# Is it possible to find a method that shows a correspondence between a known mutation and the phenotype in barley wax less mutants?

**Lovisa Kjellén Biologiska institutionen, MOB K01, HT 2015**
**Supervisors Lizette Schneider and Mats Hansson**
**Department of Biology, Lund University**

**Abstract** The wax on the stem and leafs of the barley (*Hordeum vulgare* L.) plant has a protective function and is produced by the cells on the plant's outer surfaces. There are several available barley mutants where the wax production has been stopped. Four mutants are the single-site mutants *cer-c.36*, *cer-q.42*, *cer-u.21* and the deletion mutant *cer-cqu.724*. We phenotyped 636 barley plants and collected leaf samples from all of them for DNA extraction. We used PCR with pre-designed primers to confirm that DNA had been extracted from all plants. Since the mutations in *cer-c.36*, *cer-q.42* and *cer-u.21* are already known we tried to identify the mutant plants by using restriction enzymes to cleave a PCR product on the mutant site. Then we designed specific nucleotide primers for PCR that only amplifies a region of either mutated plants or the wild type plants. This method gave some interesting results for the wild type *cer-u.21* mutant. Finally, we looked at the triple mutant *cer-cqu.724* and since it had not been sequenced yet we used primers for *cer-c.36* and *cer-u.21* to try to amplify the wild type DNA and then confirm the results by amplifying a separate sequence in the barley genome to make sure that there is DNA extracted from all plants. In the end we only obtained a result for the *cer-u.21* wild typeHowever, it should be possible to get results for the other mutants if the PRC program is optimized.

**Keywords** barley, eceriferum, designed primers, wax less mutants

## Introduction

Barley (*Hordeum vulgare* L.) is an important agricultural crop, serving as a food source for both humans and animals. Like other plants the barley plant surface is covered with a protective hydrophobic layer called cuticle, which consists of cutin and wax. This layer is produced by the plant's epidermal cells (Beisson and Ohlrogge, 2012). The cutin has two distinct layers, intracuticular waxes in the cutin polymer matrix inside the cell and coating epicuticular waxes on the surface of the cell, and these layers have a similar chemical composition of alkenes, primary alcohols, free fatty acids, aldehydes, beta-ketones, hydroxy-beta-diketones, esters and hydrocarbons (Zabka et al. 2008; Søgaard & von Wettstein-Knowles, 1987). The wax coating keeps water droplets from the outside environment of the plant separated from the water reservoirs inside. This keeps important nutrition molecules and substrates accessible for the plant and protects the plant from evaporation drought climates (Lundqvist 1992). By letting barley plants grow under conditions of water stress it has been found that barleys with leaf epicuticular wax are more drought resistant than barley without the wax (Larsson and Svenningsson 1986), also their grain yield is higher under terminal water stress conditions (González and Ayerbe 2010). The wax also provides resistance to UV-radiation, virus infection and other pathogens.

The biosynthesis of the wax is controlled by the *eceriferum* (*cer*) genes, and mutations in these genes cause reduction or complete

absence of wax. A total of 1580 *eceriferum* mutations has been assigned to 79 *cer* loci. Most of the mutations are located in the *cer-cqu* locus in the terminal end of barley chromosome 2H (Lundqvist and Lundqvist 1988). The three genes cer-*c*, *cer-q* and *cer-u*are all included in the *cqu* locus, and there are 85 *cer-cqu* locus throughout the barley genome positioned within 0.0025 cM from each other. Mutations can be obtained in each of the three genes but single mutations can also cause *cer-cq*, *cer-cu*, *cer-qu* and *cer-cqu* genotypes. It is also possible to obtain revertants from *cer-cqu* mutations. This should not be possible if the *cer-cqu* mutations are deletions (von Wettstein-Knowles and Søgaard 1981). Due to these findings, the *cer-cqu* gene has been suggested to encode a multifunctional protein that implies a polypeptide chain consisting of three functional domains corresponding to *cer-c*, *cer-q*, and *cer-u* (von Wettstein-Knowles and Søgaard B 1980; Søgaard and von Wettstein-Knowles 1987). This hypothesis was recently challenged by Marais-Schneider et al. (2016), who suggested three genes, *MLOC_59804*, *MLOC_13397* and *AK373499*, as candidates for *cer-c*, *cer-q*, and *cer-u*, respectively (see Fig. 1). In the present study, we explore four segregating mapping populations based on mutants *cer-c.36*, *cer-q.42*, *cer-u.21* and *cer-cqu.724*, and investigate whether there is a 100% match between mutations in *MLOC_59804*, *MLOC_13397* and *AK373499*, and mutant phenotypes. We develop PCR-based genotyping for this task.

## Results

### Phenotyping of barley plants

624 plants from four segregated mapping populations were phenotyped in categories according to whether they had wax or not on their spikes and leaf respectively. The $F_2$-mapping populations were *cer-c.36* x Quench, *cer-q.42* x Quench, *cer-u.21* x Quench and *cer-cqu.724* x Quench. The *cer-c.36*, *cer-q.42* and *cer-cqu.724* arecategorized as "spike and leaf sheath" mutants while *cer-u.21* is a "partial" mutant (Lundqvist and von Wettstein 1962). Our phenotyping showed that the *cer-c.36* mapping population had 76% wild type and 24% mutant phenotypes, while *cer-q.42* had 72% wild type and 28% mutant, *cer-u.21* had 77% wild type and 23% mutant, and *cer-cqu.724* had 66% wild type and 34% mutant (see Table A-1 in Appendix A).

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WT_cerC         GAAGGCTCCGCG------CTGGCTATCGGAACAGCAAATCCTGCGAACAAGGTGTCCCAA
cerC_mut        GAAGGCTCCGCGGCAATGCTGGCAAT-GGAACAGCAAATCCTGCGAACAAGGTGTCCCAA
                ************      ***** ** **********************************

WT_cerQ         CGGCGAGGTGGACGACGAATTCTACCCATTAATCCGCAAGTACAAGGATGGCCGGATCGA
cerQ_mut        CGGCGAGGTGGACGACGAATTCTACC-ATTAATCCGCAAGTACAAGGATGGCCGGATCGA
                ************************ **********************************

WT_cerU         GACGCCCTCGGCAAGTTGAAGCTGGTATGATACGCATATAGTATGGATGGACATTAAACC
cerU_Mut        GACGCCCTCGGCAAGTTGAAGCTGGTCTGCTACGCATATAGTATGGATGGACATTAAACC
                ************************ ** ****************************
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**Fig. 1** The wild type sequences of *MLOC_59804*, *MLOC_13397* and *AK373499* and the corresponding sequences of these genes in mutants *cer-c.36*, *cer-q.42*, and *cer-u.21* (alignments madeusing ClustalOmega at ). All three mutations damage the production of wax on the barley plant's surface. The mutation which is thought to be responsible for the wax less phenotype in *cer-c.36* and *cer-q.42* is a deletion of a cytosine while *cer-u.21* is a point mutation where an adenine has changed to a cytosine. The triple mutant *cer-cqu* has a large deletion of the entire gene cluster.


**Fig. 2** Designed primer to separate wild type and mutant DNA sequences. **a** For conducting PCR amplifiation of the wild type *cer-u.21* plant is special primers constructed that binds to the complimentary DNA strand. **b** When the same primer is used in conducting PCR amplifiation of the mutant *cer-u.21* plant is there a mismatch at the last nucleotide that the primer cannot bind to complimentary DNA binding site and there will not be a PCR product.

***cer-c.36***

The mapping population was amplified by PCR and the wild type and mutant genotypes were distinguished by restriction enzyme digestion. When we analyzed cer-c.36 we found that the restriction enzyme Hpy1881 would theoretically cleave the wild type PCR product in four fragments of 229, 184, 284 and 85 bp while only cleaving the mutant PCR product in three fragments of 223, 184 and 306 bp. The results of the first attempt looked promising on the gel but all attempts to refine the reaction to see the wildtype 85 bp band on a gel failed.

***cer-u.21***

Since there were no restriction enzymes that could cleave the gene at the mutated site we decided to construct a specific primer that only binds to either the wild type DNA or the mutated DNA (see Fig. 2a, 2b). This means that it should only be possible to get a PCR product in the plant of interest for either wild type or mutant. The result for the designed wild type primers was successful (see Fig. 3) and we obtained a clear match between a wild type or heterozygous genotype and a wild type phenotype (see Table A-1). To confirm the results, we tried to design a primer that would give the opposite reaction, that is, a primer that would generate a PCR product with the mutant plants. However, this did not work.

During PCR of the wild type and the mutant plants the double stranded DNA has been denatured and the designed primer for the wild type binds to the complementary strand of the wild type strand (see Fig. 2a). However, when the primer comes across the mutant strand it does not fit and cannot bind to the strand (see Fig. 2b). The reaction also has a reverse primer that binds to both of the plants but since there only is a forward primer to the wild type plant there will only be a PCR product generated for the wild type. This mutation was also a bit difficult to phenotype since the mutated plants had a thin wax layer.

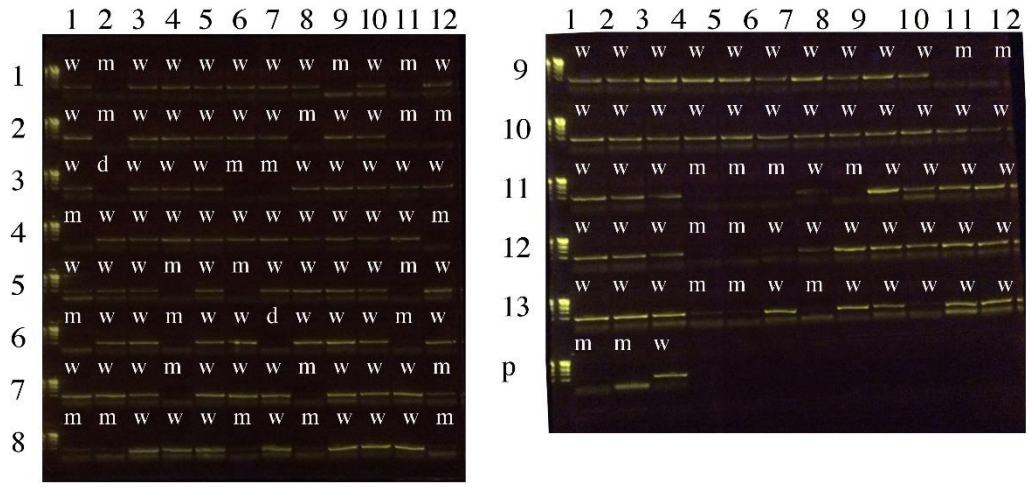


**Fig. 3** The *cer-u.21* with primers designed to produce a PCR product only in the wild type plants that has been run in a 2% agarose gel. The genotypes are indicated for a total of 159 plants, 156 that are numbered from 1.1 to 13.12, as well as two mother mutated plants and a wild type father plant. The phenotypes (see Table A-1) have been marked with letters where "w" means that the plant is a wild type, "m" that it is a mutant and "d" that the plant is dead. These results only prove that the wild type plant has the *cer-u.21* gene and not that the mutant plant does not.

***cer-q.42***

We could not find any restriction enzymes that could distinguish the PCR products of plants in the cer-q.42 mapping population. Instead we tried to repeat the designed primers PCR reaction of the cer-u.21. However, none of the reactions worked (hence, no data shown).

***cer-cqu.724***

The *cer-cqu.724* mutations had not been sequenced yet. Therefore, we did not know exactly what the deletion site looked like. However, since the deleted region includes all three domains this could provide a method to distinguish wild type plants from *cer-cqu.724* mutant plants by the use of the also their respective primer binding regions. This would generate a PCR product in the wild type and heterozygous plants but not in the mutant plants. To make sure that all samples had DNA extracted, a control PCR was designed from another part of the plant genome. The control segment showed that DNA had been extracted, but the *cer-c.36* reaction did not match with the phenotyping. Instead the primers for *cer-u.21* was tried and after that failed, the designed primers for the *cer-u.21* wild type was unsuccessfully tried.

**Discussion**

This project had two parts: phenotyping of barley plants and then matching plants with a specific gene to the phenotype. During phenotyping we started with the assumption that each plant either had wax on their spikes and leafs or that wax was completely absent, but we discovered that this not was the case. The mutations of the *cer-u.21* population were difficult to phenotype. Its wild type plant had a distinct white layer of wax on the stem, leaf and spikes, but the mutant also had a thin layer of wax, especially on the stem but also a thin layer on the spikes. We found an explanation for this in Lundqvist and von Wettstein (1962) who identified different groups of wax less mutations. The *cer-u.21* is categorized as a "partial" mutant, while *cer-c.36*, *cer-q.42* and *cer-cqu.724*, belong to the "spike and leaf sheath" mutants. Another difference between the *cer-u.21* and the other three populations is that the *cer-u.21* is a point mutation, while the other three are deletions. The *cer-c.36* and *cer-q.42* are missing a cytosine while the *cer-cqu.724* is missing the entire *cer-c*, *-q*, *-u* segment. The *cer-c*, *-q*, and *-u* mutations affect three different steps in the pathway to β-diketones, hydroxy-β-diketones and esterified alkan-2-oils synthesis (von Wettstein-Knowles

1976). The *cer-q* mutation partially stops the esterified alkan-2-oils and completely stops the pathway of β-diketones and hydroxy-β-diketones. The *cer-c* mutation blocks the pathway of β-diketones and hydroxy-β-diketones. While the *cer-u* mutation only blocks the hydroxy-β-diketones this could also explain the difficulty in phenotyping (von Wettstein-Knowles and Søgaard 1980). It was, however, the *cer-u.21* population of the "partial" mutant that we were able to match with the genotype (see Fig. 3).

In the genetic analysis we obtained some results that might prove useful for *cer-u.21* but failed to obtain results in the other three populations. To confirm the result of the wild type *cer-u.21* reaction another reaction had to be made that only would generate a PCR product in the mutant plants of the population, but we failed to obtain such a result. It seemed promising to use the method of designed primers since it generated the *cer-u.21* wild type result but we did not have enough time in the lab to optimize the reactions for the others. In order to optimize the reactions in the future the protocols from the Sequence Manipulation Suite (Stothard 2000) should be consulted. All the reactions had a G and C nucleotide content of 40–60% which is recommended in the protocol. The optimization for all the reactions used the same procedure but only the *cer-u.21* wild type worked. It does not seem that these reactions failed because of temperature differences between the forward and reverse primers since the *cer-u.21* wild type reaction had a theoretical annealing temperature difference of 10°C and the other reactions had about the same annealing temperature differences. The problem might be related to the primer concentrations or salt concentrations in the reaction mixtures. Also, the wildtype reaction of *cer-u.21* was made before we ordered the other primes, and it is possible that we did not do the reaction exactly the same way so that the primer concentrations became different, which might be why the reaction worked for the *cer-u.21* but not in the following trials.

We did design primers for the *cer-c.36* reaction when the cleavage of restriction enzyme failed, however we did not have time to order them and the the next step for this mutant population is to try these primers out. The forward primer for the wild type that we suggest is the 5'-GCGGCAATGCTGGCTATC and use it together with the reverse primer of 5'-GAGCATCTCCCCATTGCCAA. For the mutant reaction we suggest a forward primer 5'-GCTCCGCGGCAATGCTGGCAATG with the same reverse primer as above.

In this project we aimed to find methods to match genotypes and phenotypes of known mutants. The mutants in question were *cer-u.21*, which had a point mutation where an adenine changed to a cytosine, *cer-c.36* and *cer-q.42*, which had a deletion of a cytosine, and finally the deletion of the *cer-cqu.724* fragment. The phenotype of each plant was estimated by close visual inspection. We tried two methods to match the genotype, cleaving the PCR product with restriction enzymes and to create a PCR product with specially designed forward primers. We had two separate PCR reactions per plant, one for the wildtype and one for the mutant. The only result that we obtained was from the *cer-u.21* wild type. However, this is not a clear result since we have only shown that the wild type is there but we cannot see any difference between a mutant plant and a dead plant. That is why it is important to find a method that only affects the mutant plant. We still believe that the designed primer should work and the next step in the project would be to find the most optimized PCR program.

## Methods

### Plant materials and phenotyping

Barley (*Hordeum vulgare* L.) with the mutations of *cer-c.36*, *cer-q.42*, *cer-u.21*, and the deletion *cer-cqu.724* was crossed with the wax covered barley specie Quench. The $F_2$ generation of the crosseswhere then grown in a green house at 18°C with 156 plants of each cross resulting in 624 plants in total, each mutant crossing was each. The phenotypes were determined of each mutant by visually looking at the plants to see if they had wax on their outer leafs or not. A plant with a thin white powder that could be removed simply by scraping a finger on it showed that the plant had

wax. While a plant with a dark green colour and no powder represents a mutant. Some of the mutants had some wax on their stem but still differed a lot in their amount of wax from the wild type.

**DNA Extraction and Amplification**

Fresh leaves (0.5x0.5cm from the edge of the leaf) were collected from all individuals and put into the wells of a 96-well plate and were then stored in a freezer when not used. Genomic DNA was isolated and extracted from the frozen leaves using the REDExtract-N-Amp Plant PCR Kit (Sigma), 80 $\mu l$ extraction solution was added to each the leaf material, then the plates were incubated at 95 °C for 10 min and finally 80 $\mu l$ dilution buffer was added. An amplification solution was then prepared by making a master mix of 1650 $\mu l$ REDExtract-N-Amp PCR ReadyMix (containing JumpStart Taq anti-body for specific hot-start amplifications), 990 $\mu l$ water, 165 $\mu l$ forward primers, and 165 $\mu l$ reverse primers. 18 $\mu l$ of the master mix was loaded to a new 96-well plate and then 2 $\mu l$ ofthe DNA extraction solution was added and run for optimal conditions (as described below). The PCR plates were run with a total volume of 20 $\mu l$ in each well in a 100-volt electrophoresis for 10 minutes on a 2% agarose gel stained with GelGreen Nucleic Stain (Biotium) 16 $\mu l$ per gel of 60 ml TAE buffer.

**PCR and electrophoresis of each sample**

All PRC programs were conducted with 5-minute pre-heating phase of 94.0°C, then 35 cycles of 45 seconds denaturation phase at 94.0°C, annealing phase of 45 seconds at an optimized temperature (designated bellow) and elongation phase of 1 min 30 seconds at 72.0°C each cycle, followed by one last cycle the samples were put through an of 7 minutes of extra elongation at 72.0°C before cooling down to 4.0°C. To optimize the reactions, a test of eight reactions from the same plant was run in PCR with annealing temperatures varying from 55.8 to 63.9°C in order to see which one generated the most amount of PCR product.

**Table 1**. forward primers, reverse primers and annealing temperatures for the PCR reactions preformed.

| Sequence | Forward Primer | Reverse Primer | Annealing temperature (°C) |
|---|---|---|---|
| ***cer-c.36*** | 5′- TGCTGAACCACACTTCGCCG | 5′- GAGCATCTCCCCATTGCCAA | 58.8°C |
| ***cer-q.42*** | 5′- AACCCATCGAAGCAAACCTA | 5′-TCGCATTGCTATCTGGCAA | 56.0°C |
| ***cer-q.42 wild type*** | 5'-CGAGGTGGACGACGAATTCTACCC | 5′-TCGCATTGCTATCTGGCAA | 60.4°C |
| ***cer-q.42 mutant*** | 5'-CGAGGTGGACGACGAATTCTACCA | 5′-TCGCATTGCTATCTGGCAA | 55.8°C |
| ***cer-u.21*** | 5′- CGGACCTGGCAACTCGACAA | 5′-ACGATGATAACGATACCGCTGGT | 58.0°C |
| ***cer-u.21 wild type*** | 5'-CGCCCTCGGCAAGTTGAAGCTGGTA | 5′-ACGATGATAACGATACCGCTGGT | 58.8°C |
| ***cer-u.21 mutant*** | 5'-CGAGGTGGACGACGAATTCTACCA | 5′-ACGATGATAACGATACCGCTGGT | 56.7°C |
| ***cer-cqu.724*** | 5′- TGCTGAACCACACTTCGCCG | 5′- GAGCATCTCCCCATTGCCAA | 58.8°C |
| ***cer-cqu.724*** | 5′- CGGACCTGGCAACTCGACAA | 5′-ACGATGATAACGATACCGCTGGT | 58.0°C |
| ***cer-cqu.724*** | 5'-CGCCCTCGGCAAGTTGAAGCTGGTA | 5′-ACGATGATAACGATACCGCTGGT | 58.8°C |

**Designing primers, finding restriction enzymes and constructing the enzyme cleavage mix**

To design primers we used the Sequence Manipulation Suite (Stothard 2000) software, a JavaScript program which makes a PCR suitability test that estimates the probable annealing temperature, if the primer can self-anneal and if it can make hairpin formations. To find restriction enzymes that would cut at the mutation site we used NEBcutter V2.0 (New England Biolabs® inc; Vincze et al 2003). The enzyme mixture used to the *cer-c*.36 contained 0.1 µl *Hpy*1881, 1 µl CutsmartBuffer, 28,9 µl water, and 20 µl PCR product. It was incubated in 37.0°C for two hours and then loaded on to a 100-volt electrophoresis for 24 minutes on a 2% agarose gel stained with GelGreen Nucleic Stain (Biotium) 12 $\mu l$ per gel of 60 ml TAE-buffer.

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## Appendix A

**Table A-1.** Phenotyping of the 624 barley plants. Plants marked with WT are wild type, Mut are mutated and Dead plants are plants who had died before they could be phenotyped.

| Plant | Phenotype | Plant | Phenotype | Plant | Phenotype | Plant | Phenotype |
|---|---|---|---|---|---|---|---|
| Cer-c.36. 1.1 | WT | Cer-q.42 1.1 | WT | *Cer-u.21.1.1* | *WT* | Cer-cqu.724.1.1 | WT |
| Cer-c.36. 1.2 | WT | Cer-q.42 1.2 | Mut | *Cer-u.21.1.2* | *Mut* | Cer-cqu.724.1.2 | WT |
| Cer-c.36. 1.3 | Mut | Cer-q.42 1.3 | Mut | *Cer-u.21.1.3* | *WT* | Cer-cqu.724.1.3 | Mut |
| Cer-c.36. 1.4 | WT | Cer-q.42 1.4 | Mut | *Cer-u.21.1.4* | *WT* | Cer-cqu.724.1.4 | WT |
| Cer-c.36. 1.5 | Mut | Cer-q.42 1.5 | WT | *Cer-u.21.1.5* | *WT* | Cer-cqu.724.1.5 | WT |
| Cer-c.36. 1.6 | WT | Cer-q.42 1.6 | WT | *Cer-u.21.1.6* | *WT* | Cer-cqu.724.1.6 | WT |
| Cer-c.36. 1.7 | WT | Cer-q.42 1.7 | WT | *Cer-u.21.1.7* | *WT* | Cer-cqu.724.1.7 | Mut |
| Cer-c.36. 1.8 | WT | Cer-q.42 1.8 | WT | *Cer-u.21.1.8* | *WT* | Cer-cqu.724.1.8 | Mut |
| Cer-c.36. 1.9 | WT | Cer-q.42 1.9 | Mut | *Cer-u.21.1.9* | *Mut* | Cer-cqu.724.1.9 | WT |
| Cer-c.36. 1.10 | WT | Cer-q.42 1.10 | WT | *Cer-u.21.1.10* | *WT* | Cer-cqu.724.1.10 | WT |
| Cer-c.36. 1.11 | WT | Cer-q.42 1.11 | WT | *Cer-u.21.1.11* | *Mut* | Cer-cqu.724.1.11 | WT |
| Cer-c.36. 1.12 | WT | Cer-q.42 1.12 | WT | *Cer-u.21.1.12* | *WT* | Cer-cqu.724.1.12 | WT |
| | | | | | | | |
| Cer-c.36. 2.1 | WT | Cer-q.42 2.1 | Mut | *Cer-u.21.2.1* | *WT* | Cer-cqu.724.2.1 | WT |
| Cer-c.36. 2.2 | Mut | Cer-q.42 2.2 | WT | *Cer-u.21.2.2* | *Mut* | Cer-cqu.724.2.2 | WT |
| Cer-c.36. 2.3 | WT | Cer-q.42 2.3 | WT | *Cer-u.21.2.3* | *WT* | Cer-cqu.724.2.3 | WT |
| Cer-c.36. 2.4 | Mut | Cer-q.42 2.4 | Mut | *Cer-u.21.2.4* | *WT* | Cer-cqu.724.2.4 | WT |
| Cer-c.36. 2.5 | WT | Cer-q.42 2.5 | WT | *Cer-u.21.2.5* | *WT* | Cer-cqu.724.2.5 | WT |
| Cer-c.36. 2.6 | WT | Cer-q.42 2.6 | WT | *Cer-u.21.2.6* | *WT* | Cer-cqu.724.2.6 | Mut |
| Cer-c.36. 2.7 | WT | Cer-q.42 2.7 | WT | *Cer-u.21.2.7* | *WT* | Cer-cqu.724.2.7 | WT |
| Cer-c.36. 2.8 | WT | Cer-q.42 2.8 | Dead | *Cer-u.21.2.8* | *Mut* | Cer-cqu.724.2.8 | WT |
| Cer-c.36. 2.9 | WT | Cer-q.42 2.9 | Mut | *Cer-u.21.2.9* | *WT* | Cer-cqu.724.2.9 | Mut |
| Cer-c.36. 2.10 | WT | Cer-q.42 2.10 | WT | *Cer-u.21.2.10* | *WT* | Cer-cqu.724.2.10 | WT |
| Cer-c.36. 2.11 | WT | Cer-q.42 2.11 | WT | *Cer-u.21.2.11* | *Mut* | Cer-cqu.724.2.11 | WT |
| Cer-c.36. 2.12 | Mut | Cer-q.42 2.12 | WT | *Cer-u.21.2.12* | *Mut* | Cer-cqu.724.2.12 | Mut |
| | | | | | | | |
| Cer-c.36. 3.1 | WT | Cer-q.42 3.1 | WT | *Cer-u.21.3.1* | *WT* | Cer-cqu.724.3.1 | WT |
| Cer-c.36. 3.2 | WT | Cer-q.42 3.2 | Mut | *Cer-u.21.3.2* | *Dead* | Cer-cqu.724.3.2 | WT |
| Cer-c.36. 3.3 | Mut | Cer-q.42 3.3 | WT | *Cer-u.21.3.3* | *WT* | Cer-cqu.724.3.3 | WT |
| Cer-c.36. 3.4 | WT | Cer-q.42 3.4 | Dead | *Cer-u.21.3.4* | *WT* | Cer-cqu.724.3.4 | WT |
| Cer-c.36. 3.5 | WT | Cer-q.42 3.5 | WT | *Cer-u.21.3.5* | *WT* | Cer-cqu.724.3.5 | Mut |
| Cer-c.36. 3.6 | WT | Cer-q.42 3.6 | WT | *Cer-u.21.3.6* | *Mut* | Cer-cqu.724.3.6 | WT |
| Cer-c.36. 3.7 | WT | Cer-q.42 3.7 | Mut | *Cer-u.21.3.7* | *Mut* | Cer-cqu.724.3.7 | WT |
| Cer-c.36. 3.8 | WT | Cer-q.42 3.8 | Dead | *Cer-u.21.3.8* | *WT* | Cer-cqu.724.3.8 | WT |
| Cer-c.36. 3.9 | WT | Cer-q.42 3.9 | WT | *Cer-u.21.3.9* | *WT* | Cer-cqu.724.3.9 | Mut |
| Cer-c.36. 3.10 | Mut | Cer-q.42 3.10 | Mut | *Cer-u.21.3.10* | *WT* | Cer-cqu.724.3.10 | WT |
| Cer-c.36. 3.11 | Mut | Cer-q.42 3.11 | WT | *Cer-u.21.3.11* | *WT* | Cer-cqu.724.3.11 | Mut |
| Cer-c.36. 3.12 | Dead | Cer-q.42 3.12 | WT | *Cer-u.21.3.12* | *WT* | Cer-cqu.724.3.12 | WT |
| | | | | | | | |
| Cer-c.36. 4.1 | WT | Cer-q.42 4.1 | Mut | *Cer-u.21.4.1* | *Mut* | Cer-cqu.724.4.1 | WT |
| Cer-c.36. 4.2 | WT | Cer-q.42 4.2 | WT | *Cer-u.21.4.2* | *WT* | Cer-cqu.724.4.2 | WT |
| Cer-c.36. 4.3 | Mut | Cer-q.42 4.3 | Mut | *Cer-u.21.4.3* | *WT* | Cer-cqu.724.4.3 | WT |
| Cer-c.36. 4.4 | Mut | Cer-q.42 4.4 | WT | *Cer-u.21.4.4* | *WT* | Cer-cqu.724.4.4 | WT |
| Cer-c.36. 4.5 | WT | Cer-q.42 4.5 | WT | *Cer-u.21.4.5* | *WT* | Cer-cqu.724.4.5 | WT |
| Cer-c.36. 4.6 | WT | Cer-q.42 4.6 | WT | *Cer-u.21.4.6* | *WT* | Cer-cqu.724.4.6 | WT |
| Cer-c.36. 4.7 | WT | Cer-q.42 4.7 | WT | *Cer-u.21.4.7* | *WT* | Cer-cqu.724.4.7 | WT |
| Cer-c.36. 4.8 | WT | Cer-q.42 4.8 | Mut | *Cer-u.21.4.8* | *WT* | Cer-cqu.724.4.8 | Mut |
| Cer-c.36. 4.9 | WT | Cer-q.42 4.9 | WT | *Cer-u.21.4.9* | *WT* | Cer-cqu.724.4.9 | WT |
| Cer-c.36. 4.10 | WT | Cer-q.42 4.10 | Mut | *Cer-u.21.4.10* | *WT* | Cer-cqu.724.4.10 | WT |
| Cer-c.36. 4.11 | WT | Cer-q.42 4.11 | Mut | *Cer-u.21.4.11* | *WT* | Cer-cqu.724.4.11 | WT |
| Cer-c.36. 4.12 | WT | Cer-q.42 4.12 | WT | *Cer-u.21.4.12* | *Mut* | Cer-cqu.724.4.12 | WT |
| | | | | | | | |
| Cer-c.36. 5.1 | Mut | Cer-q.42 5.1 | WT | *Cer-u.21.5.1* | *WT* | Cer-cqu.724.5.1 | WT |
| Cer-c.36. 5.2 | WT | Cer-q.42 5.2 | WT | *Cer-u.21.5.2* | *WT* | Cer-cqu.724.5.2 | WT |
| Cer-c.36. 5.3 | WT | Cer-q.42 5.3 | WT | *Cer-u.21.5.3* | *WT* | Cer-cqu.724.5.3 | WT |
| Cer-c.36. 5.4 | WT | Cer-q.42 5.4 | WT | *Cer-u.21.5.4* | *Mut* | Cer-cqu.724.5.4 | Mut |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Cer-c.36. 5.5 | WT | Cer-q.42 5.5 | WT | *Cer-u.21.5.5* | *WT* | Cer-cqu.724.5.5 | WT |
| Cer-c.36. 5.6 | WT | Cer-q.42 5.6 | WT | *Cer-u.21.5.6* | *Mut* | Cer-cqu.724.5.6 | WT |
| Cer-c.36. 5.7 | WT | Cer-q.42 5.7 | WT | *Cer-u.21.5.7* | *WT* | Cer-cqu.724.5.7 | Mut |
| Cer-c.36. 5.8 | WT | Cer-q.42 5.8 | WT | *Cer-u.21.5.8* | *WT* | Cer-cqu.724.5.8 | Mut |
| Cer-c.36. 5.9 | WT | Cer-q.42 5.9 | WT | *Cer-u.21.5.9* | *WT* | Cer-cqu.724.5.9 | WT |
| Cer-c.36. 5.10 | WT | Cer-q.42 5.10 | WT | *Cer-u.21.5.10* | *WT* | Cer-cqu.724.5.10 | WT |
| Cer-c.36. 5.11 | WT | Cer-q.42 5.11 | Mut | *Cer-u.21.5.11* | *Mut* | Cer-cqu.724.5.11 | WT |
| Cer-c.36. 5.12 | WT | Cer-q.42 5.12 | Mut | *Cer-u.21.5.12* | *WT* | Cer-cqu.724.5.12 | WT |
| | | | | | | | |
| Cer-c.36. 6.1 | WT | Cer-q.42 6.1 | WT | *Cer-u.21.6.1* | *Mut* | Cer-cqu.724.6.1 | WT |
| Cer-c.36. 6.2 | WT | Cer-q.42 6.2 | WT | *Cer-u.21.6.2* | *WT* | Cer-cqu.724.6.2 | WT |
| Cer-c.36. 6.3 | WT | Cer-q.42 6.3 | WT | *Cer-u.21.6.3* | *WT* | Cer-cqu.724.6.3 | Mut |
| Cer-c.36. 6.4 | WT | Cer-q.42 6.4 | WT | *Cer-u.21.6.4* | *Mut* | Cer-cqu.724.6.4 | WT |
| Cer-c.36. 6.5 | Mut | Cer-q.42 6.5 | WT | *Cer-u.21.6.5* | *WT* | Cer-cqu.724.6.5 | Mut |
| Cer-c.36. 6.6 | WT | Cer-q.42 6.6 | Mut | *Cer-u.21.6.6* | *WT* | Cer-cqu.724.6.6 | WT |
| Cer-c.36. 6.7 | WT | Cer-q.42 6.7 | WT | *Cer-u.21.6.7* | *Dead* | Cer-cqu.724.6.7 | WT |
| Cer-c.36. 6.8 | Mut | Cer-q.42 6.8 | WT | *Cer-u.21.6.8* | *WT* | Cer-cqu.724.6.8 | Mut |
| Cer-c.36. 6.9 | WT | Cer-q.42 6.9 | WT | *Cer-u.21.6.9* | *WT* | Cer-cqu.724.6.9 | Mut |
| Cer-c.36. 6.10 | WT | Cer-q.42 6.10 | WT | *Cer-u.21.6.10* | *WT* | Cer-cqu.724.6.10 | WT |
| Cer-c.36. 6.11 | WT | Cer-q.42 6.11 | Mut | *Cer-u.21.6.11* | *Mut* | Cer-cqu.724.6.11 | Mut |
| Cer-c.36. 6.12 | WT | Cer-q.42 6.12 | WT | *Cer-u.21.6.12* | *WT* | Cer-cqu.724.6.12 | WT |
| | | | | | | | |
| Cer-c.36.7.1 | Mut | Cer-q.42 7.1 | Mut | *Cer-u.21. 7.1* | *WT* | Cer-cqu.724.7.1 | WT |
| Cer-c.36.7.2 | Mut | Cer-q.42 7.2 | WT | *Cer-u.21. 7.2* | *WT* | Cer-cqu.724.7.2 | Mut |
| Cer-c.36.7.3 | Mut | Cer-q.42 7.3 | WT | *Cer-u.21. 7.3* | *WT* | Cer-cqu.724.7.3 | WT |
| Cer-c.36.7.4 | WT | Cer-q.42 7.4 | WT | *Cer-u.21. 7.4* | *Mut* | Cer-cqu.724.7.4 | Mut |
| Cer-c.36.7.5 | WT | Cer-q.42 7.5 | Mut | *Cer-u.21. 7.5* | *WT* | Cer-cqu.724.7.5 | WT |
| Cer-c.36.7.6 | WT | Cer-q.42 7.6 | WT | *Cer-u.21. 7.6* | *WT* | Cer-cqu.724.7.6 | Mut |
| Cer-c.36.7.7 | Mut | Cer-q.42 7.7 | WT | *Cer-u.21. 7.7* | *WT* | Cer-cqu.724.7.7 | Mut |
| Cer-c.36.7.8 | WT | Cer-q.42 7.8 | WT | *Cer-u.21. 7.8* | *Mut* | Cer-cqu.724.7.8 | WT |
| Cer-c.36.7.9 | WT | Cer-q.42 7.9 | WT | *Cer-u.21. 7.9* | *WT* | Cer-cqu.724.7.9 | WT |
| Cer-c.36.7.10 | Mut | Cer-q.42 7.10 | WT | *Cer-u.21. 7.10* | *WT* | Cer-cqu.724.7.10 | Mut |
| Cer-c.36.7.11 | WT | Cer-q.42 7.11 | Mut | *Cer-u.21. 7.11* | *WT* | Cer-cqu.724.7.11 | WT |
| Cer-c.36.7.12 | Mut | Cer-q.42 7.12 | Mut | *Cer-u.21. 7.12* | *Mut* | Cer-cqu.724.7.12 | Mut |
| | | | | | | | |
| Cer-c.36.8.1 | WT | Cer-q.42 8.1 | Mut | *Cer-u.21. 8.1* | *Mut* | Cer-cqu.724.8.1 | WT |
| Cer-c.36.8.2 | WT | Cer-q.42 8.2 | WT | *Cer-u.21. 8.2* | *Mut* | Cer-cqu.724.8.2 | WT |
| Cer-c.36.8.3 | WT | Cer-q.42 8.3 | WT | *Cer-u.21. 8.3* | *WT* | Cer-cqu.724.8.3 | WT |
| Cer-c.36.8.4 | WT | Cer-q.42 8.4 | WT | *Cer-u.21. 8.4* | *WT* | Cer-cqu.724.8.4 | WT |
| Cer-c.36.8.5 | WT | Cer-q.42 8.5 | Mut | *Cer-u.21. 8.5* | *WT* | Cer-cqu.724.8.5 | WT |
| Cer-c.36.8.6 | WT | Cer-q.42 8.6 | WT | *Cer-u.21. 8.6* | *Mut* | Cer-cqu.724.8.6 | WT |
| Cer-c.36.8.7 | WT | Cer-q.42 8.7 | Mut | *Cer-u.21. 8.7* | *WT* | Cer-cqu.724.8.7 | Mut |
| Cer-c.36.8.8 | Mut | Cer-q.42 8.8 | Mut | *Cer-u.21. 8.8* | *Mut* | Cer-cqu.724.8.8 | WT |
| Cer-c.36.8.9 | Mut | Cer-q.42 8.9 | Mut | *Cer-u.21. 8.9* | *WT* | Cer-cqu.724.8.9 | WT |
| Cer-c.36.8.10 | WT | Cer-q.42 8.10 | WT | *Cer-u.21. 8.10* | *WT* | Cer-cqu.724.8.10 | Mut |
| Cer-c.36.8.11 | WT | Cer-q.42 8.11 | WT | *Cer-u.21. 8.11* | *WT* | Cer-cqu.724.8.11 | WT |
| Cer-c.36.8.12 | WT | Cer-q.42 8.12 | WT | *Cer-u.21. 8.12* | *Mut* | Cer-cqu.724.8.12 | Mut |
| | | | | | | | |
| Cer-c.36.9.1 | WT | Cer-q.42 9.1 | WT | *Cer-u.21. 9.1* | *WT* | Cer-cqu.724.9.1 | WT |
| Cer-c.36.9.2 | WT | Cer-q.42 9.2 | WT | *Cer-u.21. 9.2* | *WT* | Cer-cqu.724.9.2 | WT |
| Cer-c.36.9.3 | Mut | Cer-q.42 9.3 | WT | *Cer-u.21. 9.3* | *WT* | Cer-cqu.724.9.3 | WT |
| Cer-c.36.9.4 | Mut | Cer-q.42 9.4 | Mut | *Cer-u.21. 9.4* | *WT* | Cer-cqu.724.9.4 | Mut |
| Cer-c.36.9.5 | WT | Cer-q.42 9.5 | WT | *Cer-u.21. 9.5* | *WT* | Cer-cqu.724.9.5 | WT |
| Cer-c.36.9.6 | WT | Cer-q.42 9.6 | WT | *Cer-u.21. 9.6* | *WT* | Cer-cqu.724.9.6 | WT |
| Cer-c.36.9.7 | Mut | Cer-q.42 9.7 | WT | *Cer-u.21. 9.7* | *WT* | Cer-cqu.724.9.7 | Mut |
| Cer-c.36.9.8 | WT | Cer-q.42 9.8 | WT | *Cer-u.21. 9.8* | *WT* | Cer-cqu.724.9.8 | Mut |
| Cer-c.36.9.9 | Mut | Cer-q.42 9.9 | WT | *Cer-u.21. 9.9* | *WT* | Cer-cqu.724.9.9 | WT |
| Cer-c.36.9.10 | WT | Cer-q.42 9.10 | Mut | *Cer-u.21. 9.10* | *WT* | Cer-cqu.724.9.10 | WT |
| Cer-c.36.9.11 | WT | Cer-q.42 9.11 | WT | *Cer-u.21. 9.11* | *Mut* | Cer-cqu.724.9.11 | Mut |
| Cer-c.36.9.12 | WT | Cer-q.42 9.12 | Mut | *Cer-u.21. 9.12* | *Mut* | Cer-cqu.724.9.12 | WT |
| | | | | | | | |
| Cer-c.36.10.1 | Mut | Cer-q.42 10.1 | WT | *Cer-u.21. 10.1* | *WT* | Cer-cqu.724.10.1 | WT |
| Cer-c.36.10.2 | WT | Cer-q.42 10.2 | WT | *Cer-u.21. 10.2* | *WT* | Cer-cqu.724.10.2 | WT |
| Cer-c.36.10.3 | WT | Cer-q.42 10.3 | Mut | *Cer-u.21. 10.3* | *WT* | Cer-cqu.724.10.3 | Mut |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Cer-c.36.10.4 | WT | Cer-q.42 10.4 | WT | *Cer-u.21. 10.4* | *WT* | Cer-cqu.724.10.4 | WT |
| Cer-c.36.10.5 | WT | Cer-q.42 10.5 | WT | *Cer-u.21. 10.5* | *WT* | Cer-cqu.724.10.5 | WT |
| Cer-c.36.10.6 | WT | Cer-q.42 10.6 | Mut | *Cer-u.21. 10.6* | *WT* | Cer-cqu.724.10.6 | Mut |
| Cer-c.36.10.7 | WT | Cer-q.42 10.7 | WT | *Cer-u.21. 10.7* | *WT* | Cer-cqu.724.10.7 | WT |
| Cer-c.36.10.8 | WT | Cer-q.42 10.8 | WT | *Cer-u.21. 10.8* | *WT* | Cer-cqu.724.10.8 | WT |
| Cer-c.36.10.9 | WT | Cer-q.42 10.9 | WT | *Cer-u.21. 10.9* | *WT* | Cer-cqu.724.10.9 | WT |
| Cer-c.36.10.10 | Mut | Cer-q.42 10.10 | WT | *Cer-u.21. 10.10* | *WT* | Cer-cqu.724.10.10 | Mut |
| Cer-c.36.10.11 | WT | Cer-q.42 10.11 | Mut | *Cer-u.21. 10.11* | *WT* | Cer-cqu.724.10.11 | Mut |
| Cer-c.36.10.12 | WT | Cer-q.42 10.12 | WT | *Cer-u.21. 10.12* | *WT* | Cer-cqu.724.10.12 | WT |
| | | | | | | | |
| Cer-c.36.11.1 | Mut | Cer-q.42 11.1 | WT | *Cer-u.21. 11.1* | *WT* | Cer-cqu.724.10.13 | Mut |
| Cer-c.36.11.2 | Mut | Cer-q.42 11.2 | WT | *Cer-u.21. 11.2* | *WT* | Cer-cqu.724.10.14 | WT |
| Cer-c.36.11.3 | WT | Cer-q.42 11.3 | WT | *Cer-u.21. 11.3* | *WT* | Cer-cqu.724.10.15 | Mut |
| Cer-c.36.11.4 | WT | Cer-q.42 11.4 | WT | *Cer-u.21. 11.4* | *Mut* | Cer-cqu.724.10.16 | WT |
| Cer-c.36.11.5 | WT | Cer-q.42 11.5 | WT | *Cer-u.21. 11.5* | *Mut* | Cer-cqu.724.10.17 | Mut |
| Cer-c.36.11.6 | Mut | Cer-q.42 11.6 | Mut | *Cer-u.21. 11.6* | *Mut* | Cer-cqu.724.10.18 | WT |
| Cer-c.36.11.7 | Mut | Cer-q.42 11.7 | Mut | *Cer-u.21. 11.7* | *WT* | Cer-cqu.724.10.19 | WT |
| Cer-c.36.11.8 | WT | Cer-q.42 11.8 | Mut | *Cer-u.21. 11.8* | *Mut* | Cer-cqu.724.10.20 | Mut |
| Cer-c.36.11.9 | WT | Cer-q.42 11.9 | WT | *Cer-u.21. 11.9* | *WT* | Cer-cqu.724.10.21 | WT |
| Cer-c.36.11.10 | WT | Cer-q.42 11.10 | WT | *Cer-u.21. 11.10* | *WT* | Cer-cqu.724.10.22 | WT |
| Cer-c.36.11.11 | Mut | Cer-q.42 11.11 | WT | *Cer-u.21. 11.11* | *WT* | Cer-cqu.724.10.23 | Mut |
| Cer-c.36.11.12 | WT | Cer-q.42 11.12 | WT | *Cer-u.21. 11.12* | *WT* | Cer-cqu.724.10.24 | Mut |
| | | | | | | | |
| Cer-c.36.12.1 | WT | Cer-q.42 12.1 | WT | *Cer-u.21. 12.1* | *WT* | Cer-cqu.724.10.25 | WT |
| Cer-c.36.12.2 | WT | Cer-q.42 12.2 | WT | *Cer-u.21. 12.2* | *WT* | Cer-cqu.724.10.26 | Mut |
| Cer-c.36.12.3 | WT | Cer-q.42 12.3 | Mut | *Cer-u.21. 12.3* | *WT* | Cer-cqu.724.10.27 | WT |
| Cer-c.36.12.4 | WT | Cer-q.42 12.4 | WT | *Cer-u.21. 12.4* | *Mut* | Cer-cqu.724.10.28 | Dead |
| Cer-c.36.12.5 | WT | Cer-q.42 12.5 | WT | *Cer-u.21. 12.5* | *Mut* | Cer-cqu.724.10.29 | WT |
| Cer-c.36.12.6 | WT | Cer-q.42 12.6 | WT | *Cer-u.21. 12.6* | *WT* | Cer-cqu.724.10.30 | WT |
| Cer-c.36.12.7 | WT | Cer-q.42 12.7 | WT | *Cer-u.21. 12.7* | *WT* | Cer-cqu.724.10.31 | WT |
| Cer-c.36.12.8 | Mut | Cer-q.42 12.8 | WT | *Cer-u.21. 12.8* | *WT* | Cer-cqu.724.10.32 | WT |
| Cer-c.36.12.9 | WT | Cer-q.42 12.9 | WT | *Cer-u.21. 12.9* | *WT* | Cer-cqu.724.10.33 | WT |
| Cer-c.36.12.10 | Mut | Cer-q.42 12.10 | WT | *Cer-u.21. 12.10* | *WT* | Cer-cqu.724.10.34 | WT |
| Cer-c.36.12.11 | WT | Cer-q.42 12.11 | WT | *Cer-u.21. 12.11* | *WT* | Cer-cqu.724.10.35 | Mut |
| Cer-c.36.12.12 | WT | Cer-q.42 12.12 | Mut | *Cer-u.21. 12.12* | *WT* | Cer-cqu.724.10.36 | Mut |
| | | | | | | | |
| Cer-c.36.13.1 | Mut | Cer-q.42 13.1 | Mut | *Cer-u.21. 13.1* | *WT* | Cer-cqu.724.11.1 | Mut |
| Cer-c.36.13.2 | WT | Cer-q.42 13.2 | WT | *Cer-u.21. 13.2* | *WT* | Cer-cqu.724.11.2 | Dead |
| Cer-c.36.13.3 | WT | Cer-q.42 13.3 | WT | *Cer-u.21. 13.3* | *WT* | Cer-cqu.724.11.3 | Mut |
| Cer-c.36.13.4 | WT | Cer-q.42 13.4 | WT | *Cer-u.21. 13.4* | *Mut* | Cer-cqu.724.11.4 | Mut |
| Cer-c.36.13.5 | WT | Cer-q.42 13.5 | WT | *Cer-u.21. 13.5* | *Mut* | Cer-cqu.724.11.5 | Dead |
| Cer-c.36.13.6 | Mut | Cer-q.42 13.6 | WT | *Cer-u.21. 13.6* | *WT* | Cer-cqu.724.11.6 | Dead |
| Cer-c.36.13.7 | WT | Cer-q.42 13.7 | WT | *Cer-u.21. 13.7* | *Mut* | Cer-cqu.724.11.7 | Mut |
| Cer-c.36.13.8 | WT | Cer-q.42 13.8 | WT | *Cer-u.21. 13.8* | *WT* | Cer-cqu.724.11.8 | Mut |
| Cer-c.36.13.9 | WT | Cer-q.42 13.9 | Mut | *Cer-u.21. 13.9* | *WT* | Cer-cqu.724.11.9 | Mut |
| Cer-c.36.13.10 | WT | Cer-q.42 13.10 | WT | *Cer-u.21. 13.10* | *WT* | Cer-cqu.724.11.10 | Dead |
| Cer-c.36.13.11 | WT | Cer-q.42 13.11 | Mut | *Cer-u.21. 13.11* | *WT* | Cer-cqu.724.11.11 | Mut |
| Cer-c.36.13.12 | Mut | Cer-q.42 13.12 | Mut | *Cer-u.21. 13.12* | *WT* | Cer-cqu.724.11.12 | Mut |
| | | | | | | | |
| Cer-c.36 A | Mut | Cer-q.42 A | Mut | *Cer-u.21 A* | *Mut* | Cer-cqu.724 A | Mut |
| Cer-c.36 B | Mut | Cer-q.42 B | Mut | *Cer-u.21 B* | *Mut* | Cer-cqu.724 B | Mut |
| Quench D | WT | Quench C | WT | *Quench B* | *WT* | Quench A | WT |
| | | | | | | | |
| Total WT | 119 | Total WT | 111 | *Total WT* | *120* | Total WT | 100 |
| Total Mut | 39 | Total Mut | 45 | *Total Mut* | *38* | Total Mut | 54 |