

### 82.2.40. Carotenoid beta-hydroxylase (non-heme di-iron type)

HYD are non-heme di-iron b-hydroxylases that act primarily on b-carotene.

*Hyd-A1*{10913}. 2AL{10913}. tv: Kronos{10913}. v: UC1041{10913}.

*Hyd-B1*{10913}. 2BL{10913}. tv: Kronos{10913}. v: UC1041{10913}.

*Hyd-D1*{10913}. 2DL{10913}. tv: Kronos{10913}. v: UC1041{10913}.

*Hyd-A2*{10913}. 5AL{10913}. tv: Kronos{10913}. v: UC1041{10913}.

*Hyd-B2*{10913}. 4BL{10913}. tv: Kronos{10913}. v: UC1041{10913}.

*Hyd-D2*{10913}. 4DL{10913}. tv: Kronos{10913}. v: UC1041{10913}.

## 82.3. Endosperm storage proteins

### 82.3.1. Glutenins

These are heterogeneous mixtures of proteins comprising subunits linked by disulfide bonds. 'A' are high-molecular-weight (HMW) and 'B', 'C' and 'D' are low-molecular-weight (LMW) subunits.

Using proteomic analysis of 2D gels of seed storage proteins in 39 ditelocentric lines of cv. CS, 105 protein spots were resolved {03129}. Locations of structural genes controlling 26 spots were identified in 10 chromosomal arms (4 on 1BL, 5 on 1BS, 4 on 1DL, 4 on 1DS, 2 on 6AS, 3 on 6BS, 1 on 6DL, 1 on 6DS, 1 on 3BS and 1 on 3BL). Multiple regulators of the same protein located on various chromosome arms were observed. Two novel subunits, named 1Bz and 1Dz, were found to have very similar structures to HMW glutenin subunit 12 (encoded by *Glu-D1-2a* - see the relevant list below) and were located to chromosome arms 1BL and 1DL, respectively.

#### 82.3.1.1. Glu-1

The *Glu-1* loci, all of which are compound, encode HMW glutenin subunits.

Each *Glu-1* locus in hexaploid wheat contains two genes, the products of which were described as 'x-type' and 'y-type' based on differences in molecular weight and isoelectric point {1118}.

Other evidence has shown that these gene products differ in electrophoretic fingerprint pattern {1124} and cysteine content {1028}, and the genes themselves differ in nucleotide sequence {1470,1433,373}.

Although early evidence suggested up to 6 genes in total at each locus {1471,373}, it appears likely that only a single copy of each gene is present at the 1AL, 1BL, and 1DL loci {495}.

No 'y-type' protein from the *Glu-A1* locus has been demonstrated in hexaploid wheat {1118}, although they are found in diploid wheats {1535,798}, and sequencing experiments have shown the presence of two stop codons in the transcribed portion of the gene {10088}.

Definitive evidence that subunit 21\* {602}, which has a mobility close to that of subunit 21, is a 'x-type' protein rather than a 'y-type' protein has not been obtained. The gene coding for 'x-type' proteins within *Glu-A1* is also often silent {1118,420}.

The symbols for the genes within the *Glu-1* loci coding for 'x-type' and 'y-type' proteins will be *Glu-1-1* and *Glu-1-2*, respectively, rather than *Glu-1x* and *Glu-1y* {1470}. The genes are closely linked but recombination has been observed between *Glu-B1-1* and *Glu-B1-2* with a frequency of 3 in 3,450 {1117}. The gene order, relative to the centromere, has not been

ascertained.

The subunit nomenclature used is that devised in {1116}; however, an alternative system based upon molecular weight was proposed in {1068}. A system of naming the *Glu-A1-1*, *Glu-A1-2*, *Glu-B1-1* and *Glu-B1-2* alleles in *T. turgidum* var. *dicoccoides* is given in {796}.

In {00116}, a comparison between spelt wheats (*T. spelta*) and bread wheat was carried out for the glutenins using a nomenclature system described in {00117}.

The *Glu-1* loci may be recognised by the DNA probe pTag1290 {1471} and probe pwhe1(Dy10) {030}. Individual *Glu-1-1* loci on 1A, 1B and 1D and the *Glu-1-2* loci may be recognised by specific primers {263}.

In {00105}, the evolution of the high molecular weight glutenin loci of the A, B, D and G genomes of wheat was explored; 30 partial allele sequences were compared, designated by Greek letters (alpha, beta, gamma, etc.) (5 of which were cited as Schlumbaum, pers. comm.; the remaining 25 were deposited as GenBank, accession nos. X98583-X98592, X98711-X98715 and Y12401-Y12410). These partial alleles derive from all six *Glu-1-1* and *Glu-1-2* loci in current-day samples taken from seven species of wheat, as well as from DNA extracted from charred grain of two samples from archaeological excavations, dated 3000 and 5000 years old, respectively.

Following the first listing which considers the *Glu-1* set for hexaploid wheat as a single locus, there is a provisional listing based on x- and y- type glutenins. These are not referenced.

The importance of the HMW glutenin subunits for bread-making quality was first noted from observations in wheat cultivars of related pedigree on the effects of the presence of subunit 1 encoded by *Glu-A1a* {0197}, effects that have repeatedly been confirmed since (for example {0198,0199,01100}).

A nomenclature system for prolamins banding patterns of triticale was proposed in {03139}. Extensive allelic variation in triticale at *Glu-A1*, *Glu-B1*, *Glu-R1* and *Gli-R2* loci was reported in {03121}.

***Glu-A1***{780,1125}. [*Glt-A1*{420},*Glt-A2*{420},*Glu 1A*{1415}]. 1A{780}.1AL{781,1125}.  
s: CS\*/Hope 1A{1125}. v: CS{780,781}; various{420}.

Primers were designated that enabled Ax2\* to be distinguished from Ax1 or Ax-null {10641}.

***Glu-A1a***{1116}. 1{1116}. v: Hope.

***Glu-A1b***{1116}. 2\*{1116}. v: Bezostaya 1.

***Glu-A1c***{1116}. Null allele{1116}. v: CS.

***Glu-A1d***{1535}. v: V74, Spain{1115}.

***Glu-A1e***{1535}. v: 132c, Poland{1115}.

***Glu-A1f***{1535}. v: 112-29, Sudan{1115}.

***Glu-A1g***{1535}. v: Landrace 1600.

***Glu-A1h***{1527}. [*GLU-A1-I*{1527}]. tv: PI 94683, USSR, *T. dicoccum*.

***Glu-A1i***{1527}. [*GLU-A1-II*{1527}]. tv: CI 12213, India, *T. dicoccum*; Lambro{1523}.

***Glu-A1j***{1527}. [*GLU-A1-III*{1527}]. 1'{125}. tv: PI 352359, Germany, *T. dicoccum*.

***Glu-A1k***{478}. 26{478}. v: BT-2288{478}.

***Glu-A1l***{847}. tv: Chinook, Canada.

***Glu-A1m***{1069}. tv: Nugget Biotype 1, Canada, *T. durum*.

***Glu-A1n***{1526}. [*Glu A1-IV*{1526},*Glu-A1m*{959}]. 1'{125}. tv: Corado, Portugal{1526}.

***Glu-A1o***{1526,125}. [*Glu A1-V*{1526,125},*Glu-A1n*{959}]. 2\*\*{125}. tv: Aric 581/1{125}; PI 61189{1525}; USSR.

***Glu-A1p***{1146}. 3\*{1146}. v: David 1.

***Glu-A1q***{125}. [*Glu A1VI*{125}]. 2\*\*\*{125}. tv: Melianopus 1528.

***Glu-A1r***{1232}. 39+40{1232}. **i**: *T. thaouдар* IPSR 1020006/6\* Sicco.

***Glu-A1s***{1231}. 41+42{1231}. **i**: *T. thaouдар* G3152/6\* Sicco.

***Glu-A1t***{602}. 21\*{602}. **v**: W29323, W3879, W31169.

***Glu-A1u***{02106}. 2\*<sup>B</sup>{02106}. **v**: Bankuti 1201.

The allele designated *Glu-A1u* and *Glu-A1-1u* in the appropriate list below encodes a high molecular weight glutenin subunit (denominated 2\*<sup>B</sup>) that is identical to subunit 2\* apart from one amino acid difference involving the exchange of serine for cysteine (which itself is due to a C to G point mutation at the 1181 bp point of the coding region of 2\*). The authors of {02106} suggest that the additional cysteine residue facilitates the formation of further disulphide bonds (cf. the 1Dx5 subunit) which might lead to an improvement in gluten quality characters.

***Glu-A1v***{10327}. 2.1\* {10327} **v**: Grado{10327}; KU-1026{10327}; KU-1086{10327}; KU-1094{10327}; KU-1139{10327}.

***Glu-A1w***{10327}. 2' {10327} **v**: TRI14165/91{10327}.

***Glu-A1x***{10327}. 2' {10327}. **v**: TRI14165/91{10327}.

***Glu-A1y***{10535}. [2''{10535}]. **v**: 211.12014{10535}.

There is a possibility that *Glu-A1* alleles *i*, *j* {1527} and *k* {478} correspond to alleles *d*, *e*, *f* or *g* {1535} that were published shortly earlier. *Glu-A1m* [{1526}] was changed to *n*, because the *m* allele in {1069} has precedence. Allele *n* [{1526}] was changed to *o*. An earlier reference to an allele designated *Glu-A1d* {1411} was withdrawn {1114}. There appears to be a minor band associated with subunit 2 encoded by *Glu-A1b* {1516}; this may be the same as a band named A5 in {420}.

Six combinations involving 5 HMW subunits [1A (u-z)] are listed in {420}, from a study of 109 genotypes including representatives of botanical varieties. A number of alleles in *T. turgidum* var. *dicoccoides* populations, 12 at *Glu-A1-1* and 3 at *Glu-A1-2*, were described in {798}. In a further study using different germplasm of this species {205}, 14 alleles at *Glu-A1* were observed, including 12 not previously found; the 15 alleles included up to 15 alleles at *Glu-A1-1* (with up to 10 not previously observed), and 5 alleles at *Glu-A1-2* (with 4 not previously observed) (numbers take the null allele into account). The uncertainty in numbers is due to the very similar electrophoretic mobilities of some of the subunits compared with others observed either in this study or previously. In a study including emmers (*T. dicoccum*) {00115}, new subunits named 1<sup>+</sup> and 2<sup>-</sup> were found in accessions MG4378/1 and MG5380/1, respectively, and provisionally assigned to *Glu-A1*. Until confirmed, they are not included in the *Glu-A1* list.

***Glu-A1z***{10805}. [*Glu-A1<sup>m</sup>a*{10805}]. **dv**: PI 191146, *T. monococcum* ssp. *monococcum*{10805}.

***Glu-A1aa***{10805}. [*Glu-A1<sup>m</sup>b*{10805}]. **dv**: PI 190946, *T. monococcum* L. ssp. *monococcum*{10805}.

***Glu-A1ab***{10805}. [*Glu-A1<sup>m</sup>c* {10805}]. **dv**: PI 191098, *T. monococcum* ssp. *monococcum*{10805}.

***Glu-A1ac***{10806}. [*Glu-A<sup>u</sup>I-I* {10806}]. **dv**: PI 428319{10806}.

***Glu-A1ad***{10806}. [*Glu-A<sup>u</sup>I-II*{10806}]. **dv**: PI 428232{10806}.

***Glu-A1ae***{10806}. [*Glu-A<sup>u</sup>I-III*{10806}]. **dv**: PI 428240{10806}.

***Glu-A1af***{10806}. [*Glu-A<sup>u</sup>I-IV*{10806}]. **dv**: PI 428335{10806}.

***Glu-A1ag***{10806}. [*Glu-A<sup>u</sup>I-V*{10806}]. **dv**: PI 538741{10806}.

***Glu-A1ah***{10806}. [*Glu-A<sup>u</sup>I-VI*{10806}]. **dv**: PI 428230{10806}.

***Glu-A1ai***{10806}. [*Glu-A<sup>u</sup>I-VII*{10806}]. **dv**: PI 428253{10806}.

***Glu-A1aj***{10806}. [*Glu-A<sup>u</sup>I-VIII*{10806}]. **dv**: PI 427328{10806}.

***Glu-A1ak***{10806}. [*Glu-A<sup>u</sup>I-IX*{10806}]. **dv**: PI 428327{10806}.

***Glu-A1al***{10806}. [*Glu-A<sup>u</sup>I-X*{10806}]. **dv**: PI 428256{10806}.

***Glu-A1am***{10806}. [*Glu-A<sup>u</sup>I-XI*{10806}]. **dv**: PI 428224{10806}.

***Glu-A1an***{10806}. [*Glu-A<sup>u</sup>I-XII*{10806}]. **dv**: PI 428228{10806}.

- Glu-A1ao*{10806}. [*Glu-A<sup>u</sup>1-XIII*{10806}]. **dv**: PI 538724{10806}.  
*Glu-A1ap*{10806}. [*Glu-A<sup>u</sup>1-XIV*{10806}]. **dv**: TRI 6734{10806}.  
*Glu-A1aq*{10806}. [*Glu-A<sup>u</sup>1-XV*{10806}]. **dv**: TRI 11494{10806}.  
*Glu-A1ar*{10806}. [*Glu-A<sup>u</sup>1-XVI*{10806}]. **dv**: TRI 11495{10806}.  
*Glu-A1as*{10806}. [*Glu-A<sup>u</sup>1-XVII*{10806}]. **dv**: PI 428217{10806}.  
*Glu-A1at*{10806}. [*Glu-A<sup>u</sup>3-XVIII*{10806}]. **dv**: PI 428225{10806}.  
*Glu-A1au*{10806}. [*Glu-A<sup>u</sup>3-XIX*{10806}]. **dv**: PI 538733{10806}.  
*Glu-A1av*{10806}. [*Glu-A<sup>u</sup>3-XX*{10806}]. **dv**: PI 428196{10806}.  
*Glu-A1aw*{10806}. [*Glu-A<sup>u</sup>3-XXI*{10806}]. **dv**: PI 538724{10806}.  
*Glu-A1ax*{10806}. [*Glu-A<sup>u</sup>3-XXII*{10806}]. **dv**: PI 428191{10806}.  
*Glu-A1ay*{10806}. [*Glu-A<sup>u</sup>3-XXIII*{10806}]. **dv**: TRI 6734{10806}.  
*Glu-A1az*{10806}. [*Glu-A<sup>u</sup>3-XXIV*{10806}]. **dv**: TRI 11496{10806}.  
*Glu-B1*{107},{1125}. [*Glt-B1*{420},*Glt-B2*{420},*Glt-B3*{420},*Glu 1B*{1415}].  
 1BL{107,780,1125}. **v**: CS.  
*Glu-B1a*{1116}. 7{1116}. **v**: Flinor.  
*Glu-B1b*{1116}. 7+8{1116}. **v**: CS.  
*Glu-B1c*{1116}. 7+9{1116}. **v**: Bezostaya 1.  
*Glu-B1d*{1116}. 6+8{1116}. **v**: Hope.  
*Glu-B1e*{1116}. 20{1116}.20x+20y{03133}. **v**: Federation.  
*Glu-B1f*{1116}. 13+16{1116}. **v**: Lancota (rare).  
*Glu-B1g*{1116}. 13+19{1116}. **v**: NS 335 (rare).  
*Glu-B1h*{1116}. 14+15{1116}. **v**: Sappo (rare).  
*Glu-B1i*{1116}. 17+18{1116}. **v**: Gabo.  
*Glu-B1j*{1116}. 21{1116}.21x+21y{03116}. **v**: Dunav (rare); Foison{03116}.  
*Glu-B1k*{1116}. 22{1116}. **v**: Serbian (rare).  
*Glu-B1l*{778}. 23+24{778}. **v**: Spica D.  
*Glu-B1m*{1527}. [*GLU-B1-I*{1527}]. **tv**: PI 94640, Iran, *T. dicoccum*.  
*Glu-B1n*{1527}. [*GLU-B1-II*{1527}]. **tv**: PI 355505, Germany, *T. dicoccum*.  
*Glu-B1o*{1527}. [*GLU-B1-III*{1527}]. **tv**: PI 352354, Ethiopia, *T. dicoccum*.  
*Glu-B1p*{1527}. [*GLU-B1-IV*{1527}]. 23+18{125}. **tv**: Dritto{1523}; Ethiopia, PI  
 94655, *T. dicoccum*{1527}.  
*Glu-B1q*{1527}. [*GLU-B1-V*{1527}]. **tv**: PI 94633, Morocco, *T. dicoccum*.  
*Glu-B1r*{1527}. [*GLU-B1-VI*{1527}]. 19{125}. **tv**: PI 946669, Bulgaria, *T.*  
*dicoccum*{1527}; Lambro{1523}.  
*Glu-B1s*{478}. 7+11{478}. **v**: BT-2288.  
*Glu-B1t*{847}. **v**: Supreza, Canada.  
*Glu-B1u*{1069}. 7<sup>\*</sup>+8{1146}. **v**: Owens{1069}; Fiorello{1146}.  
*Glu-B1v*{1069}. **v**: Mondor.  
*Glu-B1w*{1069}. 6<sup>\*</sup>+8<sup>\*</sup>{1146}. **v**: Dawbull{1069}; Sieve{1146}.  
*Glu-B1x*{1526}. [*Glu-B1-VII*{1526},*Glu-B1t*{959}]. **tv**: Canoco de Grao Escuro,  
 Portugal, *T. turgidum*.  
*Glu-B1y*{1526}. [*Glu-B1-VIII*{1526},*Glu-B1u*{959}]. **tv**: Tremez Mollez, Portugal, *T.*  
*durum*.  
*Glu-B1z*{1524}. [*Glu-B1-IX*{1524},*Glu-B1v*{959}]. 7+15{125}. **tv**: Roccia, Italy, *T.*  
*durum*{1523,125}.  
*Glu-B1aa*{1524}. [*Glu-B1-X*{1524},*Glu-B1w*{959}]. **tv**: Quaduro, Italy, *T. durum*.  
*Glu-B1ab*{1523}. [*Glu-B1-XI*{1523},*Glu-B1x*{959}]. **tv**: Athena, Italy, *T. durum*.  
*Glu-B1ac*{125}. [*Glu B1XIII*{125}]. 6+16{125}. **tv**: Espa 18914, *T. durum*.  
*Glu-B1ad*{125}. [*Glu B1XIV*{125}]. 23+22{125}. **tv**: Greece 20, *T. durum*.  
*Glu-B1ae*{1146}. 18<sup>\*</sup>{1146}. **v**: David.  
*Glu-B1af*{1146}. 26+27{1146}. **v**: Cologna 1.  
*Glu-B1ag*{1146}. 28+29{1146}. **v**: Forlani.

- Glu-B1ah***{782}. null allele{782}. **v:** Olympic mutant.
- Glu-B1ai***{714}. 7{714}. **v:** Adonis.
- Glu-B1aj***{759}. 8{759}. **v:** AUS 14444, Afghanistan.
- Glu-B1ak***{899}. 7<sup>\*</sup>+8<sup>\*</sup>{899}. **v:** Norstar.
- Glu-B1al***{899}. 7<sup>OE</sup>+7<sup>OE</sup>+8<sup>\*</sup>{899}. **v:** Benkuti 1201{10196, 10197}; Glenlea{899}; Klein Universal II{10196}; Tezanos Pintos Precoz {10196}; Tobari 66{10196}.  
Other genotypes are listed in {10196}.  
Many of the cultivars carrying the over-expressed subunit 7 encoded by *Glu-B1al* show %UPP values that transcend the normal range observed for cultivars that lack this subunit {10089}, which presumably is associated in some way with its unusually high amount in the grain. The underlying cause of the increased amount may be due to an increased transcriptional rate compared to other alleles, for which a known difference in promoter sequence compared to other alleles expressing normal levels of this subunit {10090} may be responsible.  
However, there is evidence that over-expression is due to duplication of subunit 7 {10196}. In regard to subunit 8<sup>\*</sup>, evidence was presented to indicate that in Glenlea, one of the standard cultivars for the allele, this subunit is the same as subunit 8 {10808}.
- Glu-B1am***{1229}. 18{1229}. **v:** Royo.
- Glu-B1an***{1229}. 6{1229}. **v:** BG-2013.
- Glu-B1ao***{1229}. 7+16{1229}. **v:** BG-3545.
- Glu-B1ap***{1229}. 30+31{1229}. **v:** Marinar.
- Glu-B1aq***{1229}. 32+33{1229}. **v:** BG-1943.
- Glu-B1ar***{1229}. 34+35{1229}. **v:** Jeja Almendros.
- Glu-B1as***{1229}. 13{1229}. **v:** PI 348435.
- Glu-B1at***{1229}. 13+18{1229}. **v:** PI 348449.
- Glu-B1au***{1032}. 37{1032}. **v:** Shedraya Polesja.
- Glu-B1av***{03116}. [*Glu-B1r*{03116}]. 7-18{03116}. **v:** Triticor hexaploid *triticales*{03116}.
- Glu-B1aw***{03116}. [*Glu-B1s*{03116}]. 6.8-20y{03116}. **v:** Carnac hexaploid *triticales*{03116}.
- Glu-B1ax***{03137}. [*Glu-B1-XV*{03137}]. XV{03137}. **tv:** PI-190922, BG-012302 emmers{03137}.
- Glu-B1ay***{03137}. [*Glu-B1-XVI*{03137}]. XVI{03137}. **tv:** PI 277681 emmer{03137}.
- Glu-B1az***{03137}. [*Glu-B1-XVII*{03137}]. XVII{03137}. **tv:** PI 348620 emmer{03137}.
- Glu-B1ba***{03122}. [*Glu-B1-XVIII*{03122}]. 13<sup>\*</sup>+16{03122}. **v:** PI 348767 spelt {03122}.
- Glu-B1bb***{03122}. [*Glu-B1-XLX*{03122}]. 6+18{03122}. **v:** PI 348631 spelt{03122}.
- Glu-B1bc***{03138}. 6+17{03138}. **v:** ICDW 20975{03138}.
- Glu-B1bd***{03140}. 20+8{03140}. **v:** Abadja{03140}.
- Glu-B1be***{10186}. **tv:** *T. dicoccoides* Israel-A{10186}.
- Glu-B1bf***{10186}. **tv:** *T. dicoccoides* PI 481521{10186}.
- Glu-B1bg***{10186}. **tv:** *T. dicoccoides* PI 478742{10186}.
- Glu-B1bh***{10327}. 13+22{10327}. **v:** Grado{10327}; KU-1026{10327}; KU-1086{10327}; KU-1094{10327}; KU-1139{10327}.
- Glu-B1bi***{10327}. 13+22.1{10327}. **v:** KU-1135{10327}.
- Glu-B1bj***{10327}. 14<sup>\*</sup>+15<sup>\*</sup>{10327}. **v:** TRI11553/92{10327}.
- Glu-B1bk***{10327}. [*Glu-B1be*{10327}]. 6.1+22.1{10327}. **v:** Hercule{10327}; Rouguin{10327}; Schwabenkorn{10327}; SP3{10327}; Steiners Roter Tiroler{10327}.
- Glu-B1bl***{10327}. [*Glu-B1bf*{10327}]. 6.1{10327}. **v:** KU-3418{10327}; KU-3446{10327}; TRI4613/75{10327}.

***Glu-B1bm***{10327}. [*Glu-B1bg*{10327}]. 13\*+19\*{10327}. **v:** KU-3410{10327}; Renva{10327}; Rechenbergs Fruher Dinkel{10327}; Schlegel{10327}; SP1{10327}; TRI9885/74{10327}; Zeiners WeiSer{10327}.

***Glu-B1bn***{10425}. 7+19{10425}. **v:** Triticales: Lasko, Dagno, Tewo, Vision, Dato{10425}.

***Glu-B1bo***{10425}. 7+26{10425}. **v:** Triticales: Presto, Modus{10425}.

The number 26 was also used to designate a subunit encoded by *Glu-A1k* and *Glu-A1-1k*.

The alleles formerly designated *t* to *x* in {959} were renamed *x* to *ab* because allele *t* in {847} and alleles *u*, *v* and *w* in {1069} had precedence. Subunit 8 of *Glu-B1b* (7+8) is more acidic in isoelectric focusing than subunit 8 of *Glu-B1d* (6+8) {555}. Variation in the mobility of subunits designated 7 has been observed {1118}, which accords with more recent observations {714,1069}. The subunit encoded by *Glu-B1v* {1069} has the same mobility as subunit 7 of *Glu-B1c* (7+9); it could be the same subunit as 7' encoded by *Glu-B1ai* [{714}].

Variation in the staining intensity of subunit 7 in different lines was observed {1069}; a duplication of the gene encoding subunit 7 probably occurred in cultivar 'Red River 68', as evidenced by increased intensity of the subunit in SDS-PAGE and by approximately doubled intensity of restriction fragments carrying the gene in Southern blotting {9989}. Possible low gene expression at *Glu-B1* was noted for *Glu-B1w*, where subunits 6\*+8\* stain very faintly {1146}.

One of the *Glu-B1af* subunits was numbered 26 in {1146}; 26 was previously used to number the subunit encoded by *Glu-A1k* {478}. Subunit 28 of *Glu-B1ag* (28+29) {1146} is referred to as subunit 19\* in {1068}. Subunit 23 of *Glu-B1p* {23+18} and *Glu-B1ad* (23+22) {125} may not be the same subunit as that numbered 23 of *Glu-B1l* {23+24} {778}. *Glu-B1z* carried by Roccia was numbered (7+15) and named *Glu-B1-XII* in {125}; however, the earlier name, *Glu-B1-IX* {1523}, has precedence; also, {1523} states that the *Glu-B1-IX* subunit of faster mobility is slightly slower than subunit 15. Subunit 11 of *Glu-B1s* {7+11} was so numbered in {478} because its mobility is the same as one of the subunits encoded by a *Glu-D1* allele (2+11) described in {755}.

Eight alleles at *Glu-B1-1* and 10 alleles at *Glu-B1-2* in *T. turgidum* var. *dicoccoides* populations were described in {798}. In a further study using different germplasm of this species {205}, 19 alleles at *Glu-B1* were observed, including 15 not previously observed; the 19 alleles included 11 alleles at *Glu-B1-1* and 14 alleles (including the null allele) at *Glu-B1-2*, although, as the authors pointed out, it was not conclusively clear how many of these alleles were distinct from each other, or from others previously observed.

In a study including emmer wheats (*T. dicoccon*) {00115}, new subunits named 7<sup>+</sup> (in accessions MG5400/5 and MG30835/1), 8<sup>-</sup> (in accessions MG5400/5, MG30835/1, MG5333/1 and MG5507) and 13<sup>-</sup> (in accession MG5282/2) were found and provisionally assigned to *Glu-B1*. Until confirmed, they are not included in the *Glu-B1* list.

Although alleles *Glu-B1i* encoding subunits 17+18, and *Glu-B1bc* encoding subunit 6+17, apparently share a common subunit (Ax17 and By17, respectively) it is not clear that this is in fact true.

Primers were designed to distinguish subunit By8 from By8\*, for distinguishing subunit By9-containing alleles from non-By9 alleles, and for diagnosing the presence of *Glu-B1f*.

***Glu-B1bp***{10643}. 7\*\*+8 {10643}. **v:** XM1368-2{10643}; XM1404-2{10643}.

***Glu-B1bq***{10643}. 7+8\*\* {10643}.

***Glu-B1br***{10807}. 7.1+7.2+8\*{10807}. **v:** H45{10807}.

***Glu-B1bs***{10807}. 7.3+7<sup>OE</sup>+8\*{10807}. **v:** VQ0437{10807}.

***Glu-B1bt***{10809}. 17'+18'{10809}. **tv:** TGR-214{10809}.

***Glu-B1bu***{10809}. 17'+18\*{10809}. **tv:** TGR-2246{10809}.

***Glu-B1bv***{10809}. 13\*\*+8\*{10809}. **tv:** TGR-003{10809}.

- Glu-B1bw**{10809}. 8'<sup>1</sup>{10809}. **tv**: TGR-244{10809}.
- Glu-B1bx**{10810}. 7+17{10810}. **v**: CWI-59797, *T. aestivum* var. *ferrugineum*{10810}.
- Glu-B1by**{10808}. 7b<sup>\*</sup>+8{10808}. **v**: Eshimashinriki{10808}.
- Glu-B1bz**{10808}. 7<sup>OE</sup>{10808}. **v**: Attila{10808}; Darius{10808}; Cappelle-Desprez{10808}; Festin{10808}; Petrel{10808}.
- Glu-B1ca**{10808}. 6+8b<sup>\*</sup>{10808}. **v**: Appolo{10808}; Brimstone{10808}; Clement{10808}; Nidera Baguette 10{10808}; Ruso{10808}; Pepital{10808}; Thesee{10808}.
- Glu-B1cb**{10808}. 7<sup>OE</sup>+8{10808}. **v**: ACA 303{10808}; Courtot{10808}; Demai 3{10808}; Shinchunaga{10808}.
- Glu-B1cc**{10808}. 7<sup>OE</sup>+8a<sup>\*</sup>{10808}. **v**: Klein Jabal 1{10808}; Pioneer{10808}; ProINTA{10808}; Redemon{10808}.
- Glu-B1cd**{10808}. 7<sup>OE</sup>+8b<sup>\*</sup>{10808}. **v**: ACA 601{10808}.
- Glu-B1ce**{10808}. 7+8a<sup>\*</sup>{10808}. **v**: Jing 411{10808}; Tasman{10808}.
- Glu-D1**{1100,1125}. [*Glt-D1*{420},*Glt-D2*{420},*Glu 1D*{1415}].  
1DL{107,150,780,1100,1125}. **v**: CS.  
Primers were designated that enabled Dx2 to be distinguished from Dx5 and Dy10 from Dy12 {10641}.
- Glu-D1a**{1116}. 2+12{1116}. **v**: CS.
- Glu-D1b**{1116}. 3+12{1116}. **v**: Hobbit.
- Glu-D1c**{1116}. 4+12{1116}. **v**: Champlein.
- Glu-D1d**{1116}. 5+10{1116}. **v**: Hope.
- Glu-D1e**{1116}. 2+10{1116}. **v**: Flinor (rare).
- Glu-D1f**{1116}. 2.2+12{1116}. **v**: Danchi (rare).  
*Glu-D1f* is present at high frequencies in wheats of southern Japan. Its presence may be associated with white salted noodle (Udon) quality {10573}.
- Glu-D1g**{478}. 5+9{478}. **v**: BT-2288.
- Glu-D1h**{1145}. 5+12{1145}. **v**: Fiorello, Italy.  
Note that the cultivar Fiorello is given as a standard for *Glu-D1h* encoding subunits 5+12 and for *Glu-D1w* encoding subunits 5<sup>\*</sup>+10. An attempt to resolve this apparent conflict will be made in a future update.
- Glu-D1i**{107}. null{107}. **v**: Nap Hal, Nepal.
- Glu-D1j**{1146}. 2+12<sup>\*</sup>{1146}. **v**: Tudest.
- Glu-D1k**{421}. 2{421}. **s**: CS/Timstein 1D.
- Glu-D1l**{759}. 12{759}. **v**: AUS 10037, Afghanistan.
- Glu-D1m**{759}. 10{759}. **v**: AUS 13673, Afghanistan.
- Glu-D1n**{759}. 2.1+10{759}. **v**: AUS 14653, Afghanistan.
- Glu-D1o**{755}. 2.1+13{755}. **v**: AUS 14519, *T. macha*.
- Glu-D1p**{1233}. 36{1233}. **i**: Iranian landrace accession 3048/5<sup>\*</sup> Sicco.
- Glu-D1q**{124}. 2+11{124}. **v**: Flinor.
- Glu-D1r**{1229}. 2.3+12{1229}. **v**: PI 348465.
- Glu-D1s**{1032}. 38{1032}. **v**: Leningradka.
- Glu-D1t**{668}. 43+44{668}. **i**: *Ae. tauschii* accession TA2450/2<sup>\*</sup>.
- Glu-D1u**{836}. 2+10'<sup>1</sup>{836}. **v**: Coker 68-15.
- Glu-D1v**{755}. 2.1+10.1{755}. **dv**: *Ae. tauschii*.
- Glu-D1w**{03124}. 5<sup>\*</sup>+10{03124}. **v**: Fiorello{03124}.
- Note that the cultivar Fiorello is given as a standard for *Glu-D1h* encoding subunits 5+12 and for *Glu-D1w* encoding subunits 5<sup>\*</sup>+10. An attempt to resolve this apparent conflict will be made in a future update.
- Glu-D1x**{755}. 2+T2{755}.2<sup>t</sup>+12.2<sup>t</sup>{03124}. **dv**: *Ae. tauschii*.
- Glu-D1y**{755}. 3+T2{755}.3<sup>t</sup>+12.2<sup>t</sup>{03124}. **dv**: *Ae. tauschii*.
- Glu-D1z**{755}. 3+10{755}. **dv**: *Ae. tauschii*.

- Glu-D1aa*{755}. 3+10.3{755}. **dv:** *Ae. tauschii*.  
*Glu-D1ab*{755}. 4.1+10{755}. **dv:** *Ae. tauschii*.  
*Glu-D1ac*{755}. 4+10{755}. **dv:** *Ae. tauschii*.  
*Glu-D1ad*{755}. 5.1+10.2{755}. **dv:** *Ae. tauschii*.  
*Glu-D1ae*{1578}. 2.1+T2{1578}. 2.1<sup>t</sup>+12.2<sup>t</sup>{03124}. **dv:** *Ae. tauschii*.  
*Glu-D1ag*{1578}. 1.5+T2{1578}. 1.5<sup>t</sup>+12.2<sup>t</sup>{03124}. **dv:** *Ae. tauschii*.  
*Glu-D1ah*{1578}. 1.5+10{1578}. **dv:** *Ae. tauschii*.  
*Glu-D1ai*{1578}. 2.1+10.5{1578}. **dv:** *Ae. tauschii*.  
*Glu-D1aj*{1578}. 1.5+12{1578}. **dv:** *Ae. tauschii*.  
*Glu-D1ak*{1578}. 3+10.5{1578}. **dv:** *Ae. tauschii*.  
*Glu-D1al*{02107}. 2.2<sup>\*</sup>{02107}. **v:** MG315.  
*Glu-D1am*{03122}. [*Glu-D1-I*{03122}]. 2+12<sup>t</sup>{03122}. **v:** PI 348495 spelt {03122}.  
*Glu-D1an*{03122}. [*Glu-D1-II*{03122}]. 2+12<sup>\*</sup>{03122}. **v:** PI 348672 spelt {03122}.  
*Glu-D1ao*{03122}. [*Glu-D1-III*{03122}]. 2.4+12{03122}. **v:** PI 348473 spelt {03122}.  
*Glu-D1ap*{03122}. [*Glu-D1-IV*{03122}]. 2.5+12{03122}. **v:** PI 348572 spelt {03122}.  
*Glu-D1aq*{03124}. 1.5<sup>t</sup>+10.1<sup>t</sup>{03124}. **dv:** *Ae. tauschii*.  
*Glu-D1ar*{03124}. 2<sup>t</sup>+10.1<sup>t</sup>{03124}. **dv:** *Ae. tauschii*.  
*Glu-D1as*{03124}. 1.5<sup>t</sup>+10.2<sup>t</sup>{03124}. **dv:** *Ae. tauschii*.  
*Glu-D1at*{03124}. 3<sup>t</sup>+10.1<sup>t</sup>{03124}. **dv:** *Ae. tauschii*.  
*Glu-D1au*{03124}. 2.1<sup>t</sup>+10.2<sup>t</sup>{03124}. **dv:** *Ae. tauschii*.  
*Glu-D1av*{03124}. 2<sup>t</sup>+12.3<sup>t</sup>{03124}. **dv:** *Ae. tauschii*.  
*Glu-D1aw*{03124}. 1<sup>t</sup>+10<sup>t</sup>{03124}. **dv:** *Ae. tauschii*.  
*Glu-D1ax*{03124}. 1<sup>t</sup>+12<sup>t</sup>{03124}. **dv:** *Ae. tauschii*.  
*Glu-D1ay*{03124}. 1<sup>t</sup>+10.1<sup>t</sup>{03124}. **dv:** *Ae. tauschii*.  
*Glu-D1az*{03124}. 4<sup>t</sup>+12.2<sup>t</sup>{03124}. **dv:** *Ae. tauschii*.  
*Glu-D1ba*{03124}. 1<sup>t</sup>+12.3<sup>t</sup>{03124}. **dv:** *Ae. tauschii*.  
*Glu-D1bb*{03124}. 1.5<sup>t</sup>+11<sup>t</sup>{03124}. **dv:** *Ae. tauschii*.  
*Glu-D1bc*{03124}. 1.5<sup>t</sup>+10.3<sup>t</sup>{03124}. **dv:** *Ae. tauschii*.  
*Glu-D1bd*{03124}. 1<sup>t</sup>+11<sup>t</sup>{03124}. **dv:** *Ae. tauschii*.  
*Glu-D1be*{03124}. 2.1<sup>t</sup>+12.4<sup>t</sup>{03124}. **dv:** *Ae. tauschii*.  
*Glu-D1bf*{03124}. 2<sup>t</sup>+12.1<sup>t</sup>{03124}. **dv:** *Ae. tauschii*{03124}.  
*Glu-D1bg*{03124}. 3<sup>t</sup>+10.2<sup>t</sup>{03124}. **dv:** *Ae. tauschii*.  
*Glu-D1bh*{03124}. 4<sup>t</sup>+10.1<sup>t</sup>{03124}. **dv:** *Ae. tauschii*.  
*Glu-D1bi*{03124}. 4<sup>t</sup>+10.2<sup>t</sup>{03124}. **dv:** *Ae. tauschii*.  
*Glu-D1bj*{03124}. 5<sup>t</sup>+11<sup>t</sup>{03124}. **dv:** *Ae. tauschii*.  
*Glu-D1bk*{03124}. 5<sup>t</sup>+10.1<sup>t</sup>{03124}. **dv:** *Ae. tauschii*.  
*Glu-D1bl*{03124}. 5<sup>t</sup>+12.2<sup>t</sup>{03124}. **dv:** *Ae. tauschii*.  
*Glu-D1bm*{03124}. 5<sup>\*t</sup>+null{03124}. **dv:** *Ae. tauschii*.  
*Glu-D1bn*{03124}. 5<sup>\*t</sup>+12{03124}. **dv:** *Ae. tauschii*.  
*Glu-D1bo*{10091}. 5'+12{10091}. **v:** W958{10091}.

This putative new allele encodes two subunits that have very similar electrophoretic mobilities compared to subunits 5+12 encoded by *Glu-D1h*, but analysis using the specific PCR primers for Dx5 described in {10092} and {10093} shows that the x-type subunit of *Glu-D1bo*, provisionally denominated 5' {10091}, does not appear to be the same protein as subunit 5 {10091}. Definitive evidence awaits sequencing information (See note to allele *Glu-D1-ls*).

*Glu-D1k* {421} appears to have arisen as the result of a deficiency of subunit 12 from *Glu-D1a* (2+12); subunits 2 and 12 are referred to as D1 and D5 in {421}. One of the *Glu-D1o* subunits has been numbered 13 in {755}; 13 was previously used to number a subunit encoded by *Glu-B1f* (13+16) and *Glu-B1g* (13+19) {1116}. Subunit 9 of *Glu-D1g* (5+9) was so numbered in {478} because its mobility is the same as one of the subunits encoded by *Glu-B1c* (7+9).

***Glu-D1bp***{10327}. 2.1<sup>1</sup>+12{10327}. **v:** KU-1034{10327}.

***Glu-D1bq***{10304}. [*Glu-D1bp(t)*]{10304}. 2.6+12{10304}. **v:** Baidongmai{10304}; Hongdongmai{10304}; Hongkedongmai{10304}; Jinbaojin{10304}.

The complete sequence of this subunit was determined {10319}.

***Glu-D1br***{10426}. 5\*t+10.1t{10426}. **tv:** *Ae. tauschii* TD81{10426}.

Subunit 10.1t possesses a mobility slightly lower than subunit 10 in SDS-PAGE and its deduced amino acid sequence is similar to subunit 12 (8 amino acid differences) {10426}; the authors used the complete coding sequence to make phylogenetic comparisons with 19 other subunits including both x-type and y-type subunits and concluded that *Glu-1* gene duplication event probably occurred about 16.83 million years ago.

Five combinations involving 6 HMW subunits [1D (p-t)] are listed in {420}. Eleven additional *Glu-D1* alleles in *T. tauschii* were described {755}.

Seven transfers of *Glu-D1a* and 10 of *Glu-D1d* (5+10) from chromosome 1D to chromosome 1A in triticale were described {846}.

The subunit 2.2\* encoded by *Glu-D1al* and *Glu-D1-1m* in the appropriate list below has an unusually high Mr. Comparison of its N-terminal sequence and amino acid composition with those of subunit 2 (encoded by *Glu-D1-1a*) indicated that its greater Mr could be due to the presence of a larger central repetitive domain, although further evidence suggested that this does not affect the conformational properties of the subunit {02107}. The alleles originally designated *Glu-D1w* (encoding 'subunits' 2 (or 2<sup>t</sup> denoting its origin in the *Ae. tauschii* genome) +T1+T2), *Glu-D1af* (encoding 3 (or 3<sup>t</sup>)+T1+T2) and *Glu-D1ag* (encoding 1.5 (or 1.5<sup>t</sup>)+T1+T2) share the component T1 that was originally classified as a HMW glutenin. However, it has since been shown {02108} that this protein is soluble in aqueous ethanol, casting doubt upon this classification. More recently, it was shown {02109}, from one and two dimensional gel electrophoresis based upon SDS-PAGE and A-PAGE, and from N-terminal sequencing, that this protein is an omega-gliadin of unusually low electrophoretic mobility in SDS-PAGE, encoded by a locus located on the short arm of chromosome 1D, though distant (13.18 cM) from the principle gliadin-encoding locus on 1D, *Gli-D1*, and 40.20 cM from the high molecular weight encoding locus, *Glu-D1*. The authors named the locus *Gli-DT1* (see Gliadins). Reference to T1 was consequently removed from the *Glu-D1* list. As a consequence of this finding, allele *Glu-D1w* was reused for a distinct allele, and *Glu-D1af* was omitted and will be reused for a future allele, since the combinations of subunits that these alleles originally represented are no longer unique.

In {03124}, null alleles were observed for both *Glu-D1-1* and *Glu-D1-2*, which, naturally, are not necessarily the same as those previously reported for this locus, meaning that composite alleles involving them in this study and corresponding to combinations apparently already listed in the Catalogue, may, in fact, represent novel alleles. It is also found that certain subunits of apparently identical relative mobility in SDS-PAGE showed different surface hydrophobicities in RP-HPLC; and the reverse situation was also observed (the same hydrophobicity, but different electrophoretic mobilities).

It was shown {03126} that the relatively small size of a y-type HMW glutenin subunit, named 12.4<sup>t</sup> (encoded by *Glu-D1-1t* {03124} - see below) and carried by accession CPI110750 of *Ae. tauschii*, is due to the deletion of blocks of repetitive motifs, amounting to approximately 200 amino acids, probably caused by unequal crossing-over.

Alleles and subunits at *Glu-A1-1* and *Glu-A1-2*: *Glu-A1-1* encodes X-type glutenins and *Glu-A1-2* encodes y-type glutenins.

***Glu-D1bs***{10642}. 1.6<sup>t</sup>+12.3<sup>t</sup> {10642}. **dv:** *Ae. tauschii* TD16{10642}.

***Glu-D1bt***{10568}. 2.1<sup>t</sup>+12<sup>t</sup> {10568}. **v:** Syn 396{10568}.

*Glu-D1bu*{10810}. 2'+12{10810}. v: CWI-64806, *T. aestivum* var. *aestivum*{10810}.

*Glu-D1bv*{10810}. 2"+10{10810}. v: CWI-65297, *T. aestivum* var. *erythroleucon*{10810}.

*Glu-D1bw*{10810}. 2"+12{10810}. v: CWI-60509, *T. aestivum* var. *graecum*{10810}.

#### *Glu-A1-1*.

*Glu-A1-1a*. Null. v: CS.

*Glu-A1-1b*. 1. v: Hope.

*Glu-A1-1c*. 2\*. v: Bezostaya 1.

A PCR marker specific for the *Glu-A1-1c* (Ax2\*) allele was developed in {0147}.

*Glu-A1-1d*. v: V74, Spain.

*Glu-A1-1e*. v: 132c, Poland.

*Glu-A1-1f*. v: 112-29, Sudan.

*Glu-A1-1g*. v: Landrace 1600.

*Glu-A1-1h*. tv: PI 94683, USSR, *T. dicoccum*.

*Glu-A1-1i*. tv: CI 12213, India, *T. dicoccum*.

*Glu-A1-1j*. 1'. tv: PI 352359, Germany, *T. dicoccum*; Lambro.

*Glu-A1-1k*. 26. v: BT-2288.

*Glu-A1-1l*. tv: Chinook, Canada.

*Glu-A1-1m*. tv: Nugget Biotype 1, Canada.

*Glu-A1-1n*. 1". tv: Corado, Portugal.

*Glu-A1-1o*. 2\*. tv: PI 61189, USSR, Aric 581/1.

*Glu-A1-1p*. 3\*. v: David 1.

*Glu-A1-1q*. 2\*\*\*. tv: Melianopus 1528.

*Glu-A1-1r*. 39. i: *T. thaouadar* IPSR 1020006/6\* Sicco.

*Glu-A1-1s*. 41. i: *T. thaouadar* G3152/6\* Sicco.

*Glu-A1-1t*{602}. 21\*{602}. v: W29323, W 3879, W 31169.

*Glu-A1-1t* is a provisional designation; definitive evidence that subunit 21\*, which has a mobility similar to that of subunit 21, is a 'x-type' and not a 'y-type' protein has not been obtained.

*Glu-A1-1u*{02106}. 2\*B{02106}. v: Bankuti 1201.

*Glu-A1-1v*{10327}. 2.1\*{10327}. v: Grado{10327}; KU-1026{10327}; KU-1086{10327}; KU-1094{10327}; KU-1139{10327}.

*Glu-A1-1w*{10327}. 2'{10327}. v: TRI14165/91{10327}.

*Glu-A1-1x*{10535}. 2''{10535}. v: 211.12014{10535}.

#### *Glu-A1-2*.

*Glu-A1-2a*. Null. v: CS.

*Glu-A1-2b*. 40. i: *T. thaouadar* IPSR1020006/6\* Sicco.

*Glu-A1-2c*. 42. i: *T. thaouadar* G3152/6\* Sicco.

#### *Glu-B1-1*.

*Glu-B1-1a*. 7. v: CS.

A PCR marker (2373 bp) for the *Glu-B1-1a* (Bx7) allele was developed in {0145}.

*Glu-B1-1b*. 7,7\*. v: Flinor, Bezostaya 1, Owens, Norstar.

*Glu-B1-1c*. 7'. v: Adonis.

*Glu-B1-1d*. 6. v: Hope.

*Glu-B1-1e*. 20. v: Federation.

*Glu-B1-1f*. 13. v: Lancota.

*Glu-B1-1g*. 14. v: Sappo.

*Glu-B1-1h*. 17. v: Gabo.

*Glu-B1-1i*. 21.21x{03116}. v: Dunav; Foison{03116}.

*Glu-B1-1j*. 23. v: Spica D.

*Glu-B1-1k*. tv: PI 94640, Iran, *T. dicoccum*.

*Glu-B1-1l*. tv: PI 355505, Germany, *T. dicoccum*.

- Glu-B1-1m.* tv: PI 352354, Ethiopia, *T. dicoccum*.  
*Glu-B1-1n.* tv: PI 94633, Morocco, *T. dicoccum*.  
*Glu-B1-1o.* v: Supreza, Canada.  
*Glu-B1-1p.* v: Mondor.  
*Glu-B1-1q.* tv: Canoco de Grao Escuro, Portugal.  
*Glu-B1-1r.* tv: Tremez Mollez, Portugal.  
*Glu-B1-1s.* tv: Quaduro, Italy.  
*Glu-B1-1t.* tv: Athena, Italy.  
*Glu-B1-1u.* 26. v: Cologne 1.  
*Glu-B1-1v.* 28. v: Forlani.  
*Glu-B1-1w.* Null. v: Olympic mutant.  
*Glu-B1-1x.* 30. v: Marinar.  
*Glu-B1-1y.* 32. v: BG-1943.  
*Glu-B1-1z.* 34. v: Jeja Almendros.  
*Glu-B1-1aa.* 37. v: Shedraya Polesja.  
*Glu-B1-1ab.* 6\*. v: Dawbill.  
*Glu-B1-1ac*{03116}. 6.8{03116}. v: Carnac hexaploid triticale{03116}.  
*Glu-B1-1ad*{03122}. 13\*{03122}. v: PI 348767 spelt {03122}.  
*Glu-B1-1ae*{10327}. 14\*{10327}. v: TRI11553/92{10327}.  
*Glu-B1-1af*{10327}. 6.1{10327}. v: Hercule{10327}; KU-3418{10327}; KU-3446{10327}; Rouguin{10327}; Schwabenkorn{10327}; SP3{10327}; Steiners Roter Tiroler{10327}; TRI4613/75{10327}.  
*Glu-B1-1ag*{10643}. 7\*\*{10643}. v: XM1368-2{10643}.  
*Glu-B1-1ah*{899}. 7<sup>OE</sup>{899}. v: Benkuti 1201{10196,10197}; Glenlea{899}; Klein Universal II{10196}; Tezanos Pintos Precoz{10196}; Tobari{10196}.  
*Glu-B1-1ai*{10807}. 7.1{10807}. v: H45{10807}.  
*Glu-B1-1aj*{10807}. 7.2{10807}. v: H45{10807}.  
*Glu-B1-1ak*{10807}. 7.3{10807}. v: VQ0437{10807}.  
*Glu-B1-1al*{10809}. 17\*{10809}. tv: TGR-214{10809}; TGR-2246{10809}.  
*Glu-B1-1am*{10809}. 13\*\*{10809}. tv: TGR-003{10809}.  
*Glu-B1-1an*{10808}. 7b\*{10808}. v: Eshimashinriki{10808}.
- Glu-B1-2.**
- Glu-B1-2a.* 8. v: CS.  
*Glu-B1-2b.* 9. v: Bezostaya 1.  
*Glu-B1-2c.* 16. v: Lancota.  
*Glu-B1-2d.* 19. v: NS 335.  
*Glu-B1-2e.* 15. v: Sappo.  
*Glu-B1-2f.* 18. v: Gabo.  
*Glu-B1-2g.* 22. v: Serbian.  
*Glu-B1-2h.* 24. v: Spica D.  
*Glu-B1-2i.* tv: PI 355505, Germany, *T. dicoccum*.  
*Glu-B1-2j.* tv: PI 352354, Ethiopia, *T. dicoccum*.  
*Glu-B1-2k.* tv: PI 94633, Morocco, *T. dicoccum*.  
*Glu-B1-2l.* 11. v: BT-2288.  
*Glu-B1-2m.* v: Supreza, Canada.  
*Glu-B1-2n.* v: Mondor.  
*Glu-B1-2o.* 8\*. v: Dawbull.  
*Glu-B1-2p.* tv: Canoco de Grao Escuro, Portugal.  
*Glu-B1-2q.* tv: Tremez Mollez, Portugal, *T. durum*.  
*Glu-B1-2r.* tv: Quaduro, Italy, *T. durum*.  
*Glu-B1-2s.* 18\*. v: David.  
*Glu-B1-2t.* 27. v: Cologne 1.

- Glu-B1-2u*. 29. **v**: Forlani.  
*Glu-B1-2v*. Null. **v**: Olympic mutant.  
*Glu-B1-2w*. 31. **v**: Marinar.  
*Glu-B1-2x*. 33. **v**: BG-1943.  
*Glu-B1-2y*. 35. **v**: Jeja Almendros.  
*Glu-B1-2z*{03116}. 20y{03116}. **v**: Carnac hexaploid triticale{03116}.  
*Glu-B1-2aa*{03122}. 18'<sup>1</sup>{03122}. **v**: PI 348631 spelt {03122}.  
*Glu-B1-2ab*{03116}. 21y{03116}. **v**: Foison{03116}.  
*Glu-B1-2ac*{10327}. 22\*<sup>1</sup>{10327}. **v**: Grado{10327}; KU-1026{10327}; KU-1086{10327}; KU-1094{10327}; KU-1139{10327}.  
*Glu-B1-2ad*{10327}. 22.1<sup>1</sup>{10327}. **v**: Hercule{10327}; KU-1135{10327}; Rouguin{10327}; Schwabenkorn{10327}; SP3{10327}; Steiners Roter Tiroler{10327}.  
*Glu-B1-2ae*{10327}. 15\*<sup>1</sup>{10327}. **v**: TRI11553/92{10327}.  
*Glu-B1-2af*{10327}. 19\*<sup>1</sup>{10327}. **v**: KU-3410{10327}; Rechenbergs Fruher Dinkel{10327}; Renval{10327}; SP1{10327}; TRI9885/74{10327}; Zeiners Weiser Schlegel{10327}.  
*Glu-B1-2ag*{10643}. [8\*<sup>1</sup>{10643}]. **v**: XM1404-2{10643}.  
*Glu-B1-2ai*{10809}. 8'<sup>1</sup>{10809}. **tv**: TGR-244{10809}.  
*Glu-B1-2aj*{10808}. 8a\*<sup>1</sup>{10808}. **v**: Jing 411{10808}; Pioneer{10808}; Tasman{10808}.  
*Glu-B1-2ak*{10808}. 8b\*<sup>1</sup>{10808}. **v**: ACA 601{10808}; Nidera Baguette 10{10808}.

#### *Glu-D1-1*.

- Glu-D1-1a*. 2. **v**: CS.  
*Glu-D1-1b*. 3. **v**: Hobbit.  
*Glu-D1-1c*. 4. **v**: Champlein.  
*Glu-D1-1d*. 5. **v**: Hope.  
 PCR markers specific for the *Glu-D1-1d* (Dx5) allele were developed in {0145} and {0147}.  
*Glu-D1-1e*. 2.2. **v**: Danchi.  
*Glu-D1-1f*. Null. **v**: Nap Hal, Nepal.  
*Glu-D1-1g*. 2.1. **v**: AUS 14653, Afghanistan.  
*Glu-D1-1h*. 2.3. **v**: PI 348465.  
*Glu-D1-1i*. 38. **v**: Leningradka.  
*Glu-D1-1j*{668}. 43{668}. **i**: *Ae. tauschii* accession TA2450/2\*.  
*Glu-D1-1k*{755}. 4.1{755}. **dv**: *Ae. tauschii*.  
*Glu-D1-1l*{1578}. 1.5{1578}.D<sup>1</sup>x1.5{10306}. **dv**: *Ae. tauschii* accession SQ-214{10306}.  
 A restriction enzyme based method named the 'restricted deletion method' was used to characterize the ORF of this subunit {10306} (as in the case of subunit D<sup>1</sup>y10 encoded by *Glu-D1-2u* {10306}). Allele-specific PCR markers were developed based upon SNPs located at the non-repetitive N-terminal {10320}.  
*Glu-D1-1m*{02107}. 2.2\*<sup>1</sup>{02107}. **v**: MG315.  
*Glu-D1-1n*{03122}. 2.4{03122}. **v**: PI 348473 spelt{03122}.  
*Glu-D1-1o*{03122}. 2.5{03122}. **v**: PI 3484572 spelt{03122}.  
*Glu-D1-1p*{03124}. 1<sup>1</sup>{03124}. **dv**: *Ae. tauschii*{03124}.  
*Glu-D1-1q*{03124}. 5\*<sup>1</sup>{03124}. **dv**: *Ae. tauschii*{03124}.  
*Glu-D1-1r*{755}. 5.1{755}. **dv**: *Ae. tauschii*.

This allele was designated *Glu-D1-1j* in the 1998 Catalogue edition.

- Glu-D1-1s*{10091}. 5'<sup>1</sup>{10091}. **v**: W958{10091}.

This putative allele encodes a subunit, provisionally denominated 5' {10091}, that has a very similar electrophoretic mobility compared to subunit 5 encoded by *Glu-D1-1d*, but analysis using the specific PCR primers for Dx5 described in {10092} and {10093} shows that it does not appear to be the same protein as subunit 5 {10091}. Definitive evidence awaits sequencing information (See note to allele *Glu-D1bo*).

*Glu-D1-It*{10304}. 2.6{10304}. **v:** Baidongmai{10305}; Jinbaojin{10305}; Hongdongmai{10305}; Hongkedongmai{10305}.

*Glu-D1-Iu*{10327}. 2.1<sup>1</sup>{10327}. **v:** KU-1034{10327}.

*Glu-D1-Iv*{10642}. [1.6<sup>1</sup>{10642}]. **dv:** *Ae. tauschii* TD16{10642}.

#### *Glu-D1-2.*

*Glu-D1-2a.* 12. **v:** CS.

A PCR marker (612 bp) for the *Glu-D1-2a* (Dy12) allele was developed in {0145}.

*Glu-D1-2b.* 10. **v:** Hope.

PCR markers (576 bp and 2176bp) for the *Glu-D1-2b* (Dy10) allele were developed in {0145} and {0147}, respectively.

*Glu-D1-2c.* 9. **v:** BT-2288.

*Glu-D1-2d.* Null. **v:** Nap Hal, Nepal.

*Glu-D1-2e.* 12\*. **v:** Tudest.

*Glu-D1-2f.* 13. **v:** AUS 14519, *T. macha*.

*Glu-D1-2g.* 36. **i:** Iranian landrace 3048/5\* Sicco.

*Glu-D1-2h.* 11. **v:** Flinor.

*Glu-D1-2i*{668}. 44{668}. **i:** *Ae. tauschii* TA2450/2\*.

*Glu-D1-2j*{836}. 10<sup>1</sup>{836}. **v:** Coker 68-15.

*Glu-D1-2k*{755}. T1{755}. **dv:** *Ae. tauschii*.

*Glu-D1-2l*{755}. T2{755}. **dv:** *Ae. tauschii*.

*Glu-D1-2m*{755}. 10.1{755}. **dv:** *Ae. tauschii*.

*Glu-D1-2n*{755}. 10.2{755}. **dv:** *Ae. tauschii*.

*Glu-D1-2o*{755}. 10.3{755}. **dv:** *Ae. tauschii*.

*Glu-D1-2p*{1578}. 10.5{1578}. **dv:** *Ae. tauschii*.

*Glu-D1-2q*{03122}. 12<sup>1</sup>{03122}. **v:** PI-348495 spelt wheat accession{03122}.

*Glu-D1-2r*{03124}. 12.1<sup>1</sup>{03124}. **dv:** *Ae. tauschii*.

*Glu-D1-2s*{03124}. 12.3<sup>1</sup>{03124}. **dv:** *Ae. tauschii*.

*Glu-D1-2t*{03124}. 12.4<sup>1</sup>{03124}. **dv:** *Ae. tauschii*.

*Glu-D1-2u*{10306}. D<sup>1</sup>y10{10306}. **v:** *Ae. tauschii* accession SQ-214{10306}.

A restriction enzyme based method named the 'restricted deletion method' was used to characterize the ORF of this subunit {10306} (as in the case of subunit 1.5 (or D<sup>1</sup>x1.5 {10306}) encoded by *Glu-D1-1l* {10306}). This subunit was first recognized as being different from subunit 1- encoded by *Glu-D1-2b* in hexaploid wheat in {10307}.

*Glu-Ag<sup>1</sup>I*{374}. 1Ag<sup>1</sup>{374}. **ad:** Vilmorin 27/*Th. intermedium*.

*Glu-EI*{781}. 1ES{781}. **ad:** CS/*E. elongata*.

HMW glutenin y-type subunit Ee1.5 encoded by this locus was sequenced {10439} and compared with other y-type subunits, particularly subunit 1Dy10. It has major deletions in its middle region and is one of the smallest known HMW glutenin subunits. It has an additional Cys residue in the middle of the repetitive domain, but lacks one Cys residue commonly found towards the end of this domain. These changes may influence inter- or intra-molecular disulphide bond formation.

Four {10660, 10661} and 11 {10662} alleles were observed in *Agropyron elongatum* (E<sup>°</sup> genome, 2n = 10X = 70) and named *Aex1* to *Aex5* (producing x-type subunits) and *Aey1* to *Aey10* (producing y-type subunits). *Aex4*, *Aey7* and *Aey9* were very similar to three alleles in the diploid progenitor *Lophopyrum elongatum* {10439, 10663}. The C-terminal regions of three of the y-type subunits (products of *Aey8*, *Aey9* and *Aey10*) were more similar to x-type subunits than to other y-type subunits {10662}. The subunit from *Aex4* contained an additional cysteine residue, which may be associated with good processing quality in wheat introgression lines {10662}. Allele *Aey-4* was a chimeric gene formed by recombination of two other genes {10662}.

*Glu-E1a*{781}. **ad:** CS/*L. elongatum* W0622{781}.

- Glu-E1b**{10644}. **ad**: Langdon/*L. elongatum* DGE-1{10644}. **al**: *L. elongatum* PI 531719{10644}.
- Glu-H1**{781}. [*Hor* 3{1337}]. 1H{781}.1HL{1337}. **ad**: CS/Betzes{781}. **al**: Various barley cultivars{1337}.
- Glu-H<sup>ch</sup>1**. 1H<sup>ch</sup>{1123}. **ad**: CS/*H. chilense*.  
38 accessions (natural populations) of *Hordeum chilense* carrying the following 10 subunits were used as the maternal parents of 121 lines of primary tritordeum, and evaluations for associations with bread-making quality initiated {03114}. Subunits 1<sup>Hch</sup>, 2<sup>Hch</sup> and 3<sup>Hch</sup> were previously referred to as H<sup>ch</sup>a, H<sup>ch</sup>b and H<sup>ch</sup>c {03112}.
- Glu-H<sup>ch</sup>1a**{03114}. 1<sup>Hch</sup>{03114}. **al**: *H. chilense* Accession H1{03114}.
- Glu-H<sup>ch</sup>1b**{03114}. 2<sup>Hch</sup>{03114}. **al**: *H. chilense* Accession H11{03114}.
- Glu-H<sup>ch</sup>1c**{03114}. 3<sup>Hch</sup>{03114}. **al**: *H. chilense* Accession H7{03114}.
- Glu-H<sup>ch</sup>1d**{03114}. 4<sup>Hch</sup>{03114}. **al**: *H. chilense* Accession H16{03114}.
- Glu-H<sup>ch</sup>1e**{03114}. 5<sup>Hch</sup>{03114}. **al**: *H. chilense* Accession H47{03114}.
- Glu-H<sup>ch</sup>1f**{03114}. 6<sup>Hch</sup>{03114}. **al**: *H. chilense* Accession H220{03114}.
- Glu-H<sup>ch</sup>1g**{03114}. 7<sup>Hch</sup>{03114}. **al**: *H. chilense* Accession H293{03114}.
- Glu-H<sup>ch</sup>1h**{03114}. 8<sup>Hch</sup>{03114}. **al**: *H. chilense* Accession H297{03114}.
- Glu-H<sup>ch</sup>1i**{03114}. 9<sup>Hch</sup>{03114}. **al**: *H. chilense* Accession H252{03114}.
- Glu-H<sup>ch</sup>1j**{03114}. 10<sup>Hch</sup>{03114}. **al**: *H. chilense* Accession H210{03114}.
- Glu-H<sup>L</sup>1**{1037}. 1H<sup>L</sup>{1037}. **ad**: CS/*E. trachycaulum*.
- Glu-R1**{781,1356}. [*Sec* 3{1336}]. 1R{781,1336}.1RL{1356,1340}. **ad**: CS/Imperial; Holdfast/ King II{1340}. **tr**: CS Imperial 1DS.1RL{1356}.
- Glu-R1a**{03116}. 1<sup>r</sup>-4<sup>r</sup>{03116}. **v**: Indiana hexaploid triticales{03116}.
- Glu-R1b**{03116}. 2<sup>r</sup>-6.5<sup>r</sup>{03116}. **v**: Graal hexaploid triticales{03116}.
- Glu-R1c**{03116}. 6<sup>r</sup>-13<sup>r</sup>{03116}. **v**: Almao hexaploid triticales{03116}.
- Glu-R1d**{03116}. 2<sup>r</sup>-9<sup>r</sup>{03116}. **v**: Olympus hexaploid triticales{03116}.
- Glu-R1e**{03116}. 6.5<sup>r</sup>{03116}. **v**: Clercal hexaploid triticales{03116}.
- Glu-R1f**{03115}. 0.8<sup>r</sup>-6<sup>r</sup>{03115}. **v**: Carmara hexaploid triticales{03115}.
- Glu-R1g**{03115}. 5.8<sup>r</sup>{03115}. **v**: Arrayan hexaploid triticales{03115}.

There is a difficulty in the assignment of subunit 6<sup>r</sup> in the *Glu-R1-1* and *Glu-R1-2* lists, since it appears as an x-type subunit in allele *Glu-R1c* and as a y-type subunit in allele *Glu-R1f*. It is currently provisionally assigned to the *Glu-R1-1* list since, based upon its relative electrophoretic mobility, it is considered more likely to be an x-type subunit. Some of the remaining designations should also be considered as provisional since they too are not free of ambiguity.

From study of chromosome substitutions in bread wheat {03117}, it was found that a chromosome 1R carrying HMW secalin subunit 6.5<sup>r</sup> (*Glu-R1e*), originally derived from the 'Petkus' rye population, was associated with bread making quality (i) intermediate between chromosome 1A carrying the null allele *Glu-A1c* and chromosome 1A carrying HMW glutenin subunit 2\* encoded by *Glu-A1b*; (ii) equivalent to a chromosome carrying HMW glutenin subunit 7 encoded by *Glu-B1a*; and (iii) inferior to chromosomes 1D with distinct alleles.

Five new x-type subunits (plus the null allele) and four y-type subunits were reported in {10094}. They vary principally through duplications and deletions of the tri-, hexa- and nona-peptide motifs found in the central repetitive region of the subunits. Orthologous genes were found to be more closely related than paralogous genes, supporting the hypothesis that gene duplication occurred before Triticeae speciation {10095, 10094}.

**Glu-R1-1.**

- Glu-R1-1a**{03116}. 1<sup>r</sup>{03116}. **v**: Indiana hexaploid triticales{03116}.
- Glu-R1-1b**{03116}. 2<sup>r</sup>{03116}. **v**: Graal hexaploid triticales{03116}.

- Glu-R1-1c*{03116}. 6<sup>r</sup>{03116}. **v**: Alamo hexaploid triticale{03116}.  
*Glu-R1-1d*{03115}. 0.8<sup>r</sup>{03115}. **v**: Carmara hexaploid triticale{03115}.  
*Glu-R1-1e*{03115}. 5.8<sup>r</sup>{03115}. **v**: Arrayan hexaploid triticale{03115}.  
***Glu-R1-2***. 1R, 1RL.  
*Glu-R1-2a*{03116}. 4<sup>r</sup>{03116}. **v**: Indiana hexaploid triticale{03116}.  
*Glu-R1-2b*{03116}. 6.5<sup>r</sup>{03116}. **v**: Graal hexaploid triticale{03116}.  
*Glu-R1-2c*{03116}. 13<sup>r</sup>{03116}. **v**: Alamo hexaploid triticale{03116}.  
*Glu-R1-2d*{03116}. 9<sup>r</sup>{03116}. **v**: Olympus hexaploid triticale{03116}.  
***Glu-R<sup>m</sup>1***{1339}. 1R<sup>m</sup>L{1339,1340}. **ad**: CS/*S. montanum*{1339,1340}.  
***Glu-S<sup>l</sup>1***{1228}. 1S<sup>l</sup>L{1228}. **ma**: In *Ae. longissima 2/Ae. longissima 10*, *Glu-S<sup>l</sup>1*, *Glu-S<sup>l</sup>3*, one glucose phosphate isomerase locus, and three gliadin loci were mapped relative to one and other {1228} as follows: *Glu-S<sup>l</sup>1* - 15.9 cM - *Gpi-S<sup>l</sup>1* - 38 cM - *Gli-S<sup>l</sup>4* - 7.1 cM - *Glu-S<sup>l</sup>3* - 0.9 cM - *Gli-S<sup>l</sup>1* - 5.6 cM - *Gli-S<sup>l</sup>5*. *Glu-S<sup>l</sup>1* is located in 1S<sup>l</sup>L and the other loci are in 1S<sup>l</sup>S.  
***Glu-UI***{150}. 1U{150,781}. **ad**: CS/*Ae. umbellulata* {150,781}.  
***Glu-VI***{111,242,1026}. 1V{1026,111}. **ad**: CS/*D. villosum*; Creso/*D. villosum*.  
*Glu-VIa*{1651}. 71{1651}. **al**: *D. villosum*.  
*Glu-VIb*{1651}. 72{1651}. **al**: *D. villosum*.  
*Glu-VIc*{1651}. 73{1651}. **al**: *D. villosum*.  
*Glu-VId*{1651}. 74{1651}. **al**: *D. villosum*.  
*Glu-VIe*{1651}. 75{1651}. **al**: *D. villosum*.  
*Glu-VIf*{1651}. 76{1651}. **al**: *D. villosum*.  
*Glu-VIg*{1651}. 77{1651}. **al**: *D. villosum*.  
*Glu-VIh*{1651}. 78{1651}. **al**: *D. villosum*.  
*Glu-VIi*{1651}. 79{1651}. **al**: *D. villosum*.  
*Glu-VIj*{1651}. 80{1651}. **al**: *D. villosum*.  
*Glu-VIk*{1651}. null{1651}. **al**: *D. villosum*.  
*Glu-VIl*{1651}. 81+82{1651}. **al**: *D. villosum*.  
*Glu-VIm*{1651}. 83+84{1651}. **al**: *D. villosum*.  
*Glu-VIn*{1651}. 85+86{1651}. **al**: *D. villosum*.

Alleles and subunits at *Glu-VI-1* and *GLU-VI-2* : The following is analogous to the *Glu-1-1* and *Glu-1-2* lists given earlier to identify x-type and y-type subunits in wheat. It was assumed that where an allele at *Glu-VI* produces only a single subunit, it is an x-type subunit and so encoded by *Glu-VI-1* rather than by *Glu-VI-2*; the electrophoretic mobilities of the subunits are all greater, though some only marginally so, than subunit 7 encoded by *Glu-B1-1a* (an x-type subunit), and extend beyond the mobility of subunit 12 encoded by *Glu-D1-2a* (a y-type subunit) {1651}; therefore, it is quite possible that any one of the subunits designated as encoded by *Glu-VI-1* is, in fact, encoded by *Glu-VI-2*. The designation given here is intended to be the most practically useful until the identities of the genes encoding the alleles are directly established.

***Glu-VI-1***.

- Glu-VI-1a*{1651}. 71{1651}. **al**: *D. villosum*.  
*Glu-VI-1b*{1651}. 72{1651}. **al**: *D. villosum*.  
*Glu-VI-1c*{1651}. 73{1651}. **al**: *D. villosum*.  
*Glu-VI-1d*{1651}. 74{1651}. **al**: *D. villosum*.  
*Glu-VI-1e*{1651}. 75{1651}. **al**: *D. villosum*.  
*Glu-VI-1f*{1651}. 76{1651}. **al**: *D. villosum*.  
*Glu-VI-1g*{1651}. 77{1651}. **al**: *D. villosum*.  
*Glu-VI-1h*{1651}. 78{1651}. **al**: *D. villosum*.  
*Glu-VI-1i*{1651}. 79{1651}. **al**: *D. villosum*.  
*Glu-VI-1j*{1651}. 80{1651}. **al**: *D. villosum*.  
*Glu-VI-1k*{1651}. null{1651}. **al**: *D. villosum*.  
*Glu-VI-1l*{1651}. 81{1651}. **al**: *D. villosum*.

**Glu-VI-1m**{1651}. 83{1651}. **al:** *D. villosum*.

**Glu-VI-1n**{1651}. 85{1651}. **al:** *D. villosum*.

#### **Glu-VI-2.**

**Glu-VI-2a**{1651}. null{1651}. **al:** *D. villosum*.

**Glu-VI-2b**{1651}. 82{1651}. **al:** *D. villosum*.

**Glu-VI-2c**{1651}. 84{1651}. **al:** *D. villosum*.

**Glu-VI-2d**{1651}. 86{1651}. **al:** *D. villosum*.

A Chinese cultivar of *T. aestivum*, Xiaoyanmai 7, carries a subunit with electrophoretic mobility in 10% SDS-PAGE well beyond that of subunits so far observed in *T. aestivum*. It may derive from *Agropyron elongatum*, which was used in the breeding programme that led to the variety {1538}. It has not been given a subunit number or allelic designation, because its genetic control has not been elucidated.

**Glu-Ta1**{10449}. **al:** *Taenitherum crinitum* PI 204577{10449}.

**Glu-Ta1a**{10449}. **al:** *Ta. crinitum* PI 204577{10449}.

**Glu-Ta1b**{10449}. **al:** *Ta. crinitum* PI 205590{10449}.

**Glu-Ta1c**{10449}. **al:** *Ta. crinitum* PI 561094{10449}; *Ta. asperum* PI 561091{10449}; PI 561092{10449}.

**Glu-Ta1d**{10449}. **al:** *Ta. caput-medusae* PI 598389{10449}.

**Glu-Ta1e**{10449}. **al:** *Ta. caput-medusae* PI 577708{10449}.

**Glu-Ta1f**{10449}. **al:** *Ta. caput-medusae* PI 577710{10449}.

Each allele identified to date encodes two subunits, an x-type and a y-type. The x-type subunits are slower or equal in mobility to subunit Dx2 of wheat, whereas the y-type subunits are faster than subunit Dx12 {10449}. Phylogenetic analysis based upon the sequence of two genes designated *Tax* and *Tay* isolated from *Ta. crinitum* PI 204577 suggest that the *Tax* subunit was most closely related to Ax1, Cx (*Ae. caudata*), Ux (*Ae. umbellulata*) and Dx5, and the *Tay* subunit to Ay, Cy and Ry (*Secale cereale*) {10449}.

### 82.3.1.2. Glu-2

**Glu-B2**{819,277}. [**XGlu-B2**{277}]. 1BS. **s:** CS\*/Cheyenne 1B{277}. **stv:** Langdon\*/*T. turgidum* var. *dicoccoides* 1B{277}.

**Glu-B2a**{00114}. 12{00114}. **tv:** Mexicali.

**Glu-B2b**{00114}. Null{00114}. **tv:** Langdon.

*Glu-B3* was designated *Glu-B2* {589} until the name of the locus was changed in {1119}.

**Glu-B2c**{10215}. 12\*{10215}. **tv:** Alcala la Real{10215}.

### 82.3.1.3. Glu-3

The *Glu-3* loci are defined as the cluster of LMW glutenin genes previously considered a component of the compound *Gli-1* loci.

More than 30 LMW glutenin complete genes, partial genes or pseudogenes have been sequenced from *Triticum* species (reviewed in {0245}).

In *T. aestivum*, only *Glu-B3* was shown to recombine with the gliadin genes (1.7 +/- 0.8) {1355,1358}. However, in *T. durum*, recombination was observed for both *Glu-A3* and *Glu-B3* with their respective *Gli-1* loci: the map distance between *Glu-A3* and *Gli-A1* has been estimated as 1.3 +/- 0.4 cM {1242}, and that between *Glu-B3* and *Gli-B1* as 2.0 +/- 0.8 in {1144} and as 2.0 +/- 0.4 in {1242}. It appears that *Glu-B3* is proximal to *Gli-B1*, and there is some evidence that *Glu-A3* is proximal to *Gli-A1* {1242}.

Whereas hitherto it was widely thought that all LMW glutenin subunits were encoded by genes located on the chromosomes of homoeologous group 1, it has been demonstrated that, although the majority of the subunits are indeed controlled by genes on this group, some of

the C subunits must be controlled by loci elsewhere in the genome {482}.

A novel type of polymeric protein ( $M_r$  approx. 71,000) was reported in the Australian advanced breeding line DD118 {03125}. It participates in the polymeric structure of glutenin (possibly as a chain terminator), and has an  $M_r$  of approximately 71,000, could be considered as a D-subunit of LMW glutenin. However, N-terminal sequencing suggests it to be a *Gli-B1* type omega-gliadin that has acquired a cysteine residue through mutation.

In an electrophoretic survey of 51 primary tritordeums {03113}, 20 distinct whole banding patterns (a-t), each consisting of between one and three bands, were observed for D-zone prolamins exhibiting glutenin-like solubility characteristics.

In 85 Japanese common wheat cultivars and 61 elite  $F_6$  breeding lines, 3 alleles were observed at each of *Glu-A3* and *Glu-B3*, and 2 alleles at *Glu-D3* were named according to their parental origins in three doubled haploid mapping populations {03135}.

C-type LMW glutenin subunits in CS were assigned to chromosome groups 1 and 6, and shown to have sequences very similar to those of alpha- and gamma-gliadins {03134}. The authors suggest that they may be encoded by novel genes at loci tightly linked or present within the *Gli-1* and *Gli-2* loci, unlike other LMW glutenin subunits encoded by the *Glu-3* loci.

The HMW and LMW glutenin subunits carried by chromosome 1A<sup>m</sup> of *T. monococcum* accession G1777 were characterised electrophoretically and evaluated for quality characteristics using recombinant chromosome substitution lines with chromosome 1A of CS {03142}. The HMW subunits from G1777 are promising for bread-making quality, whereas its LMW subunits are promising for biscuit-making quality.

The bread wheat cv. Salmone was shown to carry two DNA fragments designated as SF720 and SF750 located on the chromosome 1B satellite and associated with the presence of two LMW glutenin subunits {03143}. However, the authors suggest that they occur at a locus other than *Glu-B3* due to their relatively high frequency of recombination with *Gli-B3*.

A naming system in which Roman numerals are assigned to whole banding patterns for the LMW glutenin subunit is given in {03131} as an alternative to the LMW-1/-2 system described in {03136}. A further system naming whole banding patterns from LMW-1 to LMW-23 in emmer wheat is described in {03137}.

In {00111}, in a study of common and durum wheats from Portugal, the authors used the nomenclature system described in {00113} for the LMW subunits in common wheat, and that described in {00114} for the LMW subunits in durum wheat. The latter system was updated according to {02110}, but has been changed herein to new alleles with the earlier durum designation {00114} given as synonyms. In {03116}, it was suggested that *Glu-B3d* (common wheat standard genetic stock) is equivalent to *Glu-B3r* (durum wheat standard genetic stock), and that (referring to article {03127}) LMW subunits observed in some Portuguese triticales could be of the durum type.

A novel storage protein gene with chimeric structure was isolated from the old Hungarian cultivar Bankuti 1201, containing gamma-gliadin sequences in the 5' region, LMW-glutenin sequences in the 3' region and a frameshift mutation leading to a completely new polypeptide in the C-terminal region. A further seven recombinant prolamins were subsequently isolated. The eight genes, designated *Ch1* to *Ch8*, seem to derive from four gamma-gliadin and three LMW-glutenin sequences and are probably the result of crossing over between the

loci *Gli-1* and *Glu-3*. However, the precise recombinational mechanism that gave rise to them has yet to be elucidated {10307}.

***Glu-A3***{1358}. 1AS{1358}. **v:** CS.

The first 7 alleles were distinguished using 5 allele-specific primer sets {10185}. Further mainly Australian genotypes with alleles *a* to *f* are listed in {10185}.

***Glu-A3a***{481}. **v:** CS.

***Glu-A3b***{481}. **v:** Gabo.

***Glu-A3c***{481}. **v:** Cheyenne.

***Glu-A3d***{481}. **v:** Cappelle Desprez, Orca; Suneca{10185}.

***Glu-A3e***{481}. **v:** Halberd{10185}; Hope, Insignia.

***Glu-A3f***{481}. **v:** Rescue.

***Glu-A3g***{00113}. **v:** Glenlea{10185}.

***Glu-A3h***{00114,03116}. [***Glu-A3d'***{03116}]. Null{00114}. **v:** Magistral hexaploid triticales{03116}.

***Glu-A3i***{02110}. 8<sup>\*</sup>+11{02110}. **tv:** Mourisco Fino.

In 112 common wheat cultivars from Argentina, 11 microsatellite alleles plus a null allele were found at the *Glu-A3* locus {03123}.

***Glu-A3j***{00114}. [***Glu-A3a***{00114}]. 6{00114}. **tv:** Mexicali.

***Glu-A3k***{00114}. [***Glu-A3b***{00114}]. 5{00114}. **tv:** Langdon.

***Glu-A3l***{00114}. [***Glu-A3c***{00114}]. 6+10{00114}. **tv:** Cocorit.

***Glu-A3m***{00114}. [***Glu-A3d***{00114}]. 6+11{00114}. **tv:** Alaga.

***Glu-A3n***{00114}. [***Glu-A3e***{00114}]. 11{00114}. **tv:** Blatfort.

***Glu-A3o***{00114}. [***Glu-A3f***{00114}]. 6+11+20{00114}. **tv:** Clarofino.

***Glu-A3p***{00114}. [***Glu-A3h***{00114}]. Null{00114}. **tv:** Jiloca.

***Glu-A3q***{10215}. [***Glu-A3i***{10215}]. 5+20{10215}. **tv:** Fanfarron{10215}.

***Glu-A3r***{03116}. [***Glu-A3d'***{03116}]. **v:** Magistral hexaploid triticales{03116}.

***Glu-A3s***{00114}. [***Glu-A3g***{00114}]. 6+10+20{00114}. **tv:** Claro de Balazote{00114}.

***Glu-A3t***{10805}. [***Glu-A3<sup>m</sup>a***{10805}]. **dv:** PI 190947, *T. monococcum* ssp. *monococcum*{10805}.

***Glu-A3u***{10805}. [***Glu-A3<sup>m</sup>b***{10805}]. **dv:** PI 190946, *T. monococcum* ssp. *monococcum*{10805}.

***Glu-A3v***{10805}. [***Glu-A3<sup>m</sup>c***{10805}]. **dv:** BGE-020466, *T. monococcum* ssp. *monococcum*{10805}.

***Glu-A3w***{10805}. [***Glu-A3<sup>m</sup>d***{10805}]. **dv:** PI 191097, *T. monococcum* ssp. *monococcum*{10805}.

***Glu-A3x***{10805}. [***Glu-A3<sup>m</sup>e***{10805}]. **dv:** BGE-013624, *T. monococcum* ssp. *monococcum*{10805}.

***Glu-A3y***{10805}. [***Glu-A3<sup>m</sup>f***{10805}]. **dv:** PI 191094, *T. monococcum* ssp. *monococcum*{10805}.

***Glu-A3z***{10806}. [***Glu-A<sup>u</sup>3-I***{10806}]. **dv:** PI 428139, *T. urartu*{10806}.

***Glu-A3aa***{10806}. [***Glu-A<sup>u</sup>3-II***{10806}]. **dv:** PI 428327, *T. urartu*{10806}.

***Glu-A3ab***{10806}. [***Glu-A<sup>u</sup>3-III***{10806}]. **dv:** PI 428340, *T. urartu*{10806}.

***Glu-A3ac***{10806}. [***Glu-A<sup>u</sup>3-IV***{10806}]. **dv:** PI 428322, *T. urartu*{10806}.

***Glu-A3ad***{10806}. [***Glu-A<sup>u</sup>3-V***{10806}]. **dv:** PI 428188, *T. urartu*{10806}.

***Glu-A3ae***{10806}. [***Glu-A<sup>u</sup>3-VI***{10806}]. **dv:** PI 428203, *T. urartu*{10806}.

***Glu-A3af***{10806}. [***Glu-A<sup>u</sup>3-VII***{10806}]. **dv:** PI 428255, *T. urartu*{10806}.

***Glu-A3ag***{10806}. [***Glu-A<sup>u</sup>3-VIII***{10806}]. **dv:** PI 428328, *T. urartu*{10806}.

***Glu-A3ah***{10806}. [***Glu-A<sup>u</sup>3-IX***{10806}]. **dv:** PI 428256, *T. urartu*{10806}.

***Glu-A3ai***{10806}. [***Glu-A<sup>u</sup>3-X***{10806}]. **dv:** PI 428217, *T. urartu*{10806}.

***Glu-A3aj***{10806}. [***Glu-A<sup>u</sup>3-XI***{10806}]. **dv:** PI 428335, *T. urartu*{10806}.

***Glu-A3ak***{10806}. [***Glu-A<sup>u</sup>3-XII***{10806}]. **dv:** PI 428186, *T. urartu*{10806}.

***Glu-A3al***{10806}. [***Glu-A<sup>u</sup>3-XIII***{10806}]. **dv:** PI 428183, *T. urartu*{10806}.

*Glu-A3am*{10806}. [*Glu-A<sup>u</sup>3-XIV*{10806}]. **dv:** TRI 11563, *T. urartu*{10806}.  
*Glu-A3an*{10806}. [*Glu-A<sup>u</sup>3-XV*{10806}]. **dv:** PI 427328, *T. urartu*{10806}.  
*Glu-A3ao*{10806}. [*Glu-A<sup>u</sup>3-XVI*{10806}]. **dv:** PI 428253, *T. urartu*{10806}.  
*Glu-A3ap*{10806}. [*Glu-A<sup>u</sup>3-XVII*{10806}]. **dv:** PI 538735, *T. urartu*{10806}.  
*Glu-A3aq*{10806}. [*Glu-A<sup>u</sup>3-XVIII*{10806}]. **dv:** PI 428225, *T. urartu*{10806}.  
*Glu-A3ar*{10806}. [*Glu-A<sup>u</sup>3-XIX*{10806}]. **dv:** PI 538733, *T. urartu*{10806}.  
*Glu-A3as*{10806}. [*Glu-A<sup>u</sup>3-XX*{10806}]. **dv:** PI 428196, *T. urartu*{10806}.  
*Glu-A3at*{10806}. [*Glu-A<sup>u</sup>3-XXI*{10806}]. **dv:** PI 538724, *T. urartu*{10806}.  
*Glu-A3au*{10806}. [*Glu-A<sup>u</sup>3-XXII*{10806}]. **dv:** PI 428191, *T. urartu*{10806}.  
*Glu-A3av*{10806}. [*Glu-A<sup>u</sup>3-XXIII*{10806}]. **dv:** TRI 6734, *T. urartu*{10806}.  
*Glu-A3aw*{10806}. [*Glu-A<sup>u</sup>3-XXIV*{10806}]. **dv:** TRI 11496, *T. urartu*{10806}.  
*Glu-A3ax*{10116}. 6.1{10116}. **tv:** Buck Cristal{10116}.

The designation of this protein (subunit 6.1) as an allele of *Glu-A3* was deduced from its electrophoretic mobility and awaits confirmation through mapping studies.

*Glu-B3*{1358}. 1BS{1358}. **v:** CS.

*Glu-B3a*{481}. **v:** CS.

*Glu-B3b*{481}. **v:** Gabo, Timstein, Hope.

*Glu-B3c*{481}. **v:** Insignia, Halberd.

*Glu-B3d*{481}. **v:** Orca.

*Glu-B3e*{481}. **v:** Cheyenne.

*Glu-B3f*{481}. **v:** Radja.

*Glu-B3g*{481}. **v:** Kharkov, Bungulla.

*Glu-B3h*{481}. **v:** Thatcher, Rescue.

*Glu-B3i*{481}. **v:** Norin-61.

*Glu-B3j*{476,02110}. 4+6<sup>+</sup>+15+19{02110}. **tv:** Duramba-B, Duramba-D, Langdon; Mourisco Fino.

*Glu-B3k*{476,02110}. 8+9+13+16+19{02110}. **tv:** ALP-153, Dural, Durati, Edmore; Faisca.

*Glu-B3l*{476}. **tv:** Gionp-1954.

*Glu-B3m*{03120}. [*Glu-B3b'*{03120}]. **v:** Soissons{03120}.

*Glu-B3n*{03120}. [*Glu-B3c'*{03120}]. **v:** Courtot{03120}.

*Glu-B3o*{03116}. [*Glu-B3i'*{03116}]. **v:** Olympus hexaploid triticales{03116}.

*Glu-B3p*{03116}. [*Glu-B3k*{03116}]. **v:** Alamo hexaploid triticales{03116}.

*Glu-B3q*{03115}. [*Glu-B3h'*{03115}]. **v:** Torote hexaploid triticales{03115}.

*Glu-B3r*{00114}. [*Glu-B3a*{00114}]. 2+4+15+19{00114}. **tv:** Mexicali.

*Glu-B3s*{00114}. [*Glu-B3b*{00114}]. 8+9+13+16{00114}. **tv:** Langdon.

*Glu-B3t*{00114}. [*Glu-B3c*{00114}]. 2+4+14+15+19{00114}. **tv:** Jiloca.

*Glu-B3u*{00114}. [*Glu-B3d*{00114}]. 2+4+15+17+19{00114}. **tv:** Mundial.

*Glu-B3w*{00114}. [*Glu-B3f*{00114}]. 2+4+15+17{00114}. **tv:** Ardente.

*Glu-B3v*{00114}. [*Glu-B3e*{00114}]. 2+4+15+16+18{00114}. **tv:** Granja Badajoz.

*Glu-B3x*{00114}. [*Glu-B3g*{00114}]. 2+4+15+16{00114}. **tv:** Claro de Balazote.

*Glu-B3y*{00114}. [*Glu-B3h*{00114}]. 1+3+14+18{00114}. **tv:** Alaga.

*Glu-B3aa*{10215}. [*Glu-B3l*{10215}]. 1+3+13<sup>\*</sup>+16{10215}. **tv:** Blancal de Nules{10215}.

*Glu-B3ab*{10804}. **v:** Hope{10804}; Nanbukomugi{10804}.

*Glu-B3ac*{10804}. **v:** ACA 801{10804}; Klein Proteo{10804}; Thesee{10804}.

*Glu-B3ad*{10804}. **v:** AC Vista{10804}; Heilo{10804}; Opata85{10804}; Ruso{10804}.

*Glu-D3*{1358,707}. 1DS{707,1358}. **v:** CS.

Three different approaches were employed to identify putative SNPs used to design gene-specific primers for LMW-GS genes, and six functional STS markers, three for *Glu-B3* and three for *Glu-D3* {10664}. These markers distinguished cultivars with different haplotypes at the *Glu-B3* and *Glu-D3* loci, but there was no clear correlation between the alleles of

cultivars defined by protein electrophoretic mobility and the separation patterns of the DNA markers, since all three *Glu-3* loci were multiple gene loci and each protein electrophoretic mobility allele was controlled by 3-6 coding genes {10665}.

*Glu-D3a*{481}. v: CS.

*Glu-D3b*{481}. v: Gabo.

*Glu-D3c*{481}. v: Insignia, Cappelle Desprez.

*Glu-D3d*{481}. v: Jufy-1{10813}; Norin-61A.

*Glu-D3e*{481}. v: Orca, Thatcher.

*Glu-D3f*{10548}. v: Cheyenne{10548}.

*Glu-D3g*{10558}. v: Hira-1{10558}.

*Glu-D3h*{10558}. v: India 115{10558}.

*Glu-D3i*{10558}. v: Bolac{10558}.

*Glu-D3j*{10558}. v: Hira-2{10558}.

*Glu-D3k*{10558}. v: Lincoln{10558}.

*Glu-D3l*{10804}. v: Heilo{10804}; Jing411{10804}; Pepital{10804}; Thesee{10804}.

*Glu-D3m*{10804}. v: Darius{10804}.

*Glu-E3*{480}. 1ES{480}. su: CS/*E. elongata*.

*Glu-S<sup>1</sup>3*{480,1228}. 1S<sup>1</sup>{480}.1S<sup>1</sup>S{1228}. su: CS/*Ae. longissima*{480,1228}. ma: In *Ae. longissima* 2/*Ae. longissima* 10 glucose phosphate isomerase locus, and three gliadin loci were mapped relative to one another in {1228} as follows: *Glu-S<sup>1</sup>1* - 15.9 cM - *Gpi-S<sup>1</sup>1* - 38 cM - *Gli-S<sup>1</sup>4* - 7.1 cM - *Glu-S<sup>1</sup>3* - 0.9 cM - *Gli-S<sup>1</sup>1* - 5.6 cM - *Gli-S<sup>1</sup>5*. *Glu-S<sup>1</sup>1* is located in 1S<sup>1</sup>L and the other loci are in 1S<sup>1</sup>S.

*Glu-U3*{480}. 1U{480}. su: CS/*Ae. umbellulata*.

A series of papers {00106, 00107, 00108 and 00109} describe considerable variation in primitive wheats not present in bread wheat (A genome species *T. boeoticum*, *T. urartu*, *T. thaouadar*, *T. aegilopoides*, *T. monococcum*, and D-genome species *T. tauschii*) for the low molecular weight subunits, sufficient to use them as a source for potentially changing flour properties in bread wheat.

In {00110}, variants for LMW glutenin subunits were reported from study of twenty-four accessions of einkorn wheat (*T. monococcum* ssp. *monococcum*). Nine of these showed two electrophoretic bands for LMW subunits, arbitrarily designated 'a' and 'b', that appeared to be associated with good bread-making quality. The isolation of a new low-molecular-weight glutenin subunit gene, located on chromosome 1D, was reported in {0350}.

#### 82.3.1.4. *Glu-4*

The following loci, *Glu-D4* and *Glu-D5*, encoding low molecular weight subunits of glutenin (30-32 kDa) were described in {02111}; the proteins encoded by them were first observed earlier {02114, 02115}, and the former was later tentatively assigned the symbol *Glu-4* {02116}, before its chromosomal location was established and the locus definitively named as *Glu-D4* in {02111}. While this locus is located on chromosome 1D (in accordance with the position on the group 1 chromosomes of the remaining glutenin encoding loci found to date), the locus *Glu-D5* is located on chromosome 7D. In SDS-PAGE, the proteins from both loci are detected only in the presence of 4-vinylpyridine added to the sample extract. Their amino acid compositions do not match those of the major prolamins groups; nonetheless, they classify as glutenins based upon solubility, immunological behaviour and N-terminal amino acid sequence (the latter suggesting an evolutionary link with the major (B and C) low molecular weight glutenin subunits).

*Glu-D4*{02111}. 1D{02111}. su: CS/Langdon 1D(1A); CS/Langdon 1D(1B){02111}.

*Glu-D4a*{02111}. v: J 24.

*Glu-D4b*{02111}. v: PBW 154.

*Glu-D4c*{02111}. Null allele. **v**: NI 4.

#### 82.3.1.5. *Glu-5*

*Glu-D5*{02111}. 7D{02111}. **su**: CS/Langdon 7D(7A); CS/Langdon 7D(7B){02111}.

*Glu-D5a*{02111}. **v**: PBW 154.

*Glu-D5b*{02111}. Null allele. **v**: K 68.

A collection of 173 *Ae. tauschii* accessions were analysed for low molecular weight glutenin subunits by SDS-PAGE {02112}. Thirty three different patterns for B-subunits and 43 for C-subunits were identified, some of which were of identical electrophoretic mobility to those observed in common wheat. Also observed were subunits with the same mobilities as the D-subunits and as the subunits encoded by the *Glu-D4* and *Glu-D5* loci. This variation represents a source of novel germplasm of potential value for breeding programmes aimed at improving the D-genome of common wheat in the context of bread-making quality.

PCR amplification of genomic DNA was used to isolate three LMW glutenin genes in cultivar Chinese Spring, named LMWG-MB1, LMWG-MB2 and LMWG-MB3 {01101}. The deduced amino-acid sequences showed a high similarity between these ORFs and with those of other LMW glutenin genes. The authors state that the study provided direct evidence that insertions and/or deletions provide a mechanistic explanation for the allelic variation, and hence the resultant evolution, of prolamin genes, and comment on relationships with gamma-secalins and beta-hordein families. Single-base substitutions at identical sites generate premature stop codons in both LMWG-MB2 and LMWG-MB3, indicating that these clones are pseudogenes.

#### 82.3.2. Gliadins

These are heterogeneous mixtures of alcohol-soluble polypeptides without quaternary structure. The *Gli-1* loci are compound and are now considered to comprise the omega-gliadin and gamma gliadin {982,1415} multigene families {494}, which in some circumstances may be divided into *Gli-1-1* and *Gli-1-2*, respectively. The LMW glutenin multigene families, which are closely linked to the *Gli-1* loci {588}, are listed separately as the *Glu-3* set {1358}; information on map distance and gene order in relation to *Glu-3* and the centromere is given in the preamble for the *Glu-3* loci. There is evidence that a few of the omega-gliadin genes are separated from the main omega-gliadin gene cluster {993}. Variation at the *Gli-1* loci was described earlier {634,996,1126} and applied in mapping experiments {1243,1125,196,422,1120}. A rational system of naming the alleles was produced by Dr. E.V. Metakovsky{988}. This nomenclature is reproduced below. A considerable number of alleles were added to the original list given in {988}, and referenced here accordingly. A few alleles have been deleted, because, following much detailed comparison, there is now doubt that they can be reliably distinguished from existing alleles {9981}. The allelic letter in these cases has not been reused. To facilitate practical use of the list, the aim was to give at least three standard cultivars from a range of countries for each allele {9981}. This was achieved for the vast majority of entries and is a change from the original list compiled from {988}, where up to two standards were given. While the three or more standards described almost always include the original standards, some have been replaced for various reasons, such as international awareness of the cultivar, availability of seed, or the ease with which an allele can be identified in a particular genetic background {9981}. In the original list, where two cultivars were given as prototypes for an allele, the first named was from the USSR and the second from elsewhere; this is no longer the case, although care was taken to include a Russian cultivar where possible, to maintain a wide base of germplasm in which the alleles are available, as well as to acknowledge the research

groups in the country where much of the pioneering work was carried out.

For discussion of null alleles at the *Gli-1* and *Gli-2* loci, see {9984}.

Recombination was observed within the gliadin multigene family at *XGli-A1* {277}. These closely linked genes may correspond to *Gli-A1* and *Gli-A5*, but they were temporarily designated *XGli-A1.1* and *XGli-A1.2* until orthology with *Gli-A1* and/or *Gli-A5* is established.

Note: The catalogue entries reproduced here only refer to alleles in *T. aestivum*; there is, however, enormous variation in the gliadins in the close relatives of wheat; see, for example, {989} for studies in *T. monococcum* (more than 80 gliadin electrophoretic patterns observed in 109 accessions), {990} for studies in *T. boeoticum* (more than 50 electrophoretic patterns in 60 accessions), and {1076} studies in *T. durum* (19 electrophoretic patterns, referring only to variation in the omega-gliadins, in 243 accessions).

In {00110}, variants for omega-gliadins were reported from study of twenty-four accessions of einkorn wheat (*T. monococcum* ssp. *monococcum*). In {00111}, in a study of common wheat and durum from Portugal, the authors used the nomenclature system described in {00112} for the omega-gliadins. In {00116}, a comparison between spelt and common wheat was carried out for the gliadins using a nomenclature system described in {00118}.

The *Gli-I* loci may be recognised by probes pcP387 {372} and pTag1436 {065}, and by specific microsatellites primers {252}. Furthermore, it was shown that probe pTag1436 differentiates gliadin alleles rather well; using this probe, families of gliadin alleles and some of their relationships were described {9988}.

Twenty eight gamma-gliadin gene sequences from GenBank were grouped into nine subgroups in {10063}. Primers were developed against some of the subgroups and the chromosomal locations of the gamma-gliadin genes were determined {10063}.

Based upon morphological observation and RFLP analysis, it was proposed that the cultivar 'Chinese Spring' is a strain of the landrace 'Chengdu-guangtou' from the Chengdu Plain, Sichuan Province; this proposal is supported by the observation that CS and the landrace share the same alleles at all nine *Gli-1*, *Gli-2* and *Glu-1* loci {see 01102}.

PCR primers GAG5 and GAG6 were applied to 35 cultivars of closely related spelt and hexaploid wheat, and to eight cultivars of durum, to yield products originating from two gamma-gliadin genes mapped to chromosomes 1B (termed GAG56B) and 1D (termed GAG56D) {01103}. Two alleles for GAG56D (differing in a 9 bp deletion/duplication and single nucleotide polymorphism) were found, one a new allele and the other previously published {01104}. Meanwhile two alleles found for GAG56B among the durum wheats correlated with the presence of gluten quality markers, gamma-gliadins 42 or 45.

1B and 1D sulphur-poor omega-gliadins in cultivar Butte 86 were characterised by RP-HPLC, SDS-PAGE, two-dimensional PAGE, amino acid composition determination and sequencing, matrix assisted laser desorption ionisation-time of flight mass spectrometry and circular dichroism spectroscopy to reveal the detailed nature of the peptides belonging to the two groups, and showing that the complexity of mixtures of the peptides of the 1B group was greater than that of the 1D group {01105}. Although circular dichroism spectra were similar for the two groups of peptides, and suggested a mainly flexible random structure, there was evidence for a significant amount of left-handed polyproline II helical conformation in the case of the 1D components. The authors placed some of the results in the context of the possible ancestor of the B-genome and relationships with the barley C-hordeins and rye omega-secalins.

Eleven new gliadin alleles were found in a collection of 52 Spanish landraces of common wheat {03141}.

A new family of low-molecular-weight gliadin genes located on groups 4 and 7 were reported in {10117}. They appear to influence rheological properties and seem to be closely related to the 17kDa epsilon hordein, important in beer foam stability.

A novel storage protein gene with chimeric structure was isolated from the old Hungarian cultivar Bankuti 1201, containing gamma-gliadin sequences in the 5' region, LMW-glutenin sequences in the 3' region and a frameshift mutation leading to a completely new polypeptide in the C-terminal region. A further seven recombinant prolamin genes were subsequently isolated. The eight genes, designated *Ch1* to *Ch8*, seem to derive from four gamma-gliadin and three LMW-glutenin sequences and are probably the result of crossing over between the loci *Gli-1* and *Glu-3*. However, the precise recombinational mechanism that gave rise to them has yet to be elucidated {10307}.

Transcriptome analysis showed the presence of proteins called avenin-like a and b. The former contained a duplicated sequence of about 120 residues and corresponded to the LMW-gliadins. The latter was not previously characterized, but may form part of the glutenin fraction and hence influence quality. These avenin-like proteins showed higher expression levels in three *Aegilops* species (*Ae. caudata*, *Ae. cylindrica* and *Ae. tauschii*) than in common wheat {10321}.

### 82.3.2.1. Gli-1

*Gli-AI*{1334,1125}. [*Gld IA*{1415}]. 1AS{150,634,1334,1607}. s: CS\*/Cheyenne{634}.  
v: CS{150,1334,1607}.

*Gli-AIa*{988}. v: Castan{991}; CS{988}; Mara{9986}; Mentana{9986}; Millewa{00119}.

*Gli-AIb*{988}. v: Bezostaya 1, Mercia{988}; Tracy{991}.

*Gli-AIc*{988}. v: Ukrainka{998}; Gazul{9985}; Sava{994}; Hopps{00119}.

*Gli-AId*{988}. v: Dankowska{988}; Cabezorro{9985}.

*Gli-AIe*{988}. v: Falchetto{988}; Open{991}; Touzelle{991}.

*Gli-AIf*{988}. v: Mironovskaya 808, Maris Freeman{988}; Arminda{991}.

Note: An allele *Gli-AIf\** is mentioned in {03130}.

*Gli-AIg*{988}. v: Gabo{988}; Adalid{9985}.

*Gli-AIh*{988}. v: Sadovo I{988}; Predela{9981}; Krajinka{9981}.

*Gli-AIi*{988}. v: Saratovskaya 36{988}.

*Gli-AIj*{988}. v: Lutescens 62{988}.

*Gli-AIk*{988}. v: Courtot{991}; Skala (heterogeneous){988}; Soissons{991}; Spada{9986}.

*Gli-AIl*{988}. v: Lesostepka 75{988}; David{9986}; Salmone{9986}; Mura{9981}.

*Gli-AIm*{988}. v: Marquis{988}; Dneprovskaya 521{988}; Carat{991}; Liocorno{9986}.

*Gli-AIn*{988}. v: Intensivnaya{988}.

*Gli-AIo*{988}. v: Odesskaya 16 (heterogeneous){988}; Oderzo{9986}; Cappelle-Desprez{991}; Capitole{991}.

*Gli-AIp*{988}. v: Pyrotrix 28{988}; Zagore{9981}.

*Gli-AIq*{988}. v: Akmolinka 1{988}.

*Gli-AIr*{988}. v: Ranniaya 73{988}; Barbilla{9985}.

*Gli-AIs*.

Although reported {9986}, this gene is omitted because it requires further confirmation {9981}.

*Gli-AIt*{9985}. v: Jeja del Pais{9985}; Milturum 553{9981}; Strela{9981}.

*Gli-AIu*{9985}. v: Candéal Alcalá{9985}.

*Gli-AIv*{9981}. v: Japhet{9981}; Rouge de Bordeaux{9981}.

*Gli-AIw*{9984,9987}. null allele v: Saratovskaya 29 (mutant){9987}; E. Mottin{9981}.

- Gli-A1x**{10805}. [*Gli-A1<sup>m</sup>a*{10805}]. **dv**: PI 191146, *T. monococcum* ssp. *monococcum*{10805}.
- Gli-A1y**{10805}. [*Gli-A1<sup>m</sup>b*{10805}]. **dv**: PI 190947 *T. monococcum* ssp. *monococcum*{10805}.
- Gli-A1z**{10805}. [*Gli-A1<sup>m</sup>c*{10805}]. **dv**: PI 190946, *T. monococcum* ssp. *monococcum*{10805}.
- Gli-A1aa**{10805}. [*Gli-A1<sup>m</sup>d*{10805}]. **dv**: PI 191097, *T. monococcum* ssp. *monococcum*{10805}.
- Gli-A1ab**{10805}. [*Gli-A1<sup>m</sup>e*{10805}]. **dv**: BGE-020466, *T. monococcum* ssp. *monococcum*{10805}.
- Gli-A1ac**{10805}. [*Gli-A1<sup>m</sup>f*{10805}]. **dv**: BGE-013626, *T. monococcum* ssp. *monococcum*{10805}.
- Gli-A1ad**{10805}. [*Gli-A1<sup>m</sup>g*{10805}]. **dv**: BGE-013628, *T. monococcum* ssp. *monococcum*{10805}.
- Gli-A1ae**{10811}. [*Gli-A<sup>u</sup>I-I*{10811}]. **dv**: PI-428333, *T. urartu*{10811}.
- Gli-A1af**{10811}. [*Gli-A<sup>u</sup>I-II*{10811}]. **dv**: PI-428319, *T. urartu*{10811}.
- Gli-A1ag**{10811}. [*Gli-A<sup>u</sup>I-III*{10811}]. **dv**: PI-428335, *T. urartu*{10811}.
- Gli-A1ah**{10811}. [*Gli-A<sup>u</sup>I-IV*{10811}]. **dv**: PI-428323, *T. urartu*{10811}.
- Gli-A1ai**{10811}. [*Gli-A<sup>u</sup>I-V*{10811}]. **dv**: PI-428231, *T. urartu*{10811}.
- Gli-A1aj**{10811}. [*Gli-A<sup>u</sup>I-VI*{10811}]. **dv**: PI-428194, *T. urartu*{10811}.
- Gli-A1ak**{10811}. [*Gli-A<sup>u</sup>I-VII*{10811}]. **dv**: PI-428256, *T. urartu*{10811}.
- Gli-A1al**{10811}. [*Gli-A<sup>u</sup>I-VIII*{10811}]. **dv**: PI-428234, *T. urartu*{10811}.
- Gli-A1am**{10811}. [*Gli-A<sup>u</sup>I-IX* {10811}]. **dv**: PI-428320, *T. urartu*{10811}.
- Gli-A1an**{10811}. [*Gli-A<sup>u</sup>I-X*{10811}]. **dv**: PI-428255, *T. urartu*{10811}.
- Gli-A1ao**{10811}. [*Gli-A<sup>u</sup>I-XI*{10811}]. **dv**: PI-428241, *T. urartu*{10811}.
- Gli-A1ap**{10811}. [*Gli-A<sup>u</sup>I-XII*{10811}]. **dv**: PI-428235, *T. urartu*{10811}.
- Gli-A1aq**{10811}. [*Gli-A<sup>u</sup>I-XIII*{10811}]. **dv**: PI-428183, *T. urartu*{10811}.
- Gli-A1ar**{10811}. [*Gli-A<sup>u</sup>I-XIV*{10811}]. **dv**: PI-428317, *T. urartu*{10811}.
- Gli-A1as**{10811}. [*Gli-A<sup>u</sup>I-XV*{10811}]. **dv**: PI-427328, *T. urartu*{10811}.
- Gli-A1at**{10811}. [*Gli-A<sup>u</sup>I-XVI*{10811}]. **dv**: PI-428327, *T. urartu*{10811}.
- Gli-A1au**{10811}. [*Gli-A<sup>u</sup>I-XVII*{10811}]. **dv**: PI-428253, *T. urartu*{10811}.
- Gli-A1av**{10811}. [*Gli-A<sup>u</sup>I-XVIII*{10811}]. **dv**: PI-428224, *T. urartu*{10811}.
- Gli-A1aw**{10811}. [*Gli-A<sup>u</sup>I-XIX*{10811}]. **dv**: PI-538727, *T. urartu*{10811}.
- Gli-A1ax**{10811}. [*Gli-A<sup>u</sup>I-XX*{10811}]. **dv**: PI-428211, *T. urartu*{10811}.
- Gli-A1ay**{10811}. [*Gli-A<sup>u</sup>I-XXI*{10811}]. **dv**: PI-538724, *T. urartu*{10811}.
- Gli-A1az**{10811}. [*Gli-A<sup>u</sup>I-XXII*{10811}]. **dv**: PI-428191, *T. urartu*{10811}.
- Gli-A1ba**{10811}. [*Gli-A<sup>u</sup>I-XXIII*{10811}]. **dv**: TRI-6735, *T. urartu*{10811}.
- Gli-A1bb**{10811}. [*Gli-A<sup>u</sup>I-XXIV*{10811}]. **dv**: TRI-11494, *T. urartu*{10811}.
- Gli-A1bc**{10811}. [*Gli-A<sup>u</sup>I-XXV*{10811}]. **dv**: TRI-6734, *T. urartu*{10811}.
- Gli-A1bd**{10811}. [*Gli-A<sup>u</sup>I-XXVI*{10811}]. **dv**: TRI-11496, *T. urartu*{10811}.
- Gli-B1**{1607,1125}. [*Gld 1B*{1243,1415},*Gld-B1*{420},*Gld-B2*{420},*Gld-B3*{420},*Gld-B4*{420},*Gld-B5*{420},*Gld-B6*{420}]. 1B{1607}.1BS{150,634}. **s**: CS\*/Cheyenne{634}. **v**: CS{1607,150}.
- Gli-B1a**{988}. **v**: CS{988}.
- Gli-B1b**{988}. **v**: Bezostaya 1{988}; Carat{991}; Marquis{988}; Liocorno{9986}; Soissons{991}.
- Gli-B1c**{988}. **v**: Siete Cerros 66{988}; Prinqual{991}; Loreto{9986}.
- Gli-B1d**{988}. **v**: Dneprovskaya 521{988}; Chopin{991}; Petrel{991}; Tiberio{9986}; Yecora{9985}; Neepawa{995}; Suneca{00119}.
- Gli-B1e**{988}. **v**: Apexal{991}; Fournil{991}; Lutescens 62{988}; Oderzo{9986}.
- Gli-B1f**{988}. **v**: Capitole{991}; Cappelle-Desprez{991}; Dankowska{988}; Maris Freeman{988}; Mercia{988}.

- Gli-BIg**{988}. v: Champstal{991}; Galahad{988}; Mara{9986}; Sadovo 1{988}; Tracy{991}.
- Gli-BIh**{988}. v: Cabezorro{9985}; Krasnodonka{988}; Pepital{991}; Rudi{991}Tincurrin{00119}.
- Gli-BIi**{988}. v: Ghurka{988}; Insignia{988}.
- Gli-BIj**{988}. v: Cluj 650{988}.
- Gli-BIk**{988}. v: Crverkapa{994}; De Carolis{9986}; Kremena{988}; Mentana{9986}.
- Gli-BIl**{988}. v: Avrova{9981}; Clement{991}; Damier{991}; Fiocco{9986}; Kavkaz{9981}.
- Gli-BIl* encodes secalins associated with the 1BL.1RS translocation.
- Gli-BIm**{988}. v: Costantino{9986}; Et.d'Choisy{991}; Pyrotrix 28{988}.
- Gli-BIn**{988}. v: Intensivnaya{988}.
- Gli-BIo**{988}. v: Aragon 03{9985}; Levent{988}; Pippo{9986}; San Rafael{9985}.
- Gli-BIp**{988}. v: Inia 66{9985}; New Pusa 834{988}.
- Gli-BIq**{9986}. v: Gallo{9986}; Goelent{991}; Goya{991}.
- Gli-BIr**{995}. v: Chinook{995}; Gazul{9985}; Sevillano{9985}.
- Gli-BIs**{9986}. v: Salmone{9986}; Resistente{9986}; E.Mottin{9981}.
- Gli-BIt**{9985}. v: Jeja del Pais{9985}.
- Gli-BIu**{9985}. v: Negrillo{9985}.
- Gli-BIv**{9985}. v: Montjuich{9985}.
- Gli-BIw**{9981}. v: Ardica{9981}; Barbilla (MCB-1017){9981}.
- Gli-BIx**{9984,9987,991}. Null allele v: Touzelle{991}; Florence Aurora{9985}.
- In 112 bread wheat cultivars from Argentina, 12 microsatellite alleles plus a null allele were found at the *Gli-BI* locus tightly linked to *Glu-B3* {03123}.
- Gli-DI**{121,1125}. [*Gld 1D*{1415},*Gld-D1*{420},*Gld-D2*{420},*Gld-D3*{420}]. 1DS{121,150,634,1334,1607}. s: CS\*/Cheyenne{634}. v: CS{121,150,1334,1607}.
- Gli-DIa**{988}. v: CS{988}; Marquis{988}; Mentana{9986}; Prinqual{991}; Saratovskaya 36{988}.
- Gli-DIb**{988}. v: Bezostaya 1{988}; Cappelle-Desprez{991}; Etoile d'Choisy{991}; Galahad{988}.
- Gli-DIc**{988}. v: Skorospelka Uluchshennaya (biotype){988,9982}.
- Gli-DId**{988}. v: De Carolis{9986}; Solo{988}.
- Gli-DIe**{988}. v: Gerek 79{988}.
- Gli-DIf**{988}. v: Carlos{991}; Gabo{988}; Maris Freeman{988}; Orso{9986}.
- Gli-DIg**{988}. v: Fournil{991}; Ghurka{988}; Mironovskaya 808{988}; Open{991}.
- Gli-DIh**{988}. v: Sadovo I{988}; Zlatostrui{9981}.
- Gli-DIi**{988}. v: Insignia{988}; Napayo (biotype){995}; San Rafael{9985}; Tselinogradka{988}.
- Gli-DIj**{988}. v: Aubain{991}; Chinook{995}; Inia 66{9985}; Petrel{991}; Promin{988}.
- Gli-DIk**{988}. v: Cargimarec{991}; Kremena{988}; Mara{9986}; Pippo{9986}.
- Gli-DIl**{988}. v: Artaban{991}; Corin{991}; Longbow{988}.
- Gli-DIm**{991}. v: Heurtebise{991}.
- Gli-DIn**{981}. v: Blanquillo de Toledo (MCB-0950){9981}.
- Gli-DIo**{9984,9987,991}. Null allele v: Darius{991}; Touzelle{991}; Saratovskaya 29 (mutant){9987}.

**Gli-Ag<sup>i</sup>1**. 1Ag<sup>i</sup>{168}. ad: Vilmorin 27/*Th. intermedium*.

**Gli-DT1**{02109}. 1DS{02109}. v: L/18913 (synthetic). dv: *Ae. tauschii* AUS18913.

A locus designated *Gli-DT1* controlling an omega-gliadin of *Ae. tauschii* was mapped on the short arm of chromosome 1D between loci *Gli-D1* (strictly *Gli-D<sup>1</sup>I*) and *Glu-D1* (strictly *Glu-D<sup>1</sup>I*), 13.18 cM proximal to the former and 40.20 cM from the latter {02109}. The only omega-gliadin to date identified as being encoded by this locus, namely T1, is of unusually low electrophoretic mobility in SDS-PAGE gels and was formally thought to be a high

molecular weight glutenin encoded by the *Glu-D<sup>1</sup>* locus of *Ae. tauschii* (see note following the *Glu-D1* list in section 'Glutenins'). The authors speculate that, due to their similar relative map positions, the loci *Gli-A4*, *Gli-D4*, *Gli-R3*, *Gli-S<sup>4</sup>* and this locus, *Gli-DT1*, form a series of 'Gli-4' orthologous loci. However, this should be interpreted in the light of the above discussion on *Gli-A3* and *Gli-A4*.

A 1,200 bp Dra I RFLP was identified as a gene-specific probe for the T1 omega-gliadin {10645}.

**Gli-DT1a**{02109}. T1. **v**: L/18913 (synthetic). **dv**: *Ae. tauschii* AUS18913.

**Gli-E1**{781}. 1ES{781}. **ad**: CS/*E. elongata*.

**Gli-H<sup>1</sup>**{1037}. 1H<sup>1</sup>p{1037}. **ad**: CS/*E. trachycaulum*.

**Gli-R1**{1334}. [*SecR1*{1356},*Sec1*{1336}]. 1RS{781,1334,1336,1340}. **ad**: CS/Imperial{781,1334,1336,1340}; Holdfast/King II{1334,1340}. **tr**: CS 1DS. Imperial 1RL{1356}.

*Sec-12* and *Sec13* are given as allelic alternatives in 1BL.1RS translocation lines by {03132}.

**Gli-R<sup>m</sup>1**{1340}. 1R<sup>m</sup>S{1340}. **ad**: CS/*S. montanum*.

**Gli-S<sup>1</sup>**{573}. 1S<sup>1</sup>{573}. **ad**: CS/*Ae. longissima*.

**Gli-UI**{1335}. 1U{1335,150}. **ad**: CS/*Ae. umbellulata*.

**Gli-VI**{1026,111}. 1V{1026,111}. **ad**: CS/*D. villosum*{1026}; Creso/*D. villosum*{111}.

In barley, the B and C hordeins are controlled by the *Hor2* and *Hor1* loci, respectively, which are linked {1341} on chromosome 1HS {1063,1153}. The map distances and homology of the proteins indicate that *Hor1*, the locus closest to the centromere, is equivalent to the omega-gliadins (*Gli-1-1*) in *Gli-1* {1338}.

Three alleles at each of the *Gli-1-1* (omega gliadin) loci were noted {1358}. The complexity of the *Gli-1* compound loci is further emphasized by a report of individual genes being separable by recombination, where *Gld-1A* (a block of gamma and omega genes) is separable by 0.3% from *Gld4-1A* (omega gliadins) which is in turn, separable by 1.5% from *Gld3-1A* (omega gliadins) {1103}.

Elsewhere, variation was described {634,996,1126} and applied in mapping experiments {107,196,422,1120,1125,1243}. Sixteen combinations of *Gli-B1* and 4 combinations of *Gli-D1* subunits are listed in {420}. Multiple alleles described in {996}, number 15 at *Gli-A1*, 18 at *Gli-B1*, and 8 at *Gli-D1*.

The *Gli-1* alleles present in 57 Yugoslav wheat varieties were reported in {994}.

### 82.3.2.2. Gli-2

**Gli-A2**{1334,1125}. [*Gld 6A*{1415}]. 6A{1334}.6AS{1122}. **v**: CS.

**Gli-A2a**{988}. **v**: Cabezorro{9985}; CS{988}; Insignia{988}; Rieti DIV{9986}.

**Gli-A2b**{988}. **v**: Aradi{9985}; Bezostaya 1{988}; Rivoli{991}; Tiberio{9986}.

**Gli-A2c**{988}. **v**: Eagle{00119}; Escualo{9985}; Loreto{9986}; Prinqual{991}; Siete Cerros 66{988}.

**Gli-A2d**{988}. **v**: Dneprovskaya 521{988}; Kenyon (biotype){995}; Mocho Sobarriba{9985}.

**Gli-A2e**{988}. **v**: Cobra{991}; Mentana{9986}; Resistente{9986}; Sadovo 1{988}; Sevillano{9985}.

**Gli-A2f**{988}. **v**: Adalid{9985}; Gala{991}; Maris Freeman{988}; Sistar{9986}.

**Gli-A2g**{988}. **v**: Cappelle-Desprez{991}; Ducat{988}; Mahissa 1{9985}; Mara{9986}.

**Gli-A2h**{988}. **v**: Apollo{991}; Basalt{9981}; Hereward{988}; Montjuich{9985}; N. Strampelli{9986}.

**Gli-A2i**{988}. **v**: Krasnodonka{988}; Lesostepka 75{988}.

**Gli-A2j**{988}. **v**: Avalon{9981}; Camp Remy{991}; E. Mottin{9981}; Recital{991}.

**Gli-A2k**{988}. **v**: Akmolinka 1{988}; Estica{991}; Pyrotrix 28{988}; Renan{991}; Zena{9986}.

- Gli-A2l*{988}. v: Chamorro{9985}; Champlain{991}; Longbow{988}.
- Gli-A2m*{988}. v: Marquis{988}; Rex{991}; Suneca{00119}.
- Gli-A2n*{988}. v: Mironovskaya 808{988}.
- Gli-A2o*{988}. v: Calatrava{9985}; Castan{991}; Glenwari{9981}; Lontra{9986}; Touzelle{991}.
- Gli-A2p*{988}. v: Cajeme 71{9985}; Capitole{991}; Clement{991}; Pliska{988}; S. Lorenzo{9986}; Yecora 70{9985}.
- Gli-A2q*{988}. v: Candeal Alcala{9985}; Montcada{9985}; Saratovskaya 39{988}.
- Gli-A2r*{988}. v: Genial{991}; Open{991}; Riband{988}.
- Gli-A2s*{988}. v: Saratovskaya 36{998}.
- Gli-A2t*{988}. v: Courtot{991}; Prostor{9981}; Rinconada{9985}; Soissons{991}.
- Gli-A2u*{988}. v: Aragon 03{9985}; Kirgizskaya Yubileinaya{988}; Saunders{995}; Titien{991}.
- Gli-A2v*{988}. v: Kzyl-Bas{988}.
- Gli-A2w*{988}. v: Bezenchukskaya 98 (biotype){988}.
- Gli-A2x*{988}. v: Solo{988}.
- Gli-A2y*{9981}. v: Gentil Rosso 202{9981}; PI 191245{9981}.
- Gli-A2z*{9986}. v: Gallo{9986}; Giuliana{9986}.
- Gli-A2aa*{9985}. v: Navarro 122{9985}.
- Gli-A2ab*{9985}. v: Navarro 150{9985}.
- Gli-A2ac*{9981}. v: Blanquillo de Barcarrota (MCB-0893){9981}.
- Gli-A2ad*{9981}. v: Hembrilla Soria (MCB-1298){9981}.
- Gli-A2ae*{9981}. v: Candeal de S.Lorenzo Parrilla (MCB-0932){9981}.
- Gli-A2af*{9981}. v: Barbilla de Leon (MCB-1292){9981}.
- Gli-A2ag*{9981}. v: Gluclub{9981}; Tincurrin{9981}.
- Gli-A2ah*{9981}. v: Candeal de Nava del Rey (MCB-0892){9981}.
- Gli-A2ai*{9981}. v: Blanquillo (MCB-0908){9981}.
- Gli-A2aj*{9984,9987}. null allele v: Saratovskaya 29 (mutant){9987}.
- Gli-A2ak*{10805}. [*Gli-A2<sup>m</sup>a*{10805}]. dv: BGE-013630, *T. monococcum* ssp. *monococcum*{10805}.
- Gli-A2al*{10805}. [*Gli-A2<sup>m</sup>b*{10805}]. dv: PI 094740, *T. monococcum* ssp. *monococcum*{10805}.
- Gli-A2am*{10805}. [*Gli-A2<sup>m</sup>c*{10805}]. dv: PI 190942, *T. monococcum* ssp. *monococcum*{10805}.
- Gli-A2an*{10805}. [*Gli-A2<sup>m</sup>d*{10805}]. dv: PI 190947, *T. monococcum* ssp. *monococcum*{10805}.
- Gli-A2ao*{10805}. [*Gli-A2<sup>m</sup>e*{10805}]. dv: PI 190946, *T. monococcum* ssp. *monococcum*{10805}.
- Gli-A2ap*{10805}. [*Gli-A2<sup>m</sup>f*{10805}]. dv: BGE-013626, *T. monococcum* ssp. *monococcum*{10805}.
- Gli-A2aq*{10805}. [*Gli-A2<sup>m</sup>g*{10805}]. dv: PI 191095, *T. monococcum* ssp. *monococcum*{10805}.
- Gli-A2ar*{10805}. [*Gli-A2<sup>m</sup>h*{10805}]. dv: BGE-001937, *T. monococcum* ssp. *monococcum*{10805}.
- Gli-A2as*{10805}. [*Gli-A2<sup>m</sup>i*{10805}]. dv: PI 191096, *T. monococcum* ssp. *monococcum*{10805}.
- Gli-A2at*{10805}. [*Gli-A2<sup>m</sup>j*{10805}]. dv: BGE-020466, *T. monococcum* ssp. *monococcum*{10805}.
- Gli-A2au*{10805}. [*Gli-A2<sup>m</sup>k*{10805}]. dv: BGE-001937, *T. monococcum* ssp. *monococcum*{10805}.
- Gli-A2av*{10805}. [*Gli-A2<sup>m</sup>l*{10805}]. dv: BGE-029108, *T. monococcum* ssp. *monococcum*{10805}.

- Gli-A2aw*{10805}. [*Gli-A2<sup>m</sup>m*{10805}]. **dv**: BGE-013627, *T. monococcum* ssp. *monococcum*{10805}.
- Gli-A2ax*{10805}. [*Gli-A2<sup>m</sup>n*{10805}]. **dv**: BGE-001937, *T. monococcum* ssp. *monococcum*{10805}.
- Gli-A2ay*{10811}. [*Gli-A<sup>u</sup>2-I*{10811}]. **dv**: PI-428333, *T. urartu*{10811}.
- Gli-A2az*{10811}. [*Gli-A<sup>u</sup>2-II*{10811}]. **dv**: PI-428320, *T. urartu*{10811}.
- Gli-A2ba*{10811}. [*Gli-A<sup>u</sup>2-II*{10811}]. **dv**: PI-428230, *T. urartu*{10811}.
- Gli-A2bb*{10811}. [*Gli-A<sup>u</sup>2-IV*{10811}]. **dv**: PI-428319, *T. urartu*{10811}.
- Gli-A2bc*{10811}. [*Gli-A<sup>u</sup>2-V*{10811}]. **dv**: PI-428239, *T. urartu*{10811}.
- Gli-A2bd*{10811}. [*Gli-A<sup>u</sup>2-VI*{10811}]. **dv**: PI-428336, *T. urartu*{10811}.
- Gli-A2be*{10811}. [*Gli-A<sup>u</sup>2-VII*{10811}]. **dv**: PI-428235, *T. urartu*{10811}.
- Gli-A2bf*{10811}. [*Gli-A<sup>u</sup>2-VIII*{10811}]. **dv**: PI-428234, *T. urartu*{10811}.
- Gli-A2bg*{10811}. [*Gli-A<sup>u</sup>2-IX*{10811}]. **dv**: PI-428183, *T. urartu*{10811}.
- Gli-A2bh*{10811}. [*Gli-A<sup>u</sup>2-X*{10811}]. **dv**: PI-428256, *T. urartu*{10811}.
- Gli-A2bi*{10811}. [*Gli-A<sup>u</sup>2-XI*{10811}]. **dv**: PI-428255, *T. urartu*{10811}.
- Gli-A2bj*{10811}. [*Gli-A<sup>u</sup>2-XII*{10811}]. **dv**: PI-428224, *T. urartu*{10811}.
- Gli-A2bk*{10811}. [*Gli-A<sup>u</sup>2-XIII*{10811}]. **dv**: PI-428208, *T. urartu*{10811}.
- Gli-A2bl*{10811}. [*Gli-A<sup>u</sup>2-XIV*{10811}]. **dv**: PI-428202, *T. urartu*{10811}.
- Gli-A2bm*{10811}. [*Gli-A<sup>u</sup>2-XV*{10811}]. **dv**: PI-428217, *T. urartu*{10811}.
- Gli-A2bn*{10811}. [*Gli-A<sup>u</sup>2-XVI*{10811}]. **dv**: PI-427328, *T. urartu*{10811}.
- Gli-A2bo*{10811}. [*Gli-A<sup>u</sup>2-XVII*{10811}]. **dv**: PI-428317, *T. urartu*{10811}.
- Gli-A2bp*{10811}. [*Gli-A<sup>u</sup>2-XVIII*{10811}]. **dv**: PI-428253, *T. urartu*{10811}.
- Gli-A2bq*{10811}. [*Gli-A<sup>u</sup>2-XIX*{10811}]. **dv**: PI-538742, *T. urartu*{10811}.
- Gli-A2br*{10811}. [*Gli-A<sup>u</sup>2-XX*{10811}]. **dv**: PI-428232, *T. urartu*{10811}.
- Gli-A2bs*{10811}. [*Gli-A<sup>u</sup>2-XXI*{10811}]. **dv**: PI-428188, *T. urartu*{10811}.
- Gli-A2bt*{10811}. [*Gli-A<sup>u</sup>2-XXII*{10811}]. **dv**: PI-428244, *T. urartu*{10811}.
- Gli-A2bu*{10811}. [*Gli-A<sup>u</sup>2-XXIII*{10811}]. **dv**: PI-538733, *T. urartu*{10811}.
- Gli-A2bv*{10811}. [*Gli-A<sup>u</sup>2-XXIV*{10811}]. **dv**: PI-428212, *T. urartu*{10811}.
- Gli-A2bw*{10811}. [*Gli-A<sup>u</sup>2-XXV*{10811}]. **dv**: TRI-6734, *T. urartu*{10811}.
- Gli-A2bx*{10811}. [*Gli-A<sup>u</sup>2-XXVI*{10811}]. **dv**: PI-428254, *T. urartu*{10811}.
- Gli-B2*{1607,1125}. [*Gld 6B*{1415}]. 6B{1607}.6BS{1122}. **v**: CS.
- Gli-B2a*{988}. **v**: CS{988}.
- Gli-B2b*{988}. **v**: Bezostaya 1{988}; Cobra{991}; Gladio{9986}; Sideral{991}.
- Gli-B2c*{988}. **v**: Courtot{991}; Escuala{9985}; Gabo{988}; Loreto{9986};  
Manital{9986}; Prinqual{991}; Siete Cerros 66{988}; Sinton{995}; Yecora 70{9985}.
- Gli-B2d*{988}. **v**: Akmolinka 1{988}; Cesar{9981}; Friedland{991}; Tselinnaya 20{988}.
- Gli-B2e*{988}. **v**: Arsenal{991}; Veronese{9986}; Zlatna Dolina{994}.
- Gli-B2f*{988}. **v**: Basalt{9981}; Maris Freeman{988}; Master{991}.
- Gli-B2g*{988}. **v**: Capitole{991}; Capelle-Desprez{991}; Galahad{988}; Forlani{9986}.
- Gli-B2h*{988}. **v**: Castan{991}; Mentana{9986}; Pane 247{9985}; Partizanka{994};  
Sadovo 1{988}; Sistar{9986}.
- Gli-B2i*{988}. **v**: Insignia{988}; Robin{9981}.
- Gli-B2j*{988}. **v**: Farnese{9986}; Funo R250{9986}; Novosadska Rana 1{994}.
- Gli-B2k*{988}. **v**: Skala{988}.
- Gli-B2l*{988}. **v**: Clement{991}; Longbow{988}; Tracy{991}.
- Gli-B2m*{988}. **v**: Mironovskaya 808{988}; Open{991}; Renan{991}.
- Gli-B2n*{988}. **v**: Japhet{9981}; Rouge de Bordeau{9981}; Solo{988}.
- Gli-B2o*{988}. **v**: Hardi{9981}; Mara{9986}; Odesskaya 16{988}; Pippo{9986};  
Rivoli{991}; Slavjanka{9981}.
- Gli-B2p*{988}. **v**: Pliska{983}; Champstal{991}; Oderzo{9986}; Recital{991};  
Gazul{9985}.
- Gli-B2q*{988}. **v**: Saratovskaya 39{988}.

- Gli-B2r*{991}. v: Arminda{991}; Estica{991}; Genial{991}.  
*Gli-B2s*{988}. v: Aquila{9981}; Saratovskaya 36{988}.  
*Gli-B2t*{988}. v: Tselinogradka{988}.  
*Gli-B2u*{988}. v: Kirgizskaya Yubileinaya{988}.  
*Gli-B2v*{988}. v: Declic{991}; Garant{991}; Libellula{9986}; Mahissa 1{9985}; Poljarka{988}.  
*Gli-B2w*{995,9986}. v: Palata{9986}; Pembina{995}; Rieti DIV{9986}.  
*Gli-B2x*{994}. v: Super Zlatna (biotype){994}; Prostor{9981}; 251/83{9981}.  
*Gli-B2y*{9986}. v: Centauro{9986}; E. Morandi{9986}.  
*Gli-B2z*{9985}. v: Maestro{9985}.  
*Gli-B2aa*{9986}. v: Salmone{9986}; E. Mottin{9981}.  
*Gli-B2ab*{991}. v: Bordier{9981}; Orepi{991}.  
*Gli-B2ac*{991}. v: Scipion{991}; Artaban{991}; Riol{991}; Lontra{9981}.  
*Gli-B2ad*{991}. v: Champion{991}; Chopin{991}.  
*Gli-B2ae*{991}. v: Priam{991}; Etoile d'Choisy{991}; Campeador{9985}; Krajinka (biotype){994}.  
*Gli-B2af*{9985}. v: Montjuich{9985}; Mocho Sobarriba{9985}.  
*Gli-B2ag*{9981}. v: Jeja del Pais{9985}; Barbilla de Leon (MCB-1292){9981}.  
*Gli-B2ah*{9981}. v: Rojo de Humanes (MCB-1262){9981}; Grano de Miracolo{9981}.  
*Gli-B2ai*{9981}. v: Blanquillo (MCB-0908){9981}.  
*Gli-B2aj*{9981}. v: Negrete de Malaga (MCB-1754){9981}.  
*Gli-B2ak*{9981}. v: HY320{9981}; Leader{9981}.  
*Gli-B2al*{9981}. v: Dankowska{991}.  
*Gli-B2am*{9981}. v: TM-275{9981}; Uralochka{9981}.  
*Gli-B2an*{9981}. v: Eagle{9981}; Glenwari{9981}.  
*Gli-B2ao*{9981}. v: Olympic{9981}; Mokoan{9981}.  
*Gli-B2ap*{9981}. v: Veda{9981}; Magnif 27{9981}.  
*Gli-B2aq*{9981}. v: Winglen{9981}; Isis{9981}.  
*Gli-B2ar*{9981}. v: Arbon{9981}; Roazon{9981}.  
*Gli-B2as*{9981}. v: Strela{9981}; Sredneuralskaya{9981}.  
*Gli-B2at*{9981}. v: Ranee{9981}; Javelin 48{9981}.  
*Gli-B2au*{9984,9987}. Null allele v: Saratovskaya 29{9987}.  
*Gli-D2*{1334,1125}. [*Gld 6D*{1415}]. 6D{1334}.6DS{1122}. v: CS.  
*Gli-D2a*{988}. v: CS{988}; Maris Freeman{988}; Sistar{9986}; Tracy{991}.  
*Gli-D2b*{988}. v: Bezostaya 1{988}; Cobra{991}; Farnese{9986}; Partizanka{994}.  
*Gli-D2c*{988}. v: Escualo{9985}; Eridano{9986}; Rieti DIV{9986}; Siete Cerros 66{988}.  
*Gli-D2d*{988}. v: Dneprovskaya 521{988}.  
*Gli-D2e*{988}. v: Dollar{9985}; Lada{9981}; Mironovskaya 808{988}; Open{991}.  
*Gli-D2f*{988}. v: Creneau{991}; Kirgizskaya Yubileinaya{988}; Rempart{991}.  
*Gli-D2g*{988}. v: Capelle-Desprez{991}; Futur{991}; Galahad{988}; Ghurka{988}; Mec{9986}.  
*Gli-D2h*{988}. v: Capitole{991}; Chinook{995}; Eagle{00119}; Garant{991}; Sadovo 1{988}; Thatcher{995}.  
*Gli-D2i*{988}. v: Insignia 49{00119}; Lario{9986}.  
*Gli-D2j*{988}. v: Arcane{991}; Gallo{9986}; Gazul{9985}; Inia 66{9985}; Mentana{9986}.  
*Gli-D2k*{988}. v: Crvencapa{944}; Kzyl-Bas{988}; Skala{988}.  
*Gli-D2l*.  
 Omitted. No reliable differences compared to existing alleles {9981}.  
*Gli-D2m*{988}. v: Marquis{988}; Rex{991}; Rinconada{9985}; Suneca{00119}; Veronese{9986}; Yecora 70{9985}.

- Gli-D2n*{988}. **v**: Castan{991}; Champlein{991}; Mahissa 1{9985}; Mercia{988}; Pippo{9986}.
- Gli-D2o*{988}. **v**: Omskaya 12{988}.  
Note: cultivars Salmone and Resistente, which carry *Gli-D2aa* {9981}, were erroneously given as standards for allele *Gli-D2o* in {9986}.
- Gli-D2p*{988}. **v**: New Pusa {988}.
- Gli-D2q*{988}. **v**: Cook{9981}; E. Mottin{9981}; Fournil{991}; Volshebnitsa (biotype){988}; Winglen{9981}; Soissons{991}.
- Gli-D2r*{988}. **v**: Kremena{988}; Mara{9986}; Montcada{9985}.
- Gli-D2s*{988}. **v**: Akmolinka 1{988}; Bezenchukskaya 98{988}; Selkirk (biotype){995}.
- Gli-D2t*{9986}. **v**: Golia{9986}; Gabo{9981}; Manital{9986}; Bokal{9981}.
- Gli-D2u*{9986}. **v**: Loreto{9986}; Martial{991}; Cibalka{9981}.
- Gli-D2v*{991}. **v**: Epiroux{991}; Arbon{991}.
- Gli-D2w*{9985}. **v**: Navarro 150{9985}; Javelin{9981}; Hopps{9981}; Canaleja{9985}.
- Gli-D2x*{9985}. **v**: Montjuich{9985}; Blanquillo{9985}.
- Gli-D2y*{9985}. **v**: Candéal Alcalá{9985}.
- Gli-D2z*{9985}. **v**: Aragón 03{9985}.
- Gli-D2aa*{9981}. **v**: Salmone{9981}; Resistente{9981}.
- Gli-D2ab*{9981}. **v**: Rojo de Boadilla de Campos (MCB-1031){9981}.
- Gli-D2ac*{9981}. **v**: Albatros{9981}.
- Gli-D2ad*{9981}. **v**: Hembrilla Soria (MCB-1298){9981}.
- Gli-D2ae*{9984,9987}. null allele **v**: Saratovskaya 29 (mutant){9987}.
- Gli-Ag<sup>i</sup>2*{374}. 6Ag<sup>i</sup>{374}. **ad**: Vilmorin 27/ *Th. intermedium*.
- Gli-R2*{781}. [*Sec 2*{1336}]. 2R{781,1336}.2RS{1340}. **ad**: CS/Imperial{781,1336,1340}; Holdfast/King II{1340}.
- Gli-R2a*{03116}. d1{03116}. **v**: Carnac hexaploid triticale{03116}.
- Gli-R2b*{03116}. d2{03116}. **v**: Mostral hexaploid triticale{03116}.
- Gli-R2c*{03116}. t1{03116}. **v**: Alamo hexaploid triticale{03116}.
- Gli-R2d*{03116}. Null{03116}. **v**: Triticor hexaploid triticale{03116}.
- Gli-R2e*{03115}. t2{03115}. **v**: Tornado hexaploid triticale{03115}.
- Gli-R<sup>m</sup>2*{1339}. 6R<sup>m</sup>{1339,1340}. **ad**: CS/*S. montanum*.  
The location of *Gli-R2* in *S. cereale* is thought to have evolved from *S. montanum* {1339} via a translocation between 2R and 6R {1530}.
- Gli-S<sup>1</sup>2*{573}. 6S<sup>1</sup>{573}. **ad,su**: CS/*Ae. longissima*.
- Gli-U2*{1335}. 6U{1335}. **ad**: CS/*Ae. umbellulata*.
- Gli-V2*{111}. 6VS{111}. **ad**: Creso/*D. villosum*.

Prior to the publication of {988}, allelic variation was demonstrated at all of the wheat *Gli-2* loci, including 13 alleles at *Gli-A2*, 11 at *Gli-B2*, and 10 at *Gli-D2*, in a study of 39 cultivars {996}.

The *Gli-2* alleles present in 57 Yugoslav wheat varieties were determined {994}.

### 82.3.2.3. Gli-3

A *Gli-3* set of loci coding for omega-type gliadins are located 22 to 31 cM proximal to *Gli-1* on the short arms of group 1 chromosomes {422,1403,589}.

*Gli-A3*{1403,1119}. [*Gld-2-1A*{1416}]. 1AS{1403}. **v**: Bezostaya 1.

Each of the following *Gli-A3* alleles, apart from *Gli-A3d*, which is a null, controls one minor omega-gliadin with molecular mass about 41k that occurs in the middle of the omega-region of APAGE fractionation. Gliadins controlled by these alleles differ in their electrophoretic mobility in APAGE in that the fastest of three known *Gli-A3*-gliadins is controlled by *Gli-A3a* and the slowest by *Gli-A3c* {9983}.

- Gli-A3a*{9983}. v: CS, Prinqual, Courtot, Tselinogradka, Bezenchukskaya 98.  
*Gli-A3b*{9983}. v: Bezostaya 1.  
*Gli-A3c*{9983}. v: Anda.  
*Gli-A3d*{9983}. Null{9983}. v: Saratovskaya 210, Kharkovskaya 6, Richelle.  
*Gli-B3*{422,1119}. [*Gld-B6*{422},*Glu-B2*{589}]. 1BS{422,589}. s: CS\*/Thatcher1B{422}.  
v: Sicco{589}.  
*Gli-B3a*{422,589,1119}. v: CS.  
*Gli-B3b*{589}. v: Sicco.  
*Gli-B3c*{422,1119}. s: CS\*/Thatcher1B.  
*Gli-R3*{164}. 1RS{164}. al: Four inbred lines (R2, J14, 8t, E2666).  
*Gli-S<sup>l</sup>3*{1228}. 1S<sup>l</sup>S{1228}. ad,su: CS/*Ae. longissima*. ma: In *Ae. longissima* 2/*Ae. longissima* 10, three gliadin loci, one glucose phosphate isomerase, and two glutenin loci were mapped relative to one another {1228} as follows: *Glu-S<sup>l</sup>1* 15.9 cM - *Gpi-S<sup>l</sup>1* - 38 cM - *Gli-S<sup>l</sup>4* - 7.1 cM - *Glu-S<sup>l</sup>3* - 0.9 cM - *Gli-S<sup>l</sup>1* - 5.6 cM - *Gli-S<sup>l</sup>5*. *Glu-S<sup>l</sup>1* is located in 1S<sup>l</sup>L and the other loci are in 1S<sup>l</sup>S.  
*Gli-V3*{111}. 4VL{111}. ad: Creso/*D. villosum*.

#### 82.3.2.4. Gli-4

It is not clear how *Gli-S<sup>l</sup>4* and *Gli-S<sup>l</sup>5* relate to the *Gli-4* and *Gli-5* sets described below. A locus designated *Gli-A4* controlling omega-gliadins in cv. Perzivan biotype 2 was mapped at 10 cM proximal to *Gli-A1* on the short arm of chromosome 1A {1205}. However, Metakovsky *et al.* {9983} have since shown that this locus and *Gli-A3* are, in fact, the same locus. Furthermore, Dubcovsky *et al.* {277} did not find evidence for the simultaneous presence of both *Gli-A3* and *Gli-A4* in five 1A or 1A<sup>m</sup> mapping populations and concluded that *Gli-A4* should be considered to be *Gli-A3* until conclusive evidence for the former is obtained. For these reasons, the locus *Gli-A4* is deleted from the catalogue.

#### 82.3.2.5. Gli-5

A locus designated *Gli-5* controlling omega-gliadins was mapped to the short arms of chromosomes 1A and 1B, distal to *Gli-1* {1147}. The map distance between *Gli-B5* and *Gli-B1* was estimated as 1.4 cM (recombination value of 1.4 +/- 0.4%), although there was significant variation in recombination values over crosses, ranging from 0 % to 5.9 % over the six crosses analysed. This variation was attributed to genotypic influence on the frequency of recombination.

- Gli-A5*{1147}. 1AS{1147}. v: Salmone.  
*Gli-A5a*{9983}. Null{9983}. v: CS.  
*Gli-A5b*{9983}. v: Marquis.  
Allele *Gli-A5b* controls two slow-moving, easily-recognizable omega-gliadins. It is present in all common wheat cultivars having alleles *Gli-A1m* and *Gli-A1r* (and, probably, in those having *Gli-A1e*, *Gli-A1l* and *Gli-A1q*), because earlier (for example, in {988}) two minor omega-gliadins encoded by *Gli-A5b* were considered to be controlled by these *Gli-A1* alleles {9983}.  
*Gli-B5*{1147}. 1BS{1147}. v: Salmone.  
*Gli-B5a*{1147}. v: CS.  
*Gli-B5b*{1147}. v: Salmone.  
In {988}, omega-gliadins controlled by *Gli-B5* (allele *Gli-B5b*) were attributed to alleles at the *Gli-B1* locus (alleles *Gli-B1c*, *i*, *k*, *m*, *n* and *o*).

#### 82.3.2.6. Gli-6

***Gli-A6***{9983,993}. 1AS{9983}.

*Gli-A6* was first explicitly described in {9983}, but it was first observed without designation in {993}. There is strong evidence that it is distinct from *Gli-A3* and *Gli-A5*, mapping distally to *Gli-A1*, with which it recombines at a frequency of 2-5%. Currently three alleles are known, of which *Gli-A6c* is particularly well-described in {9983}: the molecular mass of the omega-gliadin controlled by this allele is slightly lower than those of the omega-gliadins controlled by *Gli-A3* alleles. In {988}, the omega-gliadin controlled by *Gli-A6c* was attributed to *Gli-A1f*. *Gli-A6c* is rather frequent in common wheat and may relate to dough quality (preliminary data {9983}). *Gli-A6a* is null {9983}.

***Gli-A6a***{9983}. Null{9983}. **v:** CS, Bezostaya 1.

***Gli-A6b***{9983}. **v:** Bezenchukskaya 98.

***Gli-A6c***{9983}. **v:** Courtot, Anda, Mironovskaya 808.

### 82.3.2.7. *Gli-7*

***Gli-A7***{10547}. 1DS{10547}. **dv:** AUS18913{10547}.

The gamma-gliadin encoded by this locus co-segregated with the T1 omega-gliadin encoded by the *Gli-D'T1* locus (currently included in the Catalogue as locus (*Gli-DT1*)). *Gli-A7* was located 0.69 cM from *Gli-D'1* {10547}.

Four new classes of low molecular weight proteins related to gliadins, though not sufficiently similar to be classified as such, were reported in {02113}. One of the classes has no close association to previously described wheat endosperm proteins.

### 82.3.3. Other endosperm storage proteins

***Tri-A1***{1357, 1358}. 1AS{1357}. **v:** CS.

***Tri-A1a***. [*cs*{1358}]. **v:** CS.

***Tri-A1b***. [*h*{1358}]. **v:** Hope.

***Tri-D1***{1357,707,1358}. 1DS{1357}. **v:** CS.

***Tri-D1a***. [*cs*{1358}]. **v:** CS.

***Tri-D1b***. [*i*{1358}]. **v:** India 115.

#### 82.3.3.1. Triticin proteins

The triticin proteins {1360} or [Triplet proteins {1357}] are storage globulins with homology to pea legumins and related proteins in oats, rice and several dicotyledonous species {1360}. Triticin gene segments including its hypervariable region were PCR-amplified, with preferential amplification of *Tri-D1* for the only pair of primers giving consistent results {10322}.

## 82.4. Enzyme Inhibitors

### 82.4.1. Inhibitors of alpha-amylase and subtilisin

***Isa-A1***{908}. 2AL{908}. **v:** CS.

***Isa-A1a***{908}. **v:** CS.

***Isa-A1b***{908}. Null allele. **v:** Cajeme 71.

***Isa-B1***{908}. 2BL{908}. **v:** CS.

***Isa-B1a***{908}. **v:** CS.