer and Kellogg (1996) and Sallares and Brown (2004) both confirmed that Ae. speltoides is distinct from other species of the genus, but that the remaining species of section Sitopsis constitute a monophyletic group. In contrast, Dvořák and Zhang (1992) recovered the entire section *Sitopsis* as monophyletic, but their analysis only included species of Aegilops, Triticum, Amblyopyrum, and Lophopyrum. Two analyses based on RFLP data confirmed monophyly of section Comopyrum and recovered the relationship between Ae. caudata and Ae. umbellulata found in the present study (Dvořák and Zhang, 1992; Mason-Gamer and Kellogg, 1996). These two relationships are further supported by sequence data from the granule-bound starch synthase gene (Mason-Gamer et al., 1998), whereas the data did not support section Sitopsis even in a restricted sense. Given that the genomic designations of polyploid species of *Aegilops* correctly depict the evolutionary history of the species it seems futile to maintain the sectional division of the genus. However, phylogenetic analyses of the polyploid species are still needed to confirm or reject the suggested genome relationships.

4.3. Is Triticum monophyletic?

The genus *Triticum* consists of only two diploid and four allopolyploid species (Slageren, 1994). Disregarding the position of the polyploid species, the present phylogenetic hypothesis suggests that the diploid species, *Triticum monococcum* (A^m) and *T. urartu* (A^u), may form a monophyletic group (Fig. 4). However, *Amblyopyrum* may have to be included in the group. Many other phylogenetic analyses have confirmed monophyly of the diploid species (Huang et al., 2002a; Mason-Gamer, 2001, 2004; Mason-Gamer and Kellogg, 1996; Mason-Gamer et al., 1998; Sallares and Brown, 2004; Zhang et al., 2002), but unfortunately only one of these studies have included *Amblyopyrum*.

The phylogenetic relationships of tetraploid T. turgidum $(\mathbf{B}\mathbf{A}^{\mathbf{u}})$ and hexaploid T. aestivum $(\mathbf{B}\mathbf{A}^{\mathbf{u}}\mathbf{D})$ obviously violate monophyly of Triticum (Fig. 4). T. turgidum has received its nuclear genome from T. urartu (100% jackknife) and Ae. speltoides (100% jackknife) (Figs. 1 and 2) with the latter acting as the plastid donor (Fig. 3), and the additional genome of T. aestivum has been paternally derived from Ae. tauschii (Figs. 1-4). The phylogenetic relationships of the three wheat genomes are all strongly supported by the jackknife (100%). Accordingly, our data strongly confirm the traditional scenario of the evolution of cultivated wheat (e.g., Cox, 1998), as do most other recent phylogenetic studies of the origin of polyploid wheats. The study of Sallares and Brown (2004) based on external transcribed spacers of the 18S rRNA gene is consistent with the above hypothesis. Ae. tauschii was confirmed as the D genome donor of T. aestivum and Ae. speltoides as the **B** genome donor of

T. turgidum. The relationship between T. turgidum and Ae. speltoides was also confirmed by Zhang et al. (2002) based on studies of ITS sequence data, but T. monococcum rather than T. urartu was found as the closest relative of the A^{u} genome of T. turgidum. As representatives of Aegilops the study included only members of section Sitopsis and Ae. tauschii, hence, its conclusiveness is limited. The same restricted sampling of Aegilops species was used by Huang et al. (2002a,b), but they included multiple specimens of most species allowing for a test of intraspecific variation and species monophyly. Accordingly, the results of their studies based on sequence data from two nuclear genes, acetyl-CoA carboxylase (ACC) and 3-phosphoglycerate kinase (PGL), are more complex. Both genes recovered Ae. tauschii as the closest relative of the D genome of hexaploid wheat, but one specimen of Ae. tauschii was not member of the clade on the ACC gene tree (Huang et al., 2002a; Fig. 1). However, the position of this specimen on the neighborjoining tree is not supported on the corresponding strict consensus tree derived from parsimony analysis and monophyly of a group consisting of both specimens of Ae. tauschii plus the D genome sequence of T. aestivum was not contradicted. Considering only clades supported by parsimony the closest relatives to the A genome sequences of both tetraploid and hexaploid wheat species were the two diploid species of *Triticum*, but the resolution of the trees did not allow for a distinction between them (Huang et al., 2002a). The relationship of the **B** genome sequences of T. turgidum and T. aestivum was unresolved both on the ACC and PGK gene trees (Huang et al., 2002a). A sister group relationship to Ae. speltoides is among the solutions, but only for a subset of specimens of Ae. speltoides. Ae. tauschii and the species of section *Sitopsis* were also the only representatives of Aegilops included in a study based on sequences from 14 assumed homologous nuclear loci by Blake et al. (1999). A combined analysis of all loci revealed Ae. speltoides as the sister to T. aestivum, though some individual loci were in conflict. Buchner et al. (2004) analysing sequence data from two sulfate transporter genes confirmed the relationship of T. aestivum to Ae. tauschii and T. urartu, but only one of two gene trees confirmed the relationship to Ae. speltoides. As the study included no other diploid species of Aegilops and Triticum, its conclusiveness is very limited. Hence, the vast majority of phylogenetic evidence confirms the traditional interpretation of the origin of cultivated wheat. Some authors (e.g., Zhang et al., 2002) finding a sister group relationship between Ae. speltoides and polyploid wheats have concluded that Ae. speltoides either was the **B** genome donor or was the most closely related species to a possibly extinct donor species. However, we find no justification for invoking extinct species as genome donors to the polyploid species of wheat. Only when the sister group to a polyploid species is found to be a clade including two or more species is it become meaningful to speak about an extinct donor.

Given the phylogenetic relationships of the polyploid species of *Triticum* involving two species of *Aegilops*—one

of which might even better be referred to a separate genus Sitopsis-the genus Triticum is obviously not monophyletic. Hence, if only monophyletic genera are to be accepted all other Triticeae species, except perhaps Henrardia persica and Pseudoroegneria spp., would have to be included in one genus. This is hardly a practically acceptable solution, though suggested previously (Stebbins, 1956). The basal position of Ae. speltoides (and the B genome in polyploid wheats) may be regarded as spurious, but even if future studies show it to be incorrect a monophyletic group including diploid and polyploid species of Aegilops and Triticum will also have to include Amblyopyrum, Thinopyrum, Lophopyrum, and Crithopsis (Fig. 4). This would cause extensive name changes (or rather uses of names-most species of Triticeae have previously been included in Triti*cum*). However, in the Triticeae is has been widely accepted to recognize paraphyletic genera caused by the occurrence of wide allopolyploids, and these allopolyploids have been referred to separate polyphyletic genera (see Kellogg, 1989). Hence, the diploid species of *Triticum* has been referred to the genus Crithodium Link, the BA^u polyploids to Gigachilon Seidl, and hexaploid, BA^uD T. aestivum is the only species left in Triticum (Löve, 1984).

4.4. Future phylogenetic studies

Many of the ambiguities emerging from analysis of single or a few data sets can hopefully be solved by combined analysis of more data sets. Hence, future phylogenetic studies of *Aegilops* and *Triticum* may benefit from the many data sets already present, but a substantial amount of new data should be gathered to minimize missing entries in a combined matrix. To provide conclusive results we recommend that the taxon sampling of such studies as a minimum includes representatives of all genera or genome groups within the Triticeae. To take the potential nonmonophyly of species into account it is desirable to include more accessions of the species that a particular phylogenetic analysis is focused on.

4.5. Differential diversification rates among the **A**^{*u*} and **B** genomes

It has previously been shown that the **B** genome of polyploid wheats is more variable than any of the other two genomes (see Wendel, 2000). Being donated at a more recent date (Cox, 1998) the **D** genome in hexaploid wheat is expected to show less variation than the other genomes. However, the hybridization event leading to the formation of allotetraploid *T. turgidum* establishes an equal divergence time for the two other genomes, A^u and **B**. Provided that each genome, A^u and **B**, was donated only once (a hypothesis corroborated by the present study) a higher level of variation in the **B** genome implies a higher diversification rate of the **B** genome as compared to the A^u genome in polyploid wheat. This is supported by the present data as the number of character changes in the **B** genome of the polyploids exceeds the numbers of changes in the A^u genome by a factor four for the DMC1 sequences and by a factor two for the EF-G sequences.

Whether the rate difference is restricted to the polyploids or whether a rate difference is also a characteristic of the **B** and A^u genome donors is not clear from the present data as both donor species are represented only two randomly chosen specimens in our analyses. However, the actually observed higher numbers of character changes in both nuclear genes in the **B** genome diploids (EF–G: 5–6 changes; DMC1: 4 changes) compared to the A^u genome diploids (EF–G: 2 changes; DMC1: 0 changes) may suggest that a rate difference also exists between the diploids. Inclusion of more specimens from both species is required to test the hypothesis.

In addition to polyploid wheats, the study by Huang et al. (2002a) did include several accessions of *Ae. speltoides* but only one accession of *T. urartu*. Their Table 3 (Huang et al., 2002a: supporting information) shows substitution rates calculated for the ACC and PGK nuclear genes, with a more than 10-fold increase in the **B** genome compared to the A^{u} genome in both genes. However, the difference may be influenced by the unequal number of specimens of the two diploids, and the calculations do not allow for a distinction between rates in diploids and polyploids.

Whether the higher diversification rate of the **B** genome sequences compared to the A^u genome sequences is restricted to the polyploids or not, it is a likely reason for the hitherto greater difficulty of identifying the **B** genome donor compared to the A^u and **D** genome donors. How differential diversification rates are controlled or maintained in the polyploid species of wheat remains an open question.

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References

- Aagesen, L., Petersen, G., Seberg, O., 2005. Sequence length variation, indel costs, and congruence in sensitivity analysis. Cladistics 21, 15–30.
- Blake, N.K., Lehfeldt, B.R., lavin, M., Talbert, L.E., 1999. Phylogenetic reconstruction based on low copy DNA sequence data in an allopolyploid: the B genome of wheat. Genome 42, 351–360.
- Bowden, W.L., 1959. The taxonomy and nomenclature of the wheats, barleys, and ryes and their wild relatives. Can. J. Bot. 37, 657–684.
- Buchner, P., Prosser, I.M., Hawkesford, M.J., 2004. Phylogeny and expression of paralogous and orthologous sulphate transporter genes in diploid and hexaploid wheats. Genome 47, 526–534.
- Büren, M.von, 2001. Polymorphisms in two homologous γ -gliadin genes and the evolution of cultivated wheat. Genet. Resour. Crop Evol. 48, 205–220.

- Cha, R.S., Zarbl, H., Keohavong, P., Thilly, W.G., 1992. Mismatch amplification mutation assay (MAMA): application to the c-H-ras gene. PCR Methods Appl. 2, 14–20.
- Cox, T.S., 1998. Deepening the wheat gene pool. J. Crop Prod. 1, 1-25.
- Cronn, R., Cedroni, M., Haselkorn, T., Grover, C., Wendel, J.F., 2002. PCR-mediated recombination in amplification products derived from polyploid cotton. Theor. Appl. Genet. 104, 482–489.
- Dvořák, J., Zhang, H.-B., 1992. Reconstruction of the phylogeny of the genus Triticum from variation in repeated nucleotide sequences. Theor. Appl. Genet. 84, 419–429.
- Farris, J.S., 1983. The logical basis of phylogenetic analysis. In: Platnick, N.I., Funk, V.A. (Eds.), Advances in Cladistics, vol. 2. Columbia Univ. Press, New York, pp. 7–36.
- Galili, S., Avivi, Y., Millet, E., Feldmen, M., 2000. RFLP-based analysis of three *RbcS* subfamilies in diploid and polyploid species of wheat. Mol. Gen. Genet. 263, 674–680.
- Giorgi, D., D'Ovidio, R., Tanzarella, O.A., Porceddu, E., 2002. RFLP analysis of *Aegilops* species belonging to the *Sitopsis* section. Genet. Resour. Crop Evol. 49, 145–151.
- Goloboff, P.A., 1993. NONA Version 2.0. Published by the author.
- Goryunova, S.V., Kochieva, E.Z., Chikida, N.N., Pukhalskyi, V.A., 2004. Phylogenetic relationships and intraspecific variation of D-genome *Aegilops* L. as revealed by RAPD analysis. Russ. J. Genet. 40, 515–523.
- Helfgott, D.M., Mason-Gamer, R.J., 2004. The evolution of North American *Elymus* (Triticeae, Poaceae) allotetraploids: evidence from phosphoenolpyruvate carboxylase gene sequences. Syst. Bot. 29, 850–861.
- Hsiao, C., Chatterton, N.J., Asay, K.H., Jensen, K.B., 1995. Phylogenetic relationships of the monogenomic species of the wheat tribe, Triticeae (Poaceae), inferred from nuclear rDNA (internal transcribed spacer) sequences. Genome 38, 211–223.
- Huang, S., Sirikhachornkit, A., Su, X., Faris, J., Gill, B., Haselkorn, R., Gornicki, P., 2002a. Genes encoding plastid acetyl-CoA carboxylase and 3-phosphoglycerate kinase of the *Triticum/Aegilops* complex and the evolutionary history of polyploid wheat. Proc. Natl. Acad. Sci. USA 99, 8133–8138.
- Huang, S., Sirikhachornkit, A., Faris, J.D., Su, X., Gill, B.S., Haselkorn, R., Gornicki, P., 2002b. Phylogenetic analysis of the acetyl-CoA carboxylase and 3-phosphoglycerate kinase loci in wheat and other grasses. Plant Mol. Biol. 48, 805–820.
- Ishii, T., Mori, N., Ogihara, Y., 2001. Evaluation of allelic diversity at chloroplast microsatellite loci among common wheat and its ancestral species. Theor. Appl. Genet. 103, 896–904.
- Kellogg, E.A., 1989. Comments on genomic genera in the Triticeae (Poaceae). Am. J. Bot. 76, 796–805.
- Kellogg, E.A., Appels, R., 1995. Intraspecific and interspecific variation in 5S RNA genes are decoupled in diploid wheat relatives. Genetics 140, 325–343.
- Kellogg, E.A., Appels, R., Mason-Gamer, R.J., 1996. When genes tell different stories: the diploid genera of Triticeae. Syst. Bot. 21, 321–347.
- Kihara, H., 1924. Cytologische und genetische Studien bei wichtigen Getreidearten mit besonderer Rucksicht auf das Verhalten der Chromosomen und die Sterilität in den Bastarden. Mem. Coll. Sci. Kyoto Imp. Univ., Ser. B., V. 1, 1–200.
- Löve, Á., 1982. Generic evolution of the wheatgrasses. Biol. Zentralbl. 101, 199–212.
- Löve, Á., 1984. Conspectus of the Triticeae. Feddes Repert. 95, 425–521.
- Mason-Gamer, R.J., 2001. Origin of North American species of *Elymus* (Poaceae: Triticeae) allotetraploids based on granule-bound starch synthase gene sequences. Syst. Bot. 26, 757–768.
- Mason-Gamer, R.J., 2004. Reticulate evolution, introgression, and intertribal gene capture in an allohexaploid grass. Syst. Biol. 53, 25–37.
- Mason-Gamer, R.J., 2005. The β -amylase genes of grasses and a phylogenetic analysis of the Triticeae (Poaceae). Am. J. Bot. 92, 1045–1058.
- Mason-Gamer, R.J., Kellogg, E.A., 1996. Chloroplast DNA analysis of the monogenomic Triticeae: phylogenetic implications and genome-specific markers. In: Jauhar, P.P. (Ed.), Methods of Genome Analysis in Plants. CRC Press, Boca Raton, FLA, pp. 310–325.

- Mason-Gamer, R.J., Orme, N.L., Anderson, C.M., 2002. Phylogenetic analysis of North American *Elymus* and the monogenomic Triticeae (Poaceae) using three chloroplast DNA data sets. Genome 45, 991–1002.
- Mason-Gamer, R.J., Weil, C.F., Kellogg, E.A., 1998. Granule-bound starch synthase: structure function, and phylogenetic utility. Mol. Biol. Evol. 15, 1658–1673.
- Nixon, K.C., 2002. Winclada Version 1.00.08. Published by the author, Ithaca, New York.
- Olmstead, R.G., Sweere, J.A., 1994. Combining data in phylogenetic systematics: an empirical approach using three molecular data sets in the Solanaceae. Syst. Biol. 43, 467–481.
- Petersen, G., Seberg, O., 1997. Phylogenetic analysis of the Triticeae (Poaceae) based on *rpoA* sequence data. Mol. Phylogenet. Evol. 7, 217–230.
- Petersen, G., Seberg, O., 2000. Phylogenetic evidence for the excision of *Stowaway* miniature inverted-repeat transposable elements in Triticeae (Poaceae). Mol. Biol. Evol. 17, 1589–1596.
- Petersen, G., Seberg, O., 2002. Molecular evolution and phylogenetic application of DMC1. Mol. Phylogenet. Evol. 22, 43–50.
- Petersen, G., Seberg, O., 2003. Phylogenetic analyses of the diploid species of *Hordeum* (Poaceae) and a revised classification of the genus. Syst. Bot. 28, 293–306.
- Petersen, G., Seberg, O., 2004. On the origin of the tetraploid species *Hord-eum capense* and *H. secalinum* (Poaceae). Syst. Bot. 29, 862–873.
- Petersen, G., Seberg, O., 2005. Phylogenetic analysis of allopolyploid species. Czech. J. Genet. Plant Breed. 41, 28–37.
- Provan, J., Wolters, P., Caldwell, K.H., Powell, W., 2004. High-resolution organellar genome analysis of *Triticum* and *Aegilops* sheds new light on cytoplasm evolution in wheat. Theor. Appl. Genet. 108, 1182–1190.
- Sallares, R., Brown, T.A., 2004. Phylogenetic analysis of complete 5' external transcribed spacers of the 18S ribosomal RNA genes of diploid Aegilops and related species (Triticeae, Poaceae). Genet. Resour. Crop Evol. 51, 701–712.
- Sasanuma, T., Chabane, K., Endo, T.R., Valkoun, J., 2004. Characterization of genetic variation in and phylogenetic relationships among diploid *Aegilops* species by AFLP: incongruence of chloroplast and nuclear data. Theor. Appl. Genet. 108, 612–618.
- Seberg, O., Frederiksen, S., 2001. A phylogenetic analysis of the monogenomic Triticeae (Poaceae) based on morphology. Bot. J. Linn. Soc. 136, 75–97.
- Seberg, O., Petersen, G., in press. Phylogeny of the Triticeae (Poaceae) based on three organelle genes, two single-copy nuclear genes, and morphology. In: Columbus, J.T., Friar, E.A., Hamilton, C.W., Porter, J.M., Prince, L.M., Simpson, M.G. (Eds.), Monocots: Comparative Biology and Evolution. Rancho Santa Ana Botanic Garden, Claremont.
- Simmons, H.P., Ochoterena, H., 2000. Gaps as characters in sequencebased phylogenetic analyses. Syst. Biol. 49, 369–381.
- Slageren, M.W. van, 1994. Wild wheats: a monograph of Aegilops L. and Amblyopyrum (Jaub. & Spach) Eig (Poaceae). Wageningen Agric. Univ. Press, Wageningen.
- Sourdille, P., Tavaud, M., Charmet, G., Bernard, M., 2001. Transferability of wheat microsatellites to diploid Triticeae species carrying the A, B and D genomes. Theor. Appl. Genet. 103, 346–352.
- Stebbins, G.L., 1956. Taxonomy and the evolution of genera with special reference to the family Gramineae. Evolution 10, 235–245.
- Swofford, D.L., 2001. PAUP*: phylogenetic analysis using parsimony (*and other methods), Version 4.0b8. Sinauer, Sunderland.
- Ünlü, S., Sümer, S., 2005. PCR-based RFLP analysis of an intergenic spacer region in cpDNA of some wild wheat species. Bot. J. Linn. Soc. 148, 305–310.
- Vakhitov, V.A., Chemeris, A.V., Sabirzhanov, B.E., Akhunov, E.D., Kulikov, A.M., Nikonorov, Y.M., Gimalov, F.R., Bikbulatova, S.M., Baymiev, A.K., 2003. The phylogeny of *Triticum L.* and *Aegilops L.* inferred from comparative analysis of nucleotide sequences in rDNA promoter regions. Russ. J. Genet. 39, 1–11.

- Wang, C., Shi, S.-H., Wang, J.-B., Zhong, Y., 2000. Phylogenetic relationships of diploid species in *Aegilops* inferred from the ITS sequences of nuclear ribosomal DNA. Acta Bot. Sinica 42, 507–511. In chinese.
- Wang, G.-Z., Matsuoka, Y., Tsunewaki, K., 2000. Evolutionary features of chondriome divergence in *Triticum* (wheat) and *Aegilops* shown by RFLP analysis of mitochondrial DNAs. Theor. Appl. Genet. 100, 221–231.
- Wang, J.-B., Wang, C., Shi, S.-H., Zhong, Y., 2000a. ITS regions in diploids of *Aegilops* (Poaceae) and their phylogenetic implications. Hereditas 132, 209–213.
- Wang, J.-B., Wang, C., Shi, S.-H., Zhong, Y., 2000b. Evolution of parental ITS regions of nuclear rDNA in allopolyploid *Aegilops* (Poaeceae) species. Hereditas 133, 1–7.
- Wang, R.R.-C., Bothmer, R. von, Dvorak, J., Fedak, G., Linde-Laursen, I., Muramatsu, M., 1996. Genome symbols in the Triticeae (Poaceae). In: Wang, R.R.-C., Jensen, K.B., Jaussi, C. (Eds.), Proc. 2nd Int. Triticeae Symp.. Utah State Univ., Logan, pp. 29–34.
- Wendel, J.F., 2000. Genome evolution in polyploids. Plant Mol. Biol. 42, 225–249.
- Yen, C., Yang, J.-L., Yen, Y., 2005. Hitoshi Kihara, Áskell Löve and the modern genetic concept of the genera in the tribe Triticeae (Poaceae). Acta Phytotax. Sin. 43, 82–93.
- Zhang, W., Qu, L.-J., Gu, H., Gao, W., Liu, M., Chen, J., Chen, Z., 2002. Studies on the origin and evolution of tetraploid wheats based on the internal transcribed spacer (ITS) sequences of nuclear ribosomal DNA. Theor. Appl. Genet. 104, 1099–1106.