Short report

Population-based analysis of *POT1* variants in a cutaneous melanoma case–control cohort

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ABSTRACT

Pathogenic germline variants in the protection of telomeres 1 gene (*POT1*) have been associated with predisposition to a range of tumour types, including melanoma, glioma, leukaemia and cardiac angiosarcoma. We sequenced all coding exons of the *POT1* gene in 2928 European-descent melanoma cases and 3298 controls, identifying 43 protein-changing genetic variants. We performed POT1-telomere binding assays for all missense and stop-gained variants, finding nine variants that impair or disrupt protein–telomere complex formation, and we further define the role of variants in the regulation of telomere length and complex formation through molecular dynamics simulations. We determine that *POT1* coding variants are a minor contributor to melanoma burden in the general population, with only about 0.5% of melanoma cases carrying germline pathogenic variants in this gene, but should be screened in individuals with a strong family history of melanoma and/or multiple malignancies.

Since the discovery of pathogenic alleles of *CDKN2A* 25 years ago,[1] a number of other variants that increase melanoma risk have been uncovered by genome-wide association studies (GWAS)[2] and the genomic analysis of melanoma-predisposed families. These variants affect biological pathways related to pigmentation (such as alleles of *MC1R*, the '*red hair' gene*), naevus count, including genetic variation adjacent to *PLA2G6*, cell cycle and senescence, comprising changes in *CDKN2A* and *CDK4*, and telomere regulation.[3] Of note, pathogenic variants in the protection of telomeres 1 gene (*POT1*) have been associated with melanoma, as well as other types of cancer such as glioma,[4] leukaemia[5] and lymphoma.[6] As such, pathogenic germline *POT1* variants have recently been recognised as defining a novel tumour predisposition syndrome.[7] Genetic variation proximal to *POT1* has also been found to be associated with melanoma in recent large-scale GWAS studies.[8]

POT1 encodes a single-stranded DNA (ssDNA)–binding protein that forms part of the shelterin complex, a group of proteins that have functions in telomere protection by allowing cells to distinguish the ends of chromosomes from sites of DNA damage and also function in regulating telomere length.[9] In recent years, sequencing of melanoma-predisposed individuals has revealed a number of pathogenic alleles of *POT1* which affect the ability of POT1 to bind to ssDNA and therefore lead to longer and abnormal telomeres.[10–12] This, in turn, may promote carcinogenesis through the accumulation of damage at chromosome ends and a delay in the onset of cell senescence. Further, a recent study has identified *POT1* variants that lead to shorter telomeres,[13] emphasising the need to identify and catalogue the consequences of these genetic changes in carriers.

As estimates have suggested that *POT1* may be the second major high-penetrance melanoma susceptibility gene after *CDKN2A*, being causal of disease predisposition in 2%–4% of *CDKN2A*/*CDK4*-negative families,[10 14] it has been included in multiple panels for genetic testing of melanoma families. As such, and to inform genetic counselling, there is a need to identify which genetic variants abrogate POT1 function leading to telomere dysregulation, as well as to determine their frequency in population-ascertained melanoma cases. In this study, we performed experimental and bioinformatic analyses to identify germline variants that disrupt the POT1–ssDNA complex and lead to telomere length alterations.

This study included 2928 melanoma cases and 3298 controls, making up a total of 6226 European-descent (British) individuals from two distinct melanoma cohorts plus a population cohort (online supplemental methods). We sequenced all *POT1* coding exons on the MiSeq platform (reference transcript: ENST00000357628). After alignment, variant calling and quality filtering, we identified 43 protein-altering variants in *POT1* by Fluidigm PCR-based amplicon sequencing and validated them by target capture with Agilent SureSelect probes and Illumina sequencing (online supplemental methods, online supplemental figure 1, online supplemental table 1, online supplemental file 6). Of these, 19 have not been reported in the gnomAD 2.1 dataset.[15]

To assess whether the detected variants impair telomere regulation, we analysed the ability of in vitro-translated POT1 proteins containing all missense and stop-gained variants (38/43 variants in total (online supplemental table 1) to

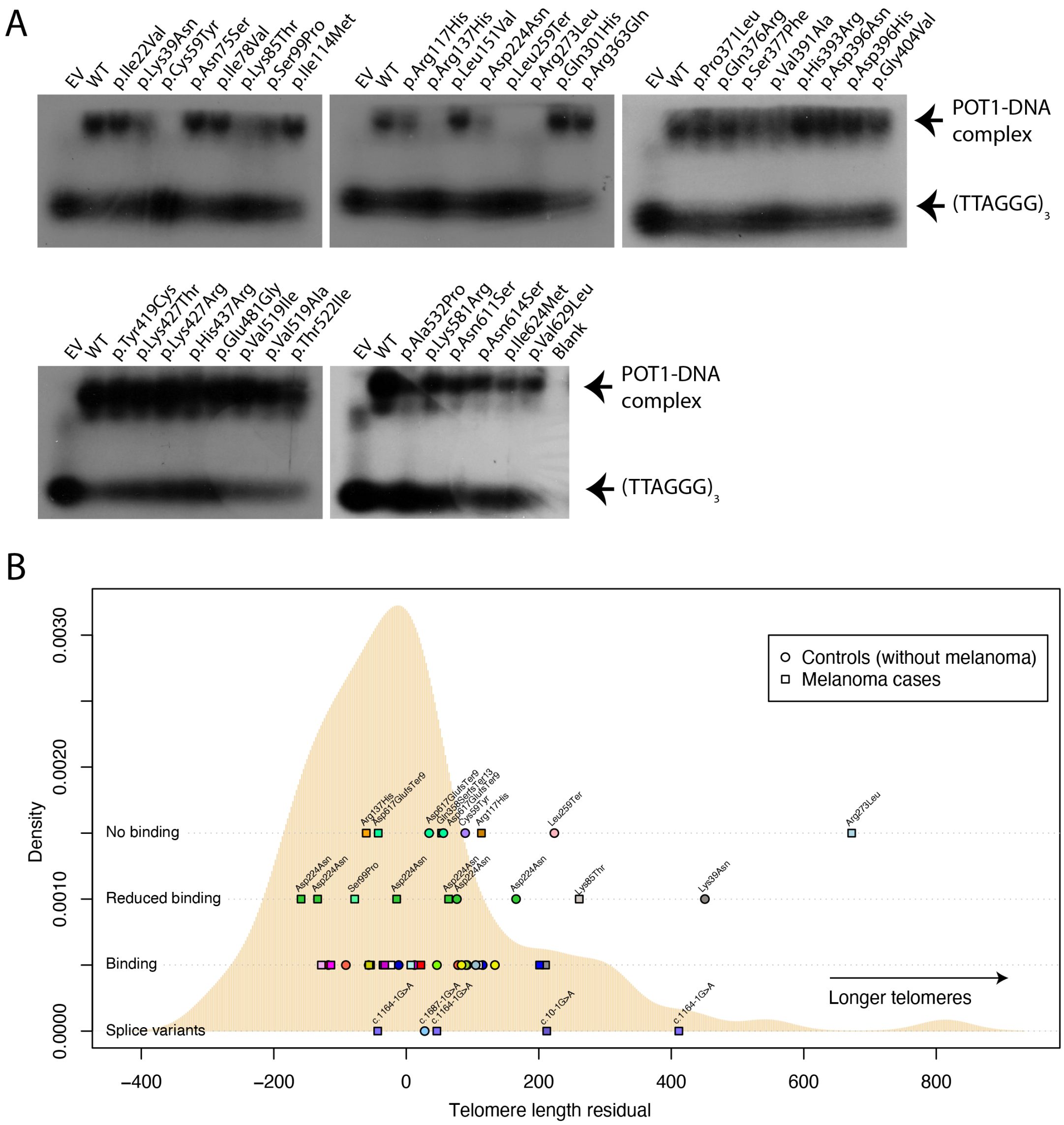

Figure 1 Biological consequences of protection of telomeres 1 gene (*POT1)* variants. (A) Electrophoretic mobility shift assays (EMSAs) are shown testing the ability of in vitro-translated mutant POT1 proteins to bind a telomere-like oligo (TTAGGGTTAGGGTTAGGG). EV, empty vector; WT, wild-type protein. (B) Telomere length of carriers of pathogenic *POT1* variants is depicted over a telomere length distribution of melanoma cases and controls with no pathogenic *POT1* variants. The distribution of the means of residuals from the linear model distribution of telomere lengths for individuals with no *POT1* variants is depicted in beige. The mean of the adjusted telomere lengths for individuals with *POT1* variants is shown on top according to the variant type (no binding, reduced binding or binding according to EMSA and splice variants). Melanoma cases are shown in squares and controls in circles. Each variant is shown in a different colour. For the 'Binding' row, the variants from left to right are p.Pro371Leu, p.Ile624Met, p.Asn611Ser, p.Lys427Thr, p.Asp396His, p.Val629Leu, p.His393Arg, p.Leu151Val, p.Asn75Ser, p.His393Arg, p.Lys581Arg, p.Glu481Gly, p.Ser377Phe, p.Asn614Ser, p.Tyr419Cys/p.Gly404Val, p.Asp396Asn, p.Ile78Val, p.Val519Ala, p.Thr522Ile, p.Ile114Met, p.Arg363Gln/p.Val391Ala, p.Lys427Arg, p.His437Arg, p.Val519Ile, p.His393Arg and p.Ala532Pro.

bind to a telomere-like oligo via electrophoretic mobility shift assay (EMSA) experiments (online supplemental methods)). Our results indicate that four variants completely disrupted POT1–ssDNA complex formation (p.Cys59Tyr, p.Arg137His, p.Leu259Ter and p.Arg273Leu), whereas a further five appear to reduce the affinity of the interaction (p.Lys39Asn, p.Lys85Thr, p.Ser99Pro, p.Arg117His and p.Asp224Asn) (figure 1A; online supplemental figure 2). Of these, six had not been reported in the gnomAD 2.1 dataset, and, of note, as expected, all variants that altered POT1-ssDNA binding fall within the *N*-terminal OB domains.

Variants were classified in three groups according to their pathogenicity: Group 1 variants were confirmed by EMSA to disrupt the POT1–ssDNA complex or were those strongly suspected as pathogenic (frameshift and splice acceptor variants). We included variants with reduced binding in this category due to their high conservation across species (online supplemental figure 3) and prior evidence that they may be pathogenic (p.Arg117His[16] and p.Asp224Asn[11]). In total, 14/43 variants were classified in this group, with 10 of these falling in the OB domains (figure 2; online supplemental tables 1 and 2). Group 2 variants were those predicted deleterious and probably damaging by both the SIFT and PolyPhen algorithms and did not disrupt POT1–ssDNA binding (4/43 variants). These variants may impair the function of the protein in other ways. The remaining variants (25) were classified into Group 3.

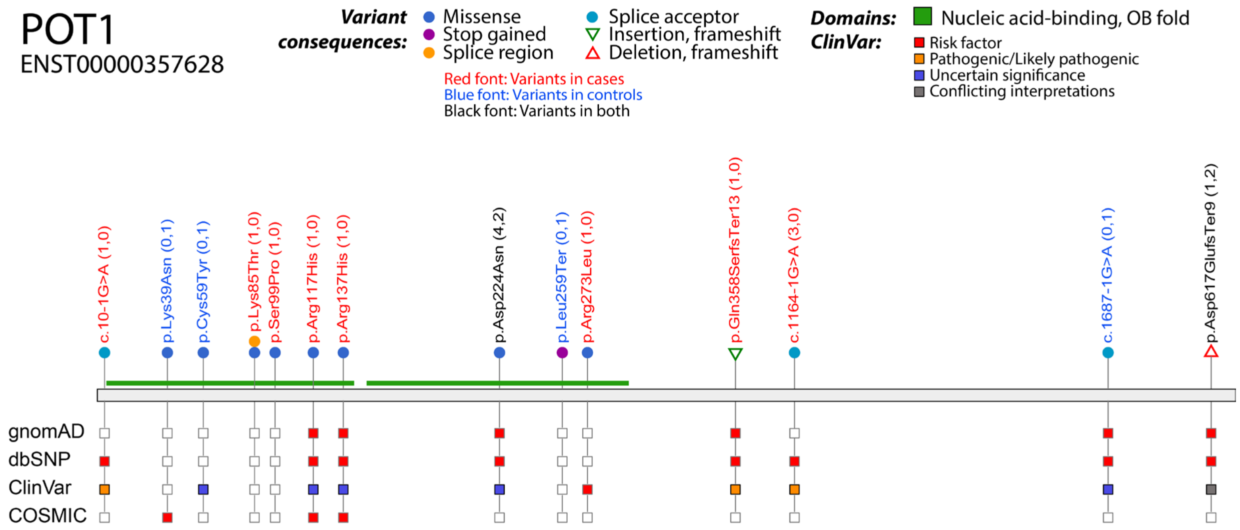

Figure 2 Schematic diagram of Group 1 POT1 variants. Variants are shown on the primary protein structure with their consequence (in a coloured circle or triangle) and their presence (red square) or absence (empty square) in publicly available datasets (gnomAD exomes v2.1, dbSNP build 151 and COSMIC v86). The ClinVar track indicates the pathogenicity prediction in ClinVar release 20220804. The OB domains are shown in green. Variants in red font colour are found in cases, those in blue font colour are found in controls and those in black are found in both cases and controls. For details on numbers of cases and controls, see online supplemental table 1. Figure created with VCF/Plotein.[22]

The majority of cases and controls in this study did not carry a *POT1* variant (94.1% cases, 95.1% controls), and the majority of those with a variant had only one variant. No person had more than two variants. In total, three persons had a Group 1 variant and a Group 3 variant (two cases, one control) while five persons had two Group 3 variants (three cases, two controls). Given the limited number of persons with two variants, each case and control is classified by their most severe mutation. For Group 1, 15 cases (0.51%) carried a variant, while 8 (0.24%) controls did (p value=0.08, OR for carrying a Group 1 variant compared with no variant (OR)=2.11, 95% CI (0.89 to 5.00)). For Groups 1+2 combined, 22 cases (0.75%) carried a variant, while 14 controls (0.42%) did (p value 0.096, OR=1.78). Finally, for Group 3, 126 cases (4.3%) carried a variant as did 149 controls (4.6%) (two-tailed Fisher's exact test, p value 0.66) indicating no evidence of increased risk associated with this variant class. Overall, then while about twice as many cases as controls carried predicted pathogenic variants in *POT1*, this difference was not conventionally statistically significant likely because of limited power even with a study this size. There were also no differences in age of onset, sex, family history or site of presentation by pathogenicity group when compared with those without one of the classified mutations (online supplemental tables 3−6).

We next sought to determine whether the variants we detected had any effect on telomere regulation. For this, we measured telomere length in *POT1* variant carriers and non-carriers from the same populations (online supplemental methods). After standardising lengths by plate and adjusting them for cohort via a linear model (online supplemental table 7, online supplemental figure 4), we observed that only the individuals carrying the p.Lys39Asn (percentile 98 when compared with controls) and the p.Arg273Leu (percentile 99 when compared with controls) variants had telomeres that were substantially longer than the mean (figure 1B). We also observed that some individuals with splice variants or variants that showed reduced DNA binding also had telomeres on the longer side of the distribution (eg, Lys85Thr, percentile 91, p.Leu259Ter, percentile 90, one individual carrying c.1164–1G>A, percentile 97) but others did not (eg, p.Ser99Pro, percentile 31, most individuals with variants in splice sites). Individuals with the p.Asp224Asn variant had telomere lengths scattered throughout the whole distribution in contrast to previous reports suggesting that these variants increase telomere length[11] (figure 1B).

Because the p.Lys39Asn, p.Cys59Tyr and p.Asp224Asn variants are found in controls and show POT1–ssDNA complex disruption, we further investigated those using molecular dynamics simulations (online supplemental methods). Our results suggest that all three variants affect the dynamics of the system when compared with the wild-type (WT) structure, as evidenced by the first and second normal modes (online supplemental figure 5A–H, online supplemental movie). Existing protein structures for POT1 also imply that there are conformational differences between the POT1–ssDNA and POT1–ACD structures.[17 18] As a result, the structural differences noted within the POT1 mutant proteins investigated here may affect shelterin complex formation, but further investigation is necessary. Additional analyses of root mean square deviation, root mean square fluctuation, residue-wise correlations, secondary structure, energy decomposition analysis and hydrogen bond interactions are all consistent with the computational results reported herein (online supplemental figure 5I-L, 6–18, online supplemental tables 8-12). MM-GBSA was used to assess the protein:DNA-binding affinities. We calculated a ΔΔH of −0.6 to –1.3, and 21.6 kcal/mol for p.Lys39Asn, p.Asp224Asn and p.Cys59Tyr, respectively. These enthalpies are in agreement with the experimental binding pattern discussed above.

Even though *POT1* seems to be the second major melanoma susceptibility gene, with 2%–4% of *CDKN2A*/*CDK4*-WT families carrying a pathogenic coding variant in this gene, its contribution to melanoma risk burden in the general population is minor, with ~0.5% of cases carrying pathogenic variants. Telomere length calculations confirm known associations of variants with longer telomeres (p.Arg273Leu,[10] p.Arg117His[11 16]) and found associations with other pathogenic variants (p.Lys39Asn, p.Lys85Thr and confirmation of longer telomere length for p.Ala532Pro, percentile 93, a variant originally reported in Ref. 11), but for other variants the association with length was not clear (eg, all three carriers of c.1164–1G>A and six of p.Asp224Asn had telomere lengths scattered throughout the distribution). Although a prior study had shown slightly longer telomeres for carriers of p.Arg117His,[11] the carrier melanoma case in this cohort had normal-length telomeres. This may reflect the many mechanisms, including other genetic variants and lifestyle, by which telomere length can be affected or the assays used for telomere analysis. Telomere length for some control individuals (without reported melanoma) with pathogenic variants (eg, p.Lys39Asn and both controls carrying p.Asp224Asn) also showed an increase in telomere length, which may portend an increased risk of tumourigenesis in these individuals or indicate that other factors are necessary for melanoma genesis.

Although in this study we have attempted to identify pathogenic *POT1* variants through DNA-binding assays, the function of POT1 proteins with variants outside the OB domains may be compromised by other mechanisms. For example, another study concluded that the *POT1* p.Ala532Pro variant shows impaired ACD binding, which may also lead to telomere dysregulation.[19] Therefore, further systematic experiments are needed to address other POT1 functions, such as telomere fragility, to provide a more complete catalogue of variants that alter protein function and therefore that lead to cancer predisposition.

While the number of *POT1* variant carriers in this study is too limited to draw strong conclusions, the lack of any statistically significant difference in age of onset between variant carriers (54.7 years) and non-carriers (54.4 years) in the general population needs some consideration. By comparison and looking at another melanoma high-penetrance gene, in the Leeds Melanoma Cohort, *CDKN2A* variant carriers have an average age of onset of 50 years (based on data included in Ref. 20). The literature contains many examples of families with particularly early ages of onset for melanoma; these extreme families likely represent the product of interactions of high penetrance variants (in genes such as *CDKN2A* and *POT1*) with contributing lower penetrance variants and risk-associated lifestyle behaviours. Therefore, the analysis of population-based samples provides a more complete description of the impact of high penetrance variants in the general population. A comparable scenario applies to breast cancer; recent analysis of the UK SEARCH study containing about 12 700 breast cancer diagnosed under the age of 70 years showed an average age of onset of 54.5 years for women without a known variant in a high penetrance gene. Only *BRCA1* and *BRCA2* variant carriers had notably earlier ages of onset (46.7 and 50.6 years, respectively), while carriers of variants in rarer predisposing genes (*CHEK2*, *PALB2*, *ATM*, *RAD51C*) had average age of onset of between 51.1 years and 58.2 years (A Antoniou, University of Cambridge, personal communication based on data in Ref. 21).

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Contributors IS-W: sequencing and telomere length data analysis, RO: sequencing data analysis, EML, MGMdlG: molecular dynamics simulation analysis, MH, KAP: qPCR assays and sample management, SO: data analysis, JH, JCT: sample management, CCW: telomere-binding assays, VI: sequence variant calling, JN-B: patient management, manuscript writing, TB: statistical analysis supervision, manuscript writing, GAC: molecular dynamics simulation analysis, manuscript writing, MI: statistical analysis supervision, DA: conceived and supervised study, manuscript writing, CDR-E: conceived and supervised study, sequencing and variant data analysis, manuscript writing.

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Competing interests None declared.

Ethics approval This study involves human participants. Samples used in this study came from three different cohorts. Their collection and use in genetic studies was approved by three different Research Ethics Boards. The Leeds Melanoma Case Control Study has recruited population-ascertained melanoma cases and the same sex and 5-year age group controls predominantly from the Yorkshire, UK geographical area since the year 2000 (NRES Committee North East—Northern and Yorkshire, MREC/01/3/057). Additionally, samples were included from the Study of Epidemiology and Risk Factors in Cancer Heredity (SEARCH) series of population-based studies in Eastern England (Cambridgeshire South Research Ethics Committee, 05/MRE05/1). Finally, controls were supplemented with samples from the Wellcome Trust Case Control Consortium (South East Multicentre Research Ethics Committee, 05/Q0106/74). Patients consented for their samples to be used in genetic studies 15+ years ago, though not for this specific study.

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Supplementary Materials

Materials and methods

Participants and sample collection. Samples used in this study came from three different cohorts.

(i) The Leeds Melanoma Case Control Study (LMC) recruited population-ascertained melanoma cases and controls. Cases came from Yorkshire and the North East of England, with recruitment starting in the year 2000 (NRES Committee North East - Northern and Yorkshire, MREC/01/3/057) [1] (**Supplementary Table 13**). Controls were recruited from the GPs of cases participating in the study and were recruited so that their age and sex distribution was similar to the distribution among cases. The controls and about half the cases were screened once at recruitment for skin lesions and were asked about family history. The remaining cases completed self-report questionnaires about family history.

(ii) Additionally, samples were included from the Study of Epidemiology and Risk Factors in Cancer Heredity (SEARCH) series of population-based studies initially in Eastern England but extended to Scotland (Cambridgeshire South Research Ethics Committee, 05/MRE05/1) [2] (**Supplementary Table 13**). Healthy control participants, *i.e*. people with no history of cancer to be used as comparisons with the cancer patients, were also recruited from 2003 to 2009 in East Anglia.

(iii) Finally, controls were supplemented with samples from the Wellcome Trust Case Control Consortium [3] (South East Multicentre Research Ethics Committee, 05/Q0106/74) (**Supplementary Table 13**). For the WTCCC controls, only basic information provided by the Wellcome Trust was available under the terms of the ethics agreement.

Sequencing and variant calling. DNA from whole blood was extracted for exon capture and sequencing. We used Fluidigm PCR-based amplicon sequencing to amplify all of the coding exons and splice junctions of the *POT1* gene in 7,024 samples and sequenced these products on the MiSeq platform by single-read sequencing. The reference sequence used was ENST00000357628. After aligning with BWA and filtering to keep only highly covered samples (Those with >94% of coding *POT1* exon bases covered >= 10 reads with MQ >= 50 and base quality >= 20), keeping only one sample out of each pair of relatives, removing samples with non-European ancestry and samples from patients that withdrew from the study, and removing related controls, 6,226 samples remained. These samples included 2,928 cases (1,574 from the Leeds Case Control Consortium and 1,354 from the SEARCH Consortium) and 3,298 controls (1,431 from the WTCCC collection, 459 from the Leeds Case Control Consortium and 1,408 from the SEARCH Consortium) (**Supplementary Table 13**). We took forward for analysis the union of calls made by HaplotypeCaller (command line below in this section) and Samtools mpileup (parameters -t DP,SP -C50 -m2 -F0.0005 -d 10000 -ug), and performed quality variant filtering (mpileup: QUAL>=20 && (DP4[2]>30 || DP4[3]>30); GATK: QUAL>=20 && AD[0:1]>30). We also removed indel calls between GRCh37 coordinates 7:124475296-124475328, as this highly repetitive region (at an intron-exon boundary) seems to be germline microsatellite unstable and may be prone to false positive calls. We called 141 different protein-altering variants (missense, stops, frameshifts and splice acceptor/donor sites) in 3,546 samples electing to use a low stringency approach so as to capture all possible variants for validation. Validation by re-sequencing with Sanger or Illumina technologies was performed for at least one sample for all detected variants, often re-sequencing all carrier samples (**Supplementary Table 14**). Illumina sequencing was performed by exome capture with Agilent Technologies probes, using the WTSI v4 Solid Tumor Panel which included other established melanoma predisposition genes such as *CDKN2A*, *BAP1* and *CDK4*. Sequencing captured all exons and exon/intron boundaries of *POT1*, and succeeded for 164 samples. Overall, 158/164 samples were covered to an average depth higher than 10x across all *POT1* coding exons (**Supplementary Table 15**). Variants were called from these data using Samtools mpileup in pooled mode. By applying this approach, we validated 40 unique variants originally identified using the Fluidigm PCR-based amplicon but importantly identified no new variant positions by this method. Capillary resequencing of variants found in the 19 samples that failed library preparation or were included in a later sequencing effort confirmed three additional variants, for a total of 43/141 protein-altering variants confirmed (**Supplementary Tables 1,2, 16**). A simplified flowchart with these analysis steps can be found in **Supplementary Figure 19**. No additional variants were called in the resequenced samples. Consequences were predicted with the Variant Effect Predictor (VEP), from Ensembl release 104, using the web tool with the GRCh37 human reference genome. Since our exon capture sequenced additional known melanoma driver genes (above) we screened all samples found to carry mutations in *POT1* to exclude the possibility that they also carried pathogenic variants in drivers *CDK4*, *CDKN2A* and *BAP1*. Three protein-coding variants were found in *CDKN2A* in *POT1* variant carriers, although these *POT1* variants were classified as benign according to our G-strand binding assays (**Supplementary Table 17**, reference transcripts *CDKN2A*: ENST00000304494, *CDK4*: ENST00000257904, *BAP1*: ENST00000460680). For the pathogenicity group classification, whenever there were two *POT1* variants found in the same patient, we classified the patient in the higher pathogenicity group. No participant had more than one Group 1 or 2 variants.

***In vitro* translation and G strand binding assays**. pEX-POT1 plasmid vectors, harboring wild-type or mutant POT1 ORF sequences downstream of a T7 promoter, were used for in vitro translation reactions with TNT coupled reticulocyte lysate kit (Promega) according to the manufacturer’s instructions. Protein expression was verified by immunoblotting an aliquot of each reaction with anti-POT1 antibodies (Abcam, ab124784). A telomeric oligonucleotide probe (GGTTAGGGTTAGGGTTAGGG) was end-labelled using [-32P] ATP (Perkin Elmer) with T4 polynucleotide kinase (New England Biolabs). Unincorporated nucleotides were removed using illustra MicroSpin G-25 columns (GE Healthcare) according to the manufacturer’s instructions. DNA-binding assays were performed by mixing 5µl translation reaction in 20 µl final volume containing binding buffer (25 mM HEPES-NaOH [pH 7.5], 100 mM NaCl, 1 mM EDTA and 5% glycerol), 1 µg poly (dI-dC) (Thermo) and 10 nM [32P]-labelled telomeric oligonucleotide probe for 10 min at room temperature. Reactions were separated on 6% DNA retardation gels (Novex) in 0.5 TBE buffer at 80 V. Gels were dried and exposed to Hyperfilm MP film (Amersham), which was developed using a Compact X4 machine (Xograph).

Analysis of telomere length by telomere repeat PCR. We measured telomere length in all Illumina re-sequenced cases and controls from the Leeds, SEARCH and WTCC cohorts who carried a potential *POT1* variant according to the initial Fluidigm analysis, as well as age and sex-matched controls (A total of 174 samples (of which 66 belong to the Leeds cohort, 86 to SEARCH and 22 to WTCC; 105 are melanoma cases and 69 are non-melanoma controls, and 48 pathogenic POT1 variant carriers and 126 non-carriers)). Telomere length was quantified by real-time PCR using the 'Absolute Human Telomere Length Quantification qPCR Assay Kit (AHTLQ)' (ScienCell Research Laboratories, CA, USA) according to the manufacturer’s instructions. Each DNA sample was amplified in two separate reactions: using the telomere (TEL) primer set; and the single copy reference (SCR) primer set. The telomere primer set recognises and amplifies telomere sequences. The SCR primer set amplifies a 100bp region on chromosome 17, and acts as a reference for normalisation.

Reactions were carried out in 20 µL volume: 1 µL DNA (5ng); 2 µL primer (TEL or SCR); 10 µL 2×GoldNStart TaqGreen qPCR master mix; and 7 µL nuclease-free water. A QuantStudio 5 Real Time PCR machine (Life Technologies, CA, USA) was used for qPCR, using a 96-well plate format. The PCR conditions were: initial denaturation at 95°C for 10 minutes, then 32 cycles of 95°C for 20 seconds, 52°C for 20 seconds and 72°C for 45 seconds. All reactions were performed in triplicate, and the same reference genomic DNA sample was included in each run. Data were analysed using the QuantStudio Design and Analysis Software version 1.4.1. (Life Technologies, CA, USA), and absolute telomere length was calculated by reference to the DNA standard using comparative ddCq according to the AHTLQ kit instructions.

A linear model adjusting for age at diagnosis, sex and cohort was done with the individuals that did not have pathogenic variants (pathogenic variants were defined as all detected variants except for p.Ile22Val, p.Gln301His, p.Gln376Arg, and p.Gly404Val, which all have a gnomAD overall allele frequency higher than 1 x 10^{-4}), whether melanoma cases or controls. The linear model showed that neither age nor sex where significantly related to the telomere length in our data. There is probably too much noise introduced by cohort origin, so we opted for using only cohort to control our data. The residuals of this linear model were used to create a telomere length distribution for this cohort. Telomere length adjustment for pathogenic variant carrier individuals was done separately with the same parameters calculated from the population distribution.

Molecular dynamics simulations of WT and variant POT1-ssDNA. Molecular dynamics (MD) simulations were performed using AMBER20's pmemd.cuda with the ff19SB force field for protein and OL15 for DNA[4–7]. The model was constructed from PDB ID 1XJV,[8, 9] using *Coot* and MolProbity to alleviate bad clashes[10, 11]. We used the Modeller interface in UCSF Chimera to incorporate missing residues,[12–14] as well as Chimera's integrated Dunbrack rotamer library to create the p.Lys39Asn, p.Cys59Tys, and p.Asp224Asn variants[15]. The systems were solvated with TIP3P water in a cube that extended 12 Å from the complex surface, and potassium was added to neutralize the charge of the system[16]. All MD simulations were run in triplicate for 250 ns while holding the number of atoms, pressure, and temperature constant (NPT ensemble) with the Langevin thermostat and barostat. A 9 Å cutoff was used for long-range non-bonded interactions with the smooth particle mesh Ewald method for electrostatics[17]. AMBER’s cpptraj program was used for root mean square deviation (RMSD), root mean square fluctuation (RMSF), hydrogen bond interactions, and secondary structure analyses[18]. Both cpptraj and the ProDy module in VMD were used for normal mode analysis[19, 20]. A Fortran90 program developed by the Cisneros group was used to perform an energy decomposition analysis (EDA) on each simulation[21]. The data.table, tidyverse, and abind packages of R were used to analyze the EDA data and hydrogen bond interactions[22–25]. The MM-GBSA method, implemented through

MMPBSA.py in AmberTools, was used to calculate the binding enthalpies between the protein and ssDNA. [26–28] VMD, UCSF Chimera, gnuplot, matplotlib, and ggplot2 were used for data visualization and image creation[14, 20, 29–31].

Command lines used. GATK HaplotypeCaller command line:

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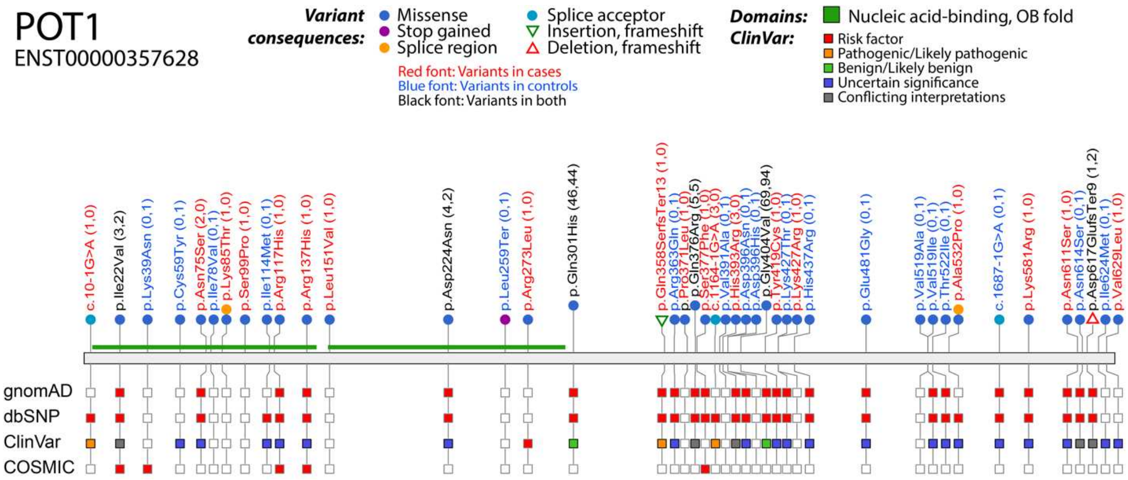
gatk_key=gatk.key tag=NA read_filter=[] disable_read_filter=[] intervals=[pot1.bed, 7:1-159138663] excludeIntervals=null
interval_set_rule=INTERSECTION interval_merging=ALL interval_padding=0 reference_
sequence=hs37d5.fa nonDeterministicRandomSeed=false disableDithering=false maxRunti
me=-1 maxRuntimeUnits=MINUTES downsampling_type=BY_SAMPLE downsample_to_fraction=null
downsample_to_coverage=500 baq=OFF baqGapOpenPena
lty=40.0 refactor_NDN_cigar_string=false fix_misencoded_quality_scores=false allow_potentially_misencoded_quality_scores=false
useOrigi
nalQualities=false defaultBaseQualities=-1 performanceLog=null BQSR=null quantize_quals=0 disable_indel_quals=false
emit_original_quals=false preserve_qscores_less_than=6 globalQScorePrior=-1.0 validation_strictness=SILENT
remove_program_records=false keep_program_records=false sample_rename_mapping_file=null unsafe=null
disable_auto_index_creation_and_locking_when_reading_rods=false no_cmdline_in_header=false sites_only=false
never_trim_vcf_format_field=false bcf=false bam_compression=null simplifyBAM=false disable_bam_indexing=false
generate_md5=false num_threads=1 num_cpu_threads_per_data_thread=1 num_io_threads=0 monitorThreadEfficiency=false
num_bam_file_handles=null read_group_black_list=null pedigree=[] pedigreeString=[] pedigreeValidationType=STRICT
allow_intervals_with_unindexed_bam=false generateShadowBCF=false variant_index_type=DYNAMIC_SEEK
variant_index_parameter=-1 logging_level=ERROR log_to_file=null help=false version=false
out=/example_path/1_gatk_haplotype_caller_with_genome_chunking/7_1-159138663.gatk_haplotype.vcf.gz
likelihoodCalculationEngine=PairHMM heterogeneousKmerSizeResolution=COMBO_MIN dbsnp=(RodBinding name=
source=UNBOUND) dontTrimActiveRegions=false maxDiscARExtension=25 maxGGAARExtension=300 paddingAroundIndels=150
paddingAroundSNPs=20 comp=[] annotation=[ClippingRankSumTest, DepthPerSampleHC] excludeAnnotation=[] debug=false
useFilteredReadsForAnnotations=false emitRefConfidence=NONE bamOutput=null bamWriterType=CALLED_HAPLOTYPES
disableOptimizations=false annotateNDA=false heterozygosity=0.001 indel_heterozygosity=1.25E-4
standard_min_confidence_threshold_for_calling=4.0 standard_min_confidence_threshold_for_emitting=4.0
max_alternate_alleles=6 input_prior=[] sample_ploidy=2 genotyping_mode=DISCOVERY alleles=(RodBinding name=
source=UNBOUND) contamination_fraction_to_filter=0.0 contamination_fraction_per_sample_file=null p_nonref_model=null
exactcallslog=null output_mode=EMIT_VARIANTS_ONLY allSitePLs=false gcpHMM=10
pair_hmm_implementation=VECTOR_LOGLESS_CACHING pair_hmm_sub_implementation=ENABLE_ALL
always_load_vector_logless_PairHMM_lib=false phredScaledGlobalReadMismappingRate=45 noFpga=false sample_name=null
kmerSize=[10, 25] dontIncreaseKmerSizesForCycles=false allowNonUniqueKmersInRef=false numPruningSamples=1
recoverDanglingHeads=false doNotRecoverDanglingBranches=false minDanglingBranchLength=4 consensus=false
maxNumHaplotypesInPopulation=128 errorCorrectKmers=false minPruning=2 debugGraphTransformations=false
allowCyclesInKmerGraphToGeneratePaths=false graphOutput=null kmerLengthForReadErrorCorrection=25
minObservationsForKmerToBeSolid=20 GVCFGQBands=[1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22,
23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57,
58, 59, 60, 70, 80, 90, 99] indelSizeToEliminateInRefModel=10 min_base_quality_score=10 includeUmappedReads=false
useAllelesTrigger=false doNotRunPhysicalPhasing=true keepRG=null justDetermineActiveRegions=false dontGenotype=false
dontUseSoftClippedBases=false captureAssemblyFailureBAM=false errorCorrectReads=false pcr_indel_model=CONSERVATIVE
maxReadsInRegionPerSample=10000 minReadsPerAlignmentStart=10 mergeVariantsViaLD=false activityProfileOut=null
activeRegionOut=null activeRegionIn=null activeRegionExtension=null forceActive=false activeRegionMaxSize=null
bandPassSigma=null maxProbPropagationDistance=50 activeProbabilityThreshold=0.002 min_mapping_quality_score=20
filter_reads_with_N_cigar=false filter_mismatching_base_and_quals=false filter_bases_not_stored=false
```

VEP command:

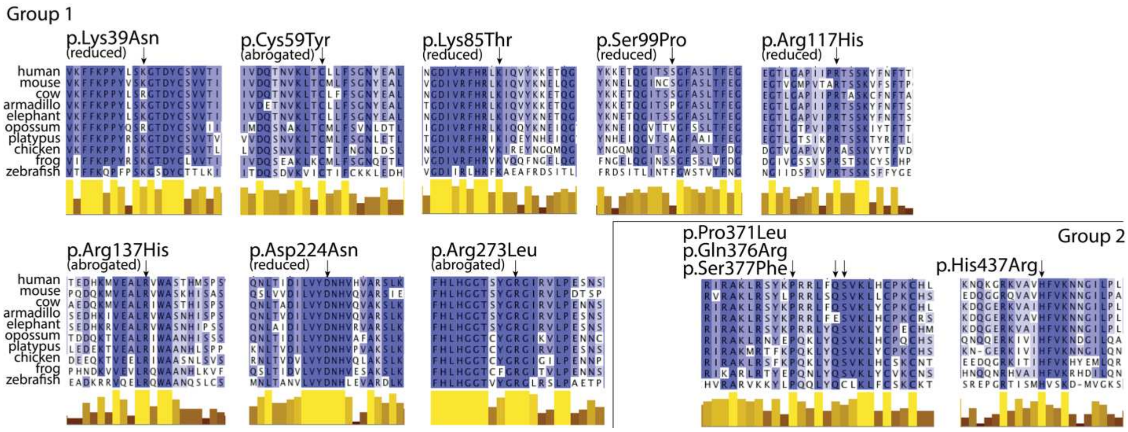
```
./vep --af --af_
 --appris --biotype --buffer_size 500 --check_existing --distance 5000 --mane --polyphen b --pubmed --regulatory --sift b --species
homo_sapiens --symbol --transcript_version --tsl --cache --input_file [input_data] --output_file [output_file] --port 3337
```

Supplementary Figures and legends

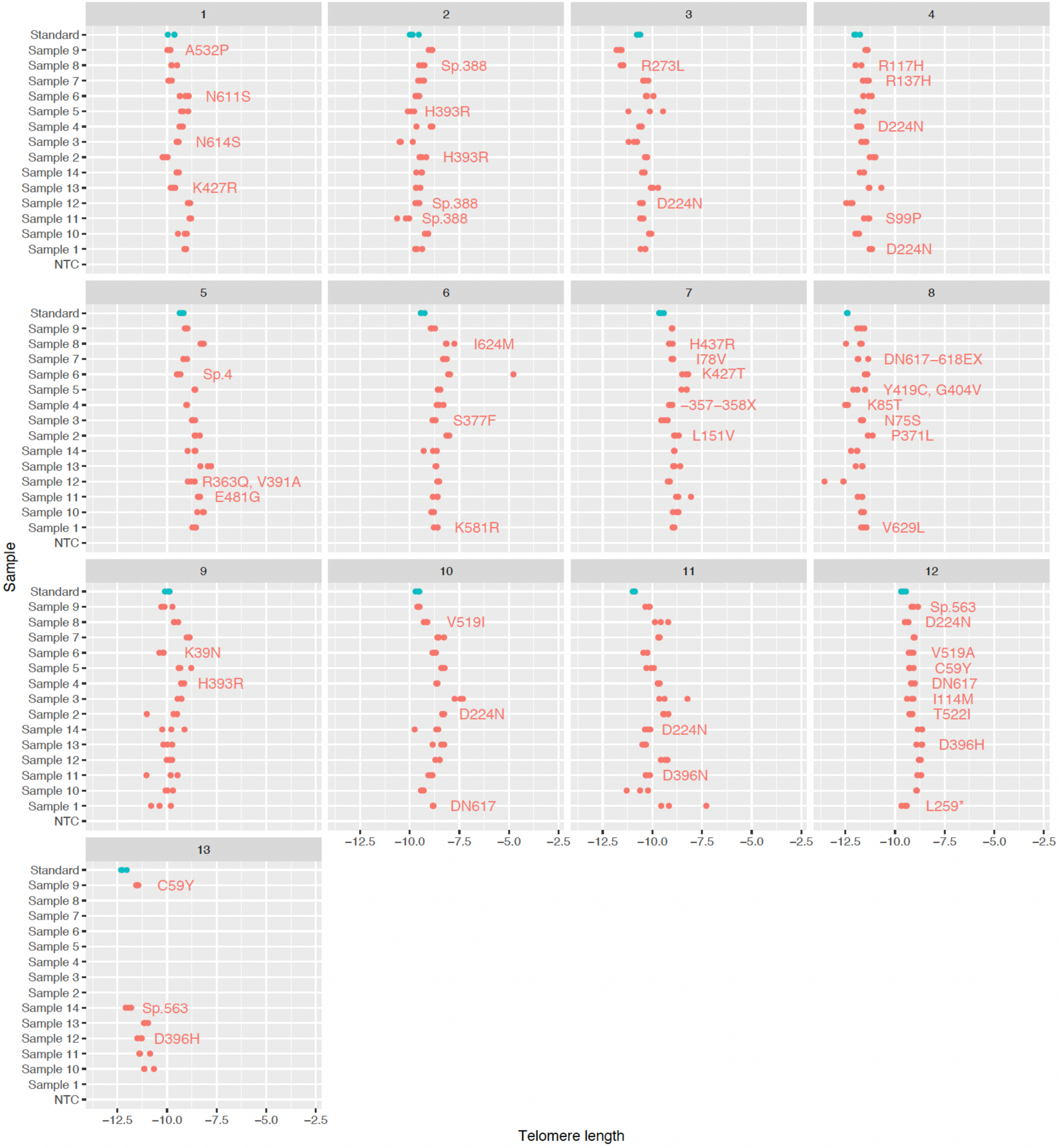


Supplementary Figure 1. Schematic diagram of POT1 variants identified in this case-control cohort study. Variants are shown on the primary protein structure with their consequence (in a colored circle or triangle) and their presence (red square) or absence (empty square) in publicly available datasets (gnomAD exomes v2.1, dbSNP build 151 and COSMIC v86). The ClinVar track indicates the pathogenicity prediction in ClinVar release 20220804. The OB domains are shown in green. Variants in red font colour are found in cases, those in blue font colour are found in controls and those in black are found in both cases and controls. For details on numbers of cases and controls see **Supplementary Table 1**. Figure created with VCF/Plotein [12].

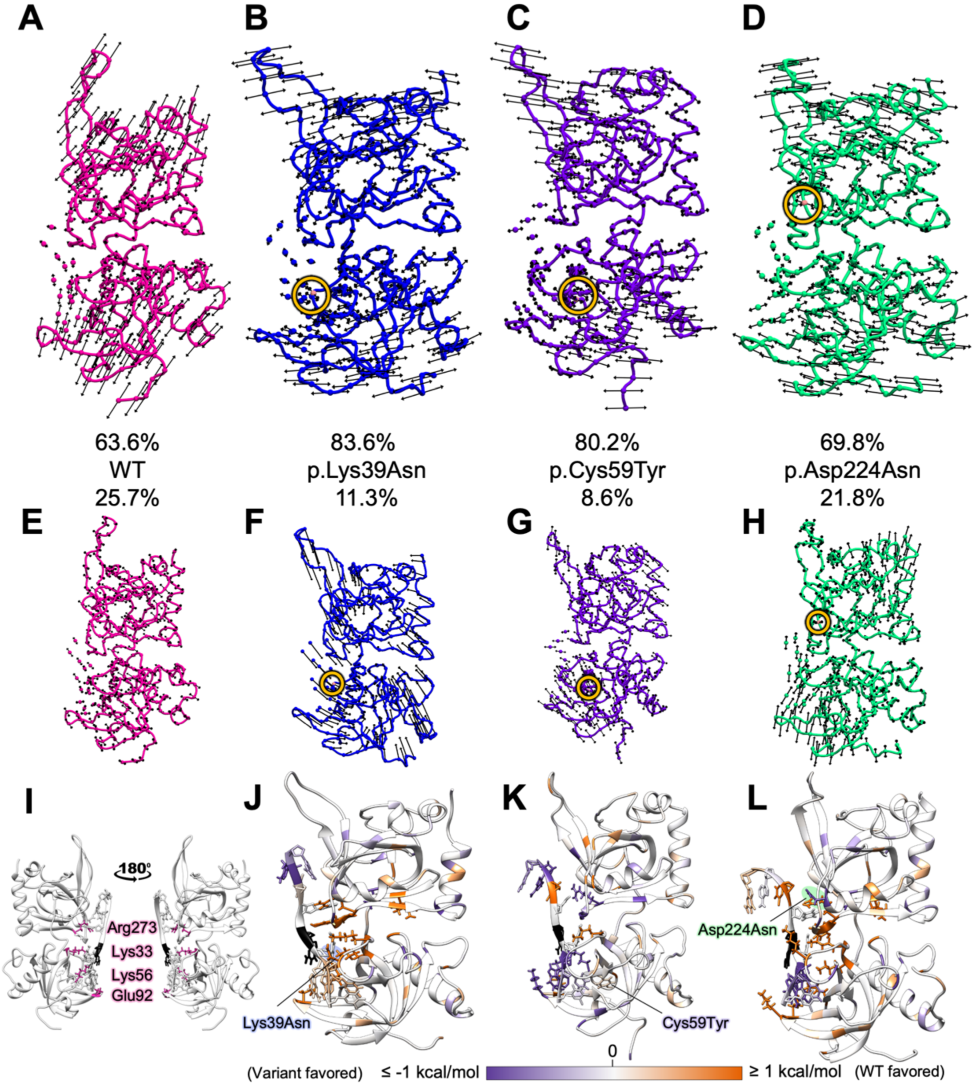
Supplementary Figure 2. Expression control for the POT1-ssDNA binding assays. The POT1 protein is shown alongside the expression of actin in each reticulocyte lysate reaction. The gels are shown in the same order as those in Figure 2A.



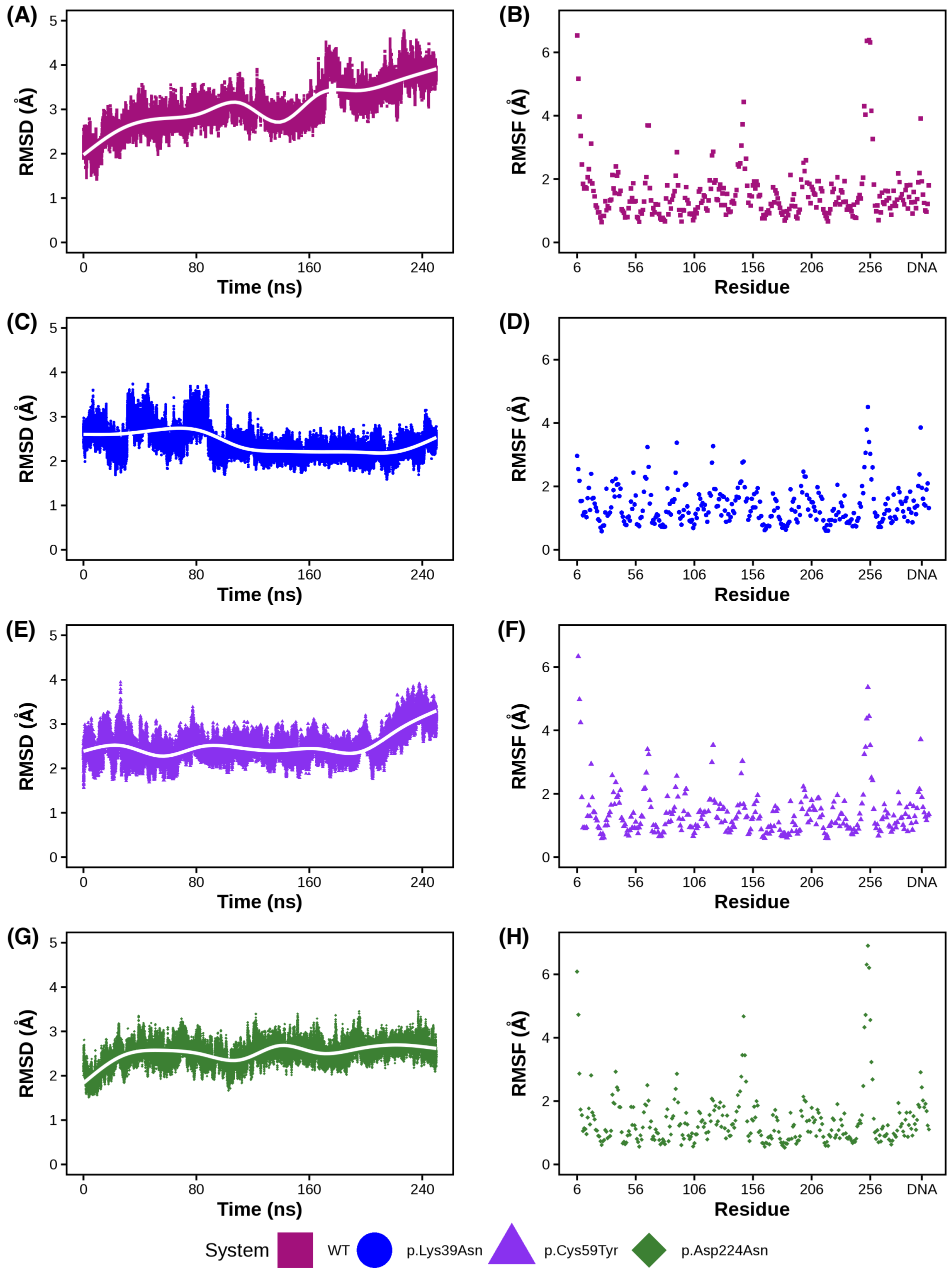
Supplementary Figure 3. Multi-species alignment of the POT1 protein sequence for missense variants in Pathogenicity Groups 1 and 2. A darker shade in an amino acid indicates higher sequence conservation across species. At the bottom, the height and color of the bars indicate sequence conservation level (taller and lighter bars indicate higher conserved residues). Protein sequences were downloaded from NCBI and are: NP_056265.2 (human), NP_598692.1 (mouse), DAA30462.1 (cow), XP_004478310.1 (armadillo), XP_003407293.1 (elephant), XP_007504312.1 (opossum), XP_001508179.2 (platypus), NP_996875.1 (chicken), AAI71328.1 (frog) and ADY16707.1 (zebrafish). Alignments were done with CLUSTAL O v 1.2.4 and rendered with Jalview.



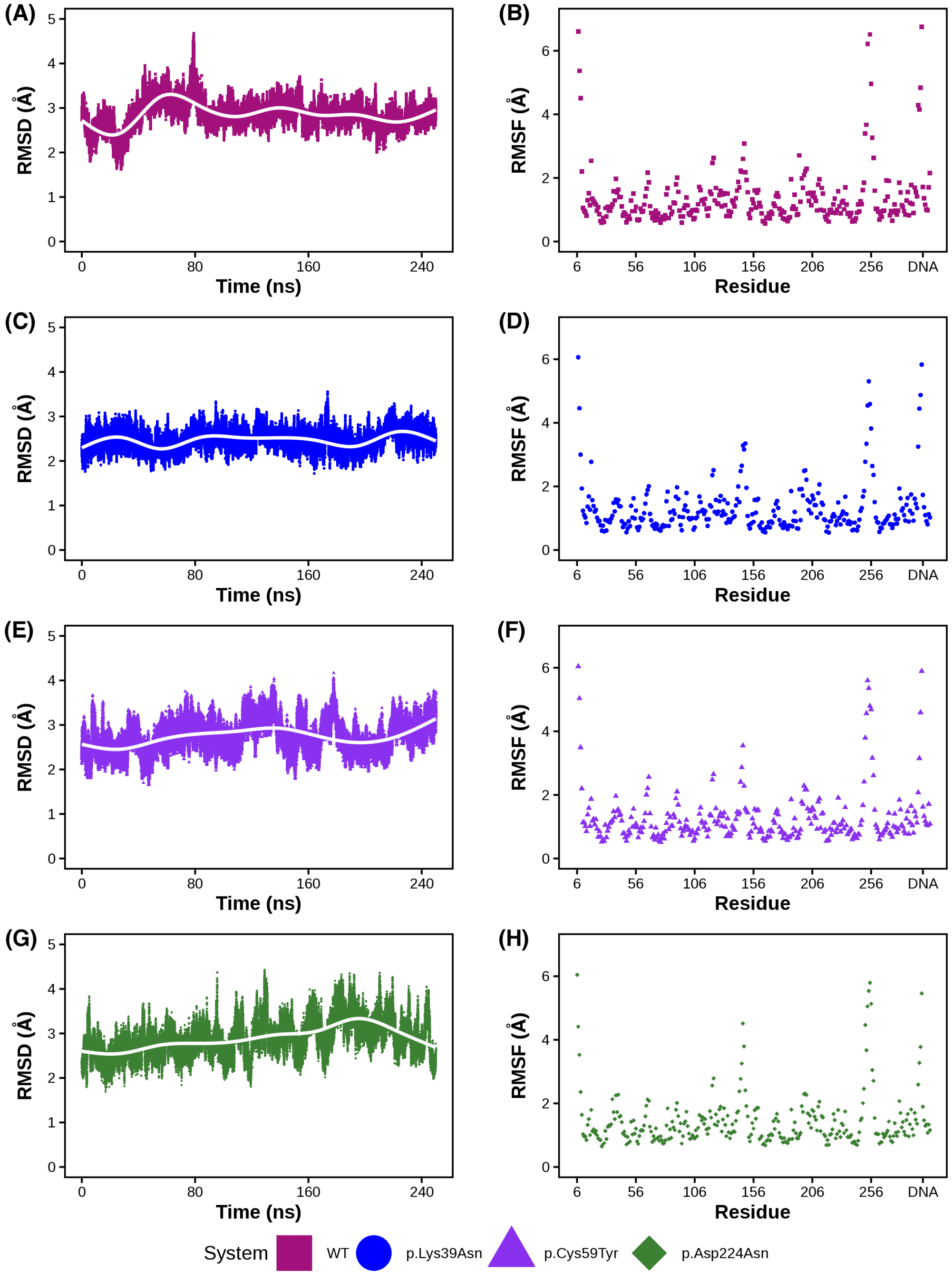
Supplementary Figure 4. Raw telomere length measurements. Each plate is shown, with the standard of known telomere length shown in the top row. Three replicates per sample were measured and are shown, the mean of measurements was used for the linear model and the distribution seen in Figure 2B. Variants carried by each sample are depicted.



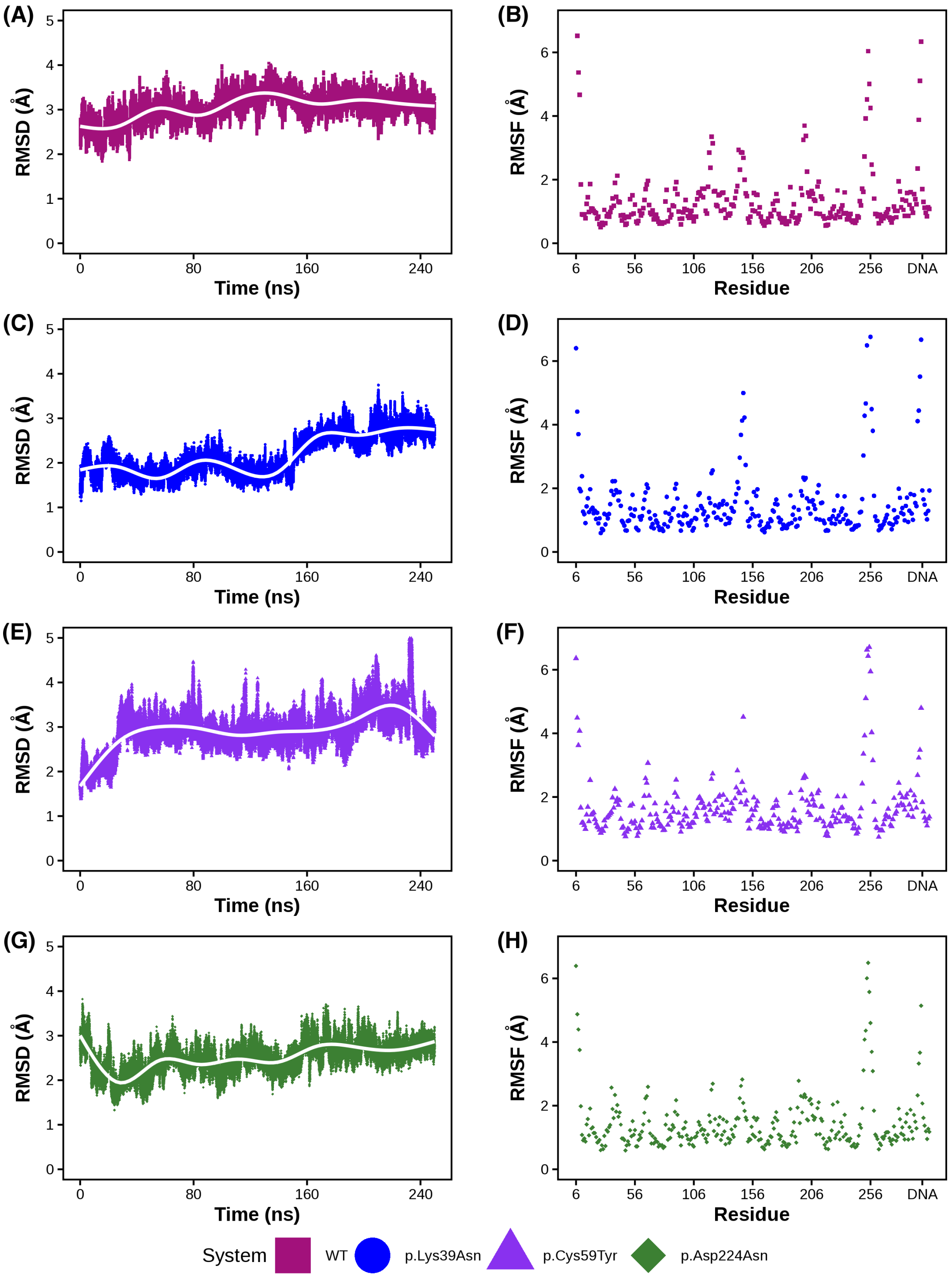
Supplementary Figure 5. **Variant differences in dynamics and non-bonded interactions.** (A–D) First and (E–H) second normal modes for (A,E) WT (B, F) K39N (C, G) C59Y and (D, H) D224N. The mutation position is colored pink and circled in yellow. (I) EDA results show that K33, K56, E92, and R73 (pink) have different non-bonded interactions with dG6 (black) across all variants when compared to WT. (J–L) Differences in the total interaction energy (Coulomb and van der Waals) with respect to the dG6 position for (J) K39N – WT, (K) C59Y – WT, and (L) D224N – WT. Interactions favored in WT are colored orange, those favored in the variant are colored, purple, and the dG6 position is colored black. All data are mapped onto the respective variant structure.



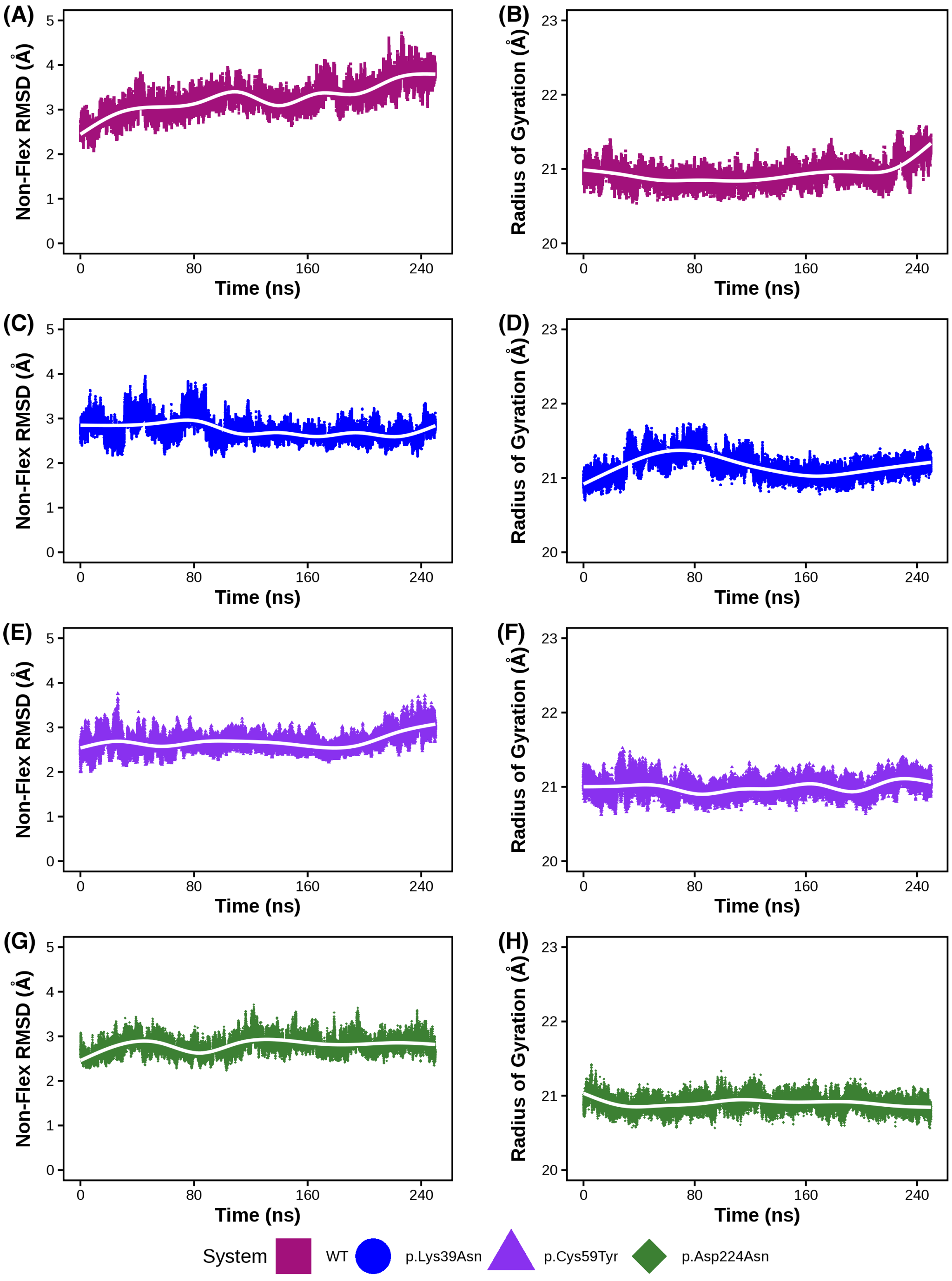
Supplementary Figure 6. RMSD and RMSF. RMSD (left) and RMSF (right) of the first MD replicate.



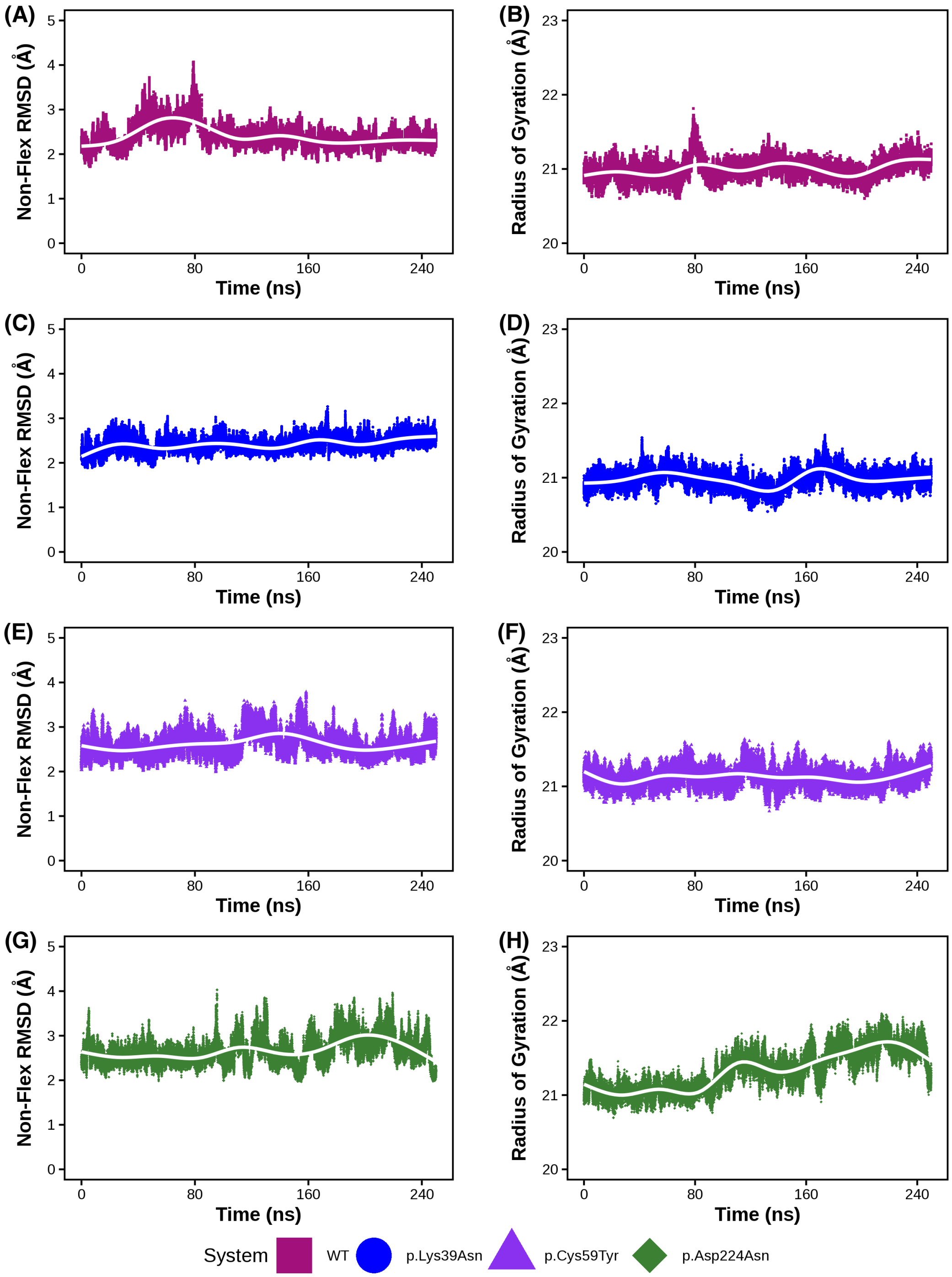
Supplementary Figure 7. RMSD and RMSF. RMSD (left) and RMSF (right) of the second MD replicate.



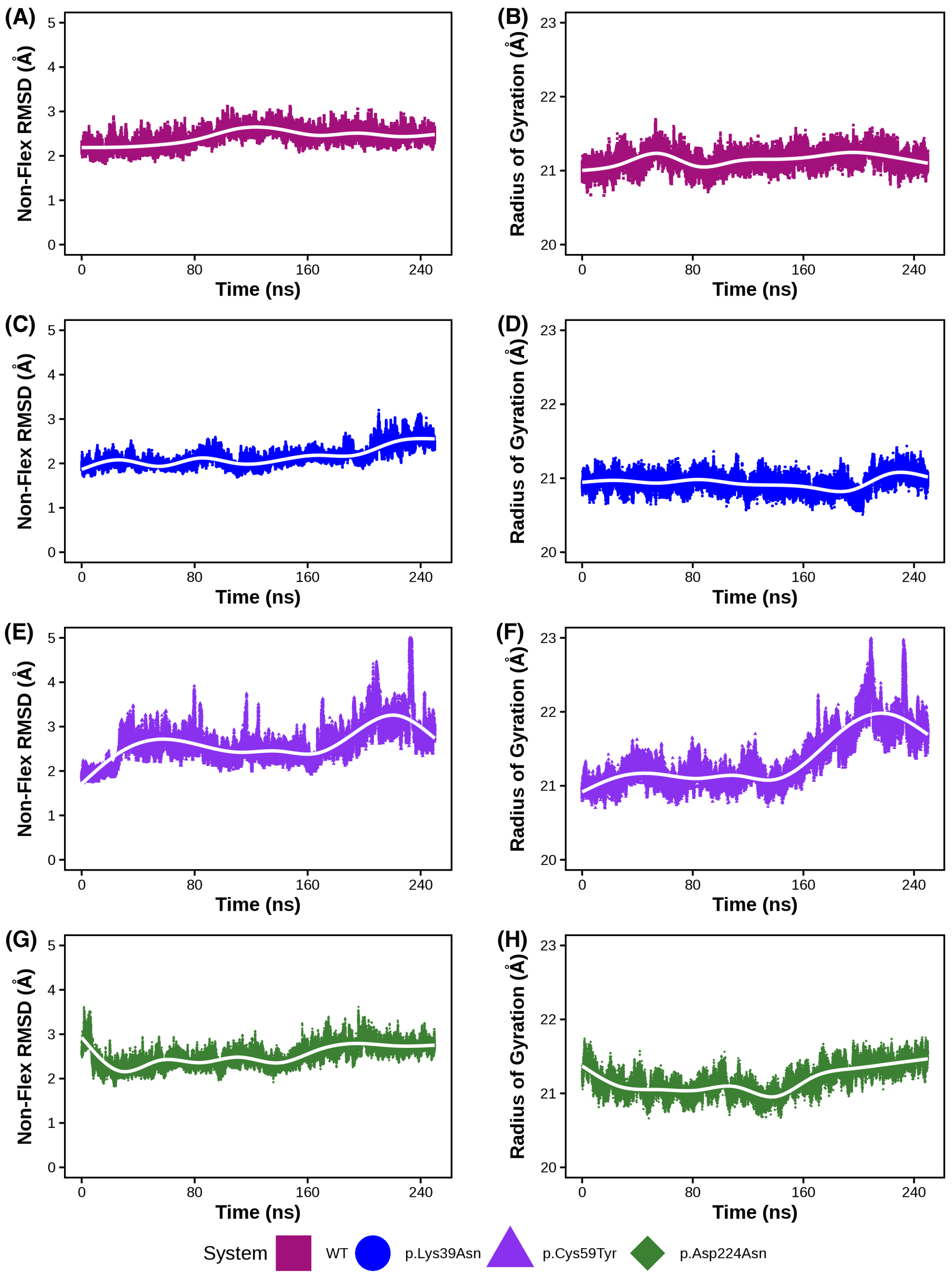
Supplementary Figure 8. RMSD and RMSF. RMSD (left) and RMSF (right) of the third MD replicate.



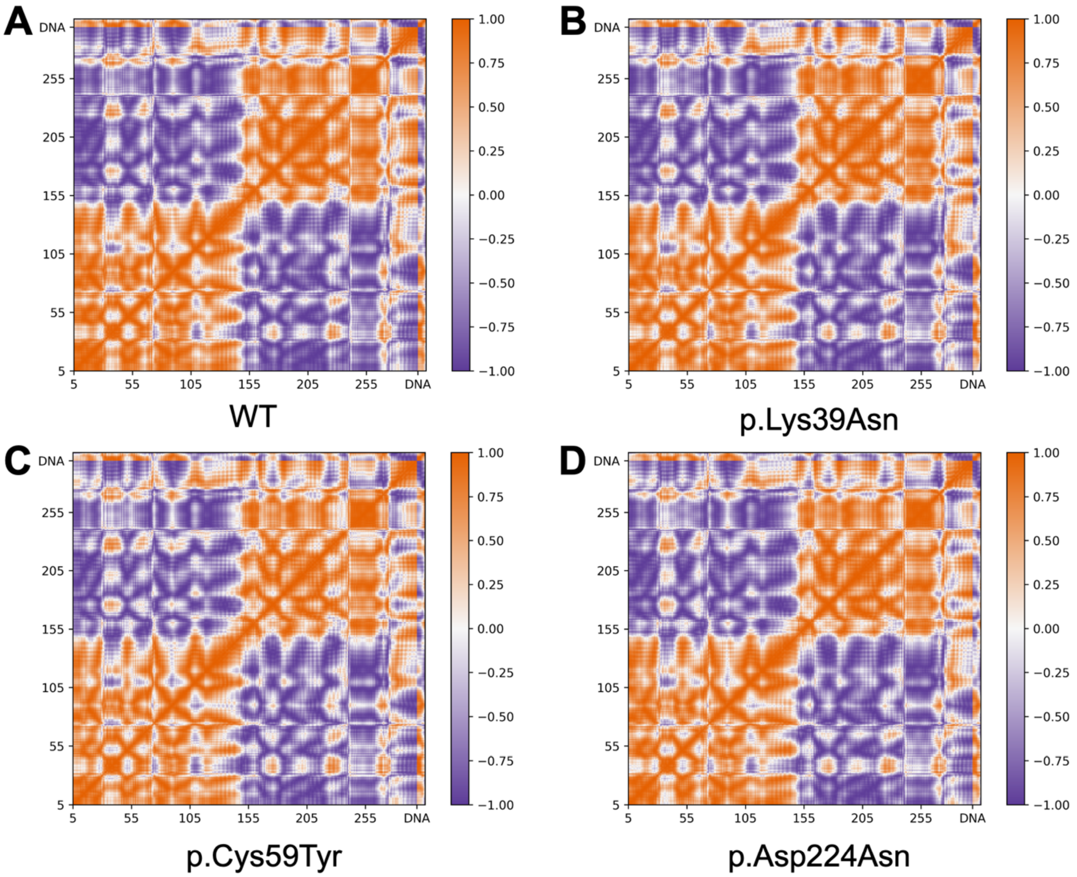
Supplementary Figure 9. Non-flexible RMSD and radius of gyration. Non-flexible RMSD (left) and radius of gyration (right) of the first MD replicate.



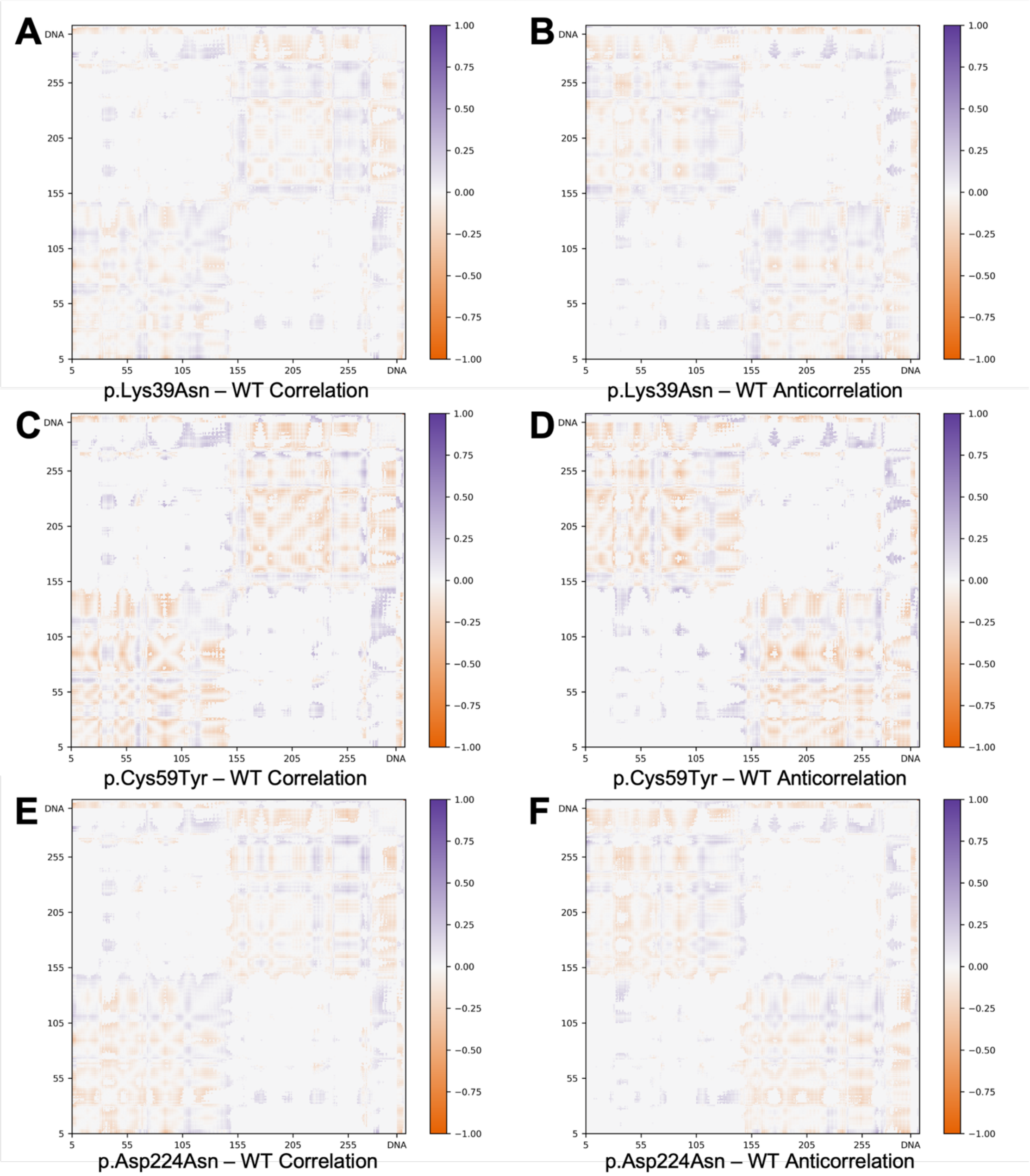
Supplementary Figure 10. Non-flexible RMSD and radius of gyration. Non-flexible RMSD (left) and radius of gyration (right) of the second MD replicate.



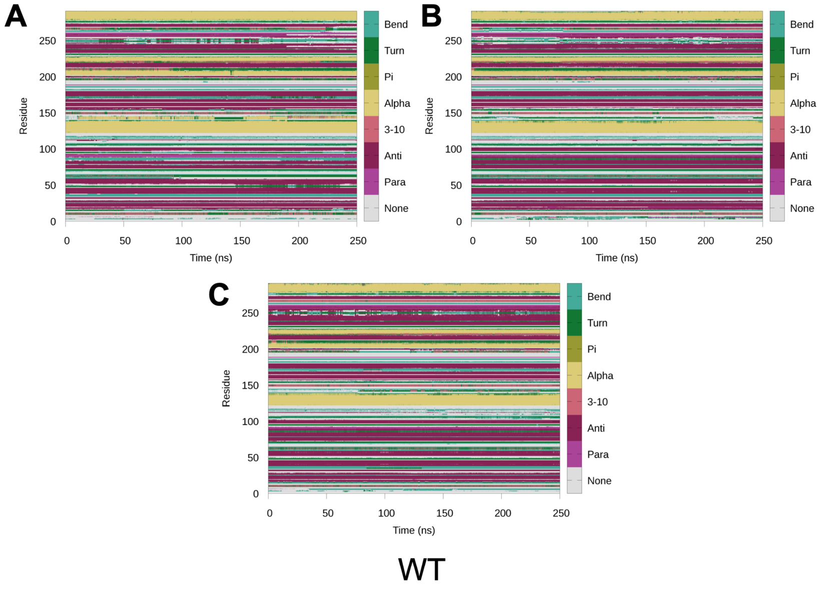
Supplementary Figure 11. Non-flexible RMSD and radius of gyration. Non-flexible RMSD (left) and radius of gyration (right) of the third MD replicate.



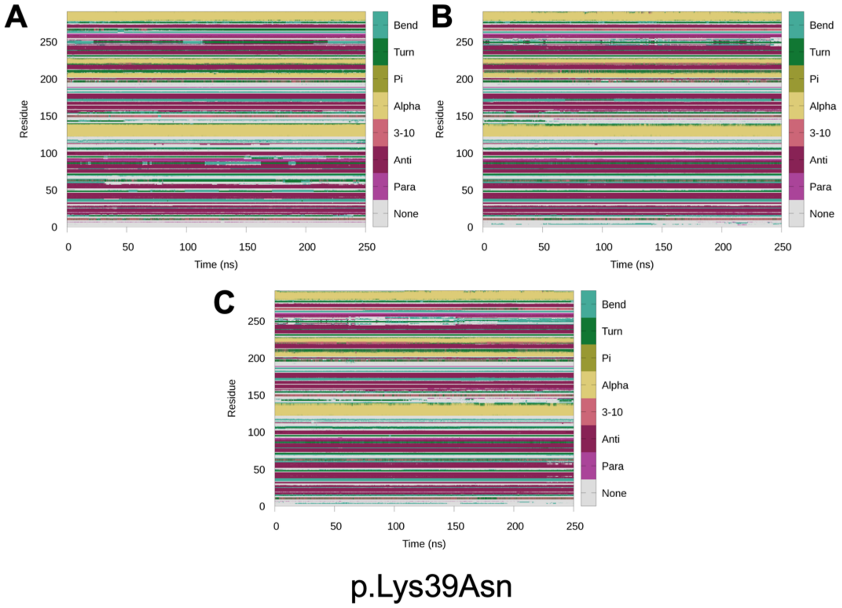
Supplementary Figure 12. Correlation matrices. Correlation matrices for (A) WT, (B) K39N, (C) C59Y, and (D) D224N. Areas of correlation are orange (1.0), areas with no correlation are white (0.0), and areas with anti-correlation are purple (-1.0).



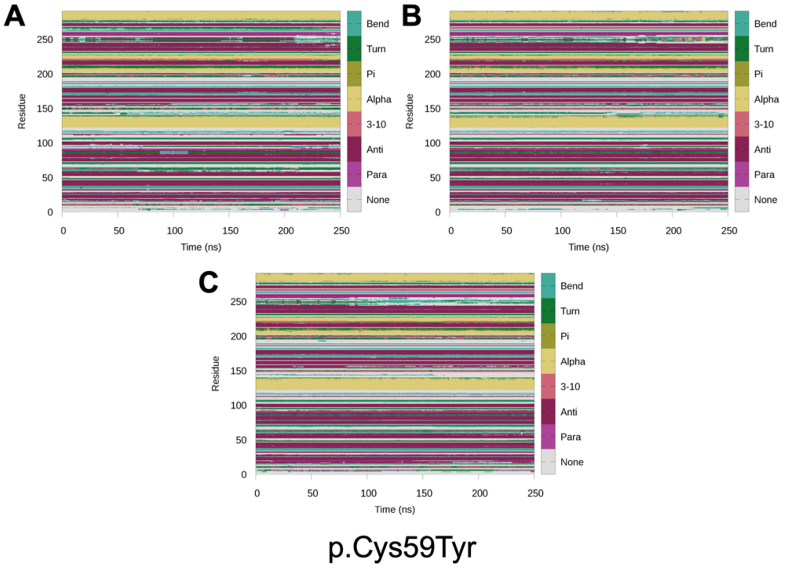
Supplementary Figure 13. Differences in correlated and anti-correlated motions. Differences in (A,C,E) correlated motions and (B,D,F) anticorrelated motions for (A–B) K39N – WT, (C–D) C59Y – WT, and (E–F) D224N – WT. Areas where that type of motion is more present in WT are orange, and areas where that type of motion is more present in the variant are purple.



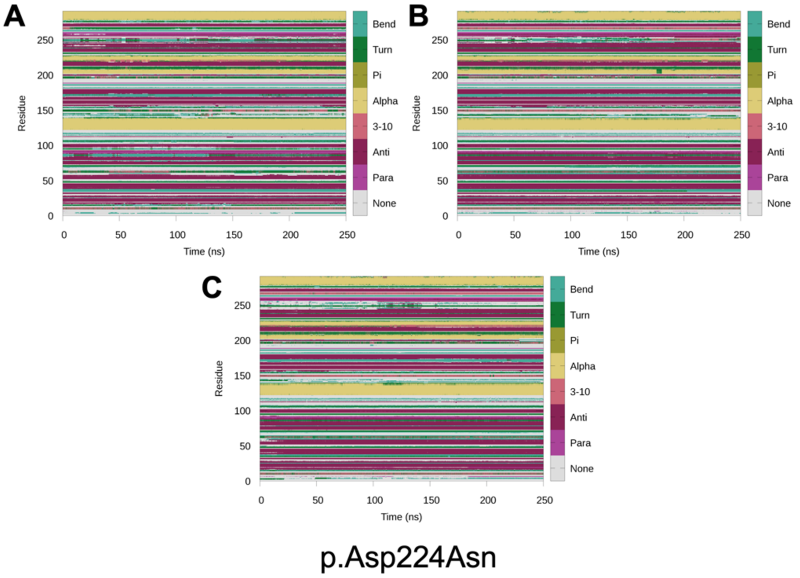
Supplementary Figure 14. WT secondary structure. Secondary structure analysis of each replicate of WT.



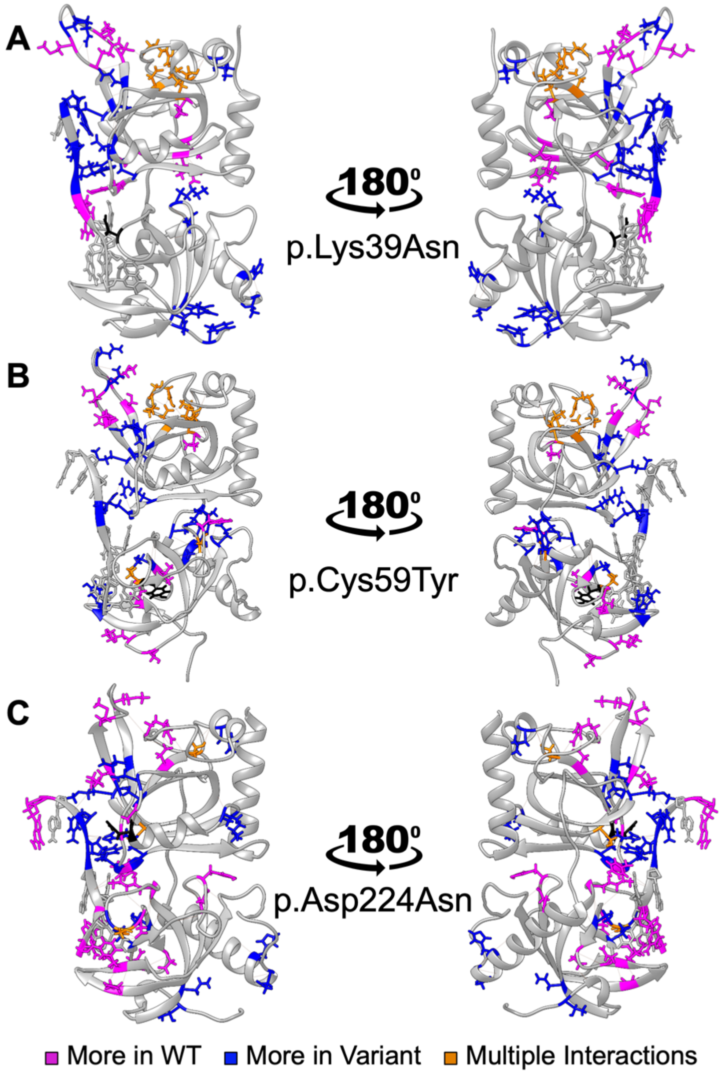
Supplementary Figure 15. K39N secondary structure. Secondary structure analysis of each replicate of K39N.



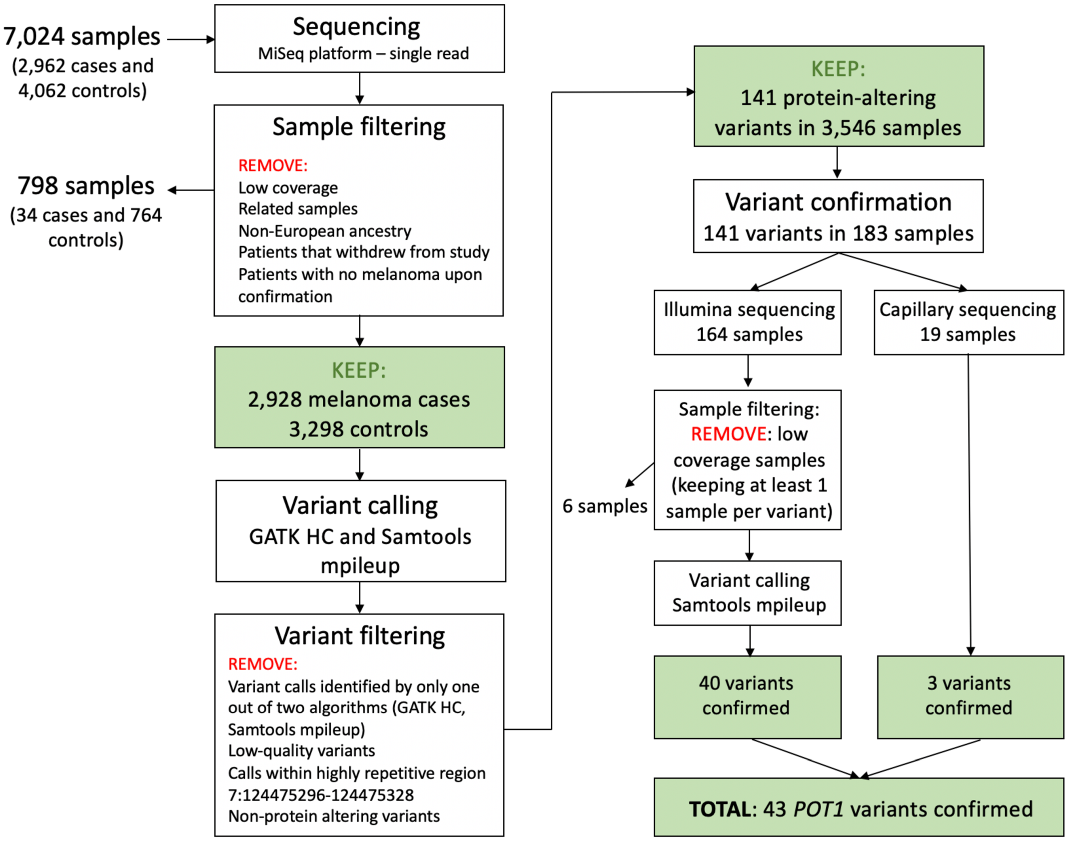
Supplementary Figure 16. C59Y secondary structure. Secondary structure analysis of each replicate of C59Y.



Supplementary Figure 17. D224N secondary structure. Secondary structure analysis of each replicate of D224N.



Supplementary Figure 18. Differences in hydrogen bond interactions. Differences in hydrogen bond interactions greater than 20% of the total simulation time for (A) WT and K39N, (B) WT and C59Y, and (C) WT and D224N. Interactions that are present for a larger percentage of simulation time in the WT are pink, and those more present in the variant structures are blue. Residues that had a combination of hydrogen bond interactions favored between both WT and the variant are shown in orange. The mutation location is shown in black, and all data are shown on the respective variant structure.



Supplementary Figure 19. Flowchart with the analysis steps followed in this study.

Supplementary Movie. First and second normal modes of the WT, K39N, C59Y, and D224N POT1-ssDNA variants from molecular dynamics simulations. The mutation position is colored pink.

Supplementary Tables and legends

Supplementary Table 1. All protein-altering variants in POT1 found in this study. Coordinates are in the GRCh37 reference genome. Consequences were predicted with VEP, Ensembl release 104, which also annotated co-existing variation, SIFT, PolyPhen and ClinVar pathogenicity predictions, and allele frequencies in the gnomAD database. All variants in this table were confirmed by resequencing of the original samples by a different method.

Supplementary Table 2. *POT1* variants classified as Group 1. Coordinates are from the GRCh37 reference genome. Consequences were predicted with VEP, Ensembl release 104, which also annotated co-existing variation, SIFT, PolyPhen and ClinVar pathogenicity predictions, and allele frequencies in the gnomAD database. All variants in this table were confirmed by resequencing of the original samples by a different method.

Supplementary Table 3. Age of onset statistics by pathogenicity group. Age of onset was not available for all participants.

Supplementary Table 4. Gender distribution by pathogenicity group in cases and controls. Please note there were two cases for which gender was unknown.

Supplementary Table 5. Family history of melanoma by pathogenicity group. *P*-value (Fisher's exact test): 0.88. Five cases were excluded from this comparison for lack of information.

Supplementary Table 6. Site of melanoma distribution by pathogenicity group.

Supplementary Table 7. Linear model used for adjusting telomere lengths by cohort.

Supplementary Table 8. Change in interactions with K39N. Residues that showed the greatest differences (K39N – WT) across systems in their total interaction energy with respect to the K39N residue. The average total interaction energy ± average standard deviation is provided. All values are in kcal mol^{-1}.

Supplementary Table 9. Change in interactions with D224N. Residues that showed the greatest differences (D224N – WT) across systems in their total interaction energy with respect to the D224N residue. The average total interaction energy ± average standard deviation is provided. All values are in kcal mol^{-1}.

Supplementary Table 10. Change in interactions with dG6 for K39N. Residues that showed the greatest differences (K39N – WT) across systems in their total interaction energy with respect to the dG6 residue. The average total interaction energy ± average standard deviation is provided. All values are in kcal mol^{-1}.

Supplementary Table 11. Change in interactions with dG6 for C59Y. Residues that showed the greatest differences (C59Y – WT) across systems in their total interaction energy with respect to the dG6 residue. The average total interaction energy ± average standard deviation is provided. All values are in kcal mol^{-1}.

Supplementary Table 12. Change in interactions with dG6 for D224N. Residues that showed the greatest differences (D224N – WT) across systems in their total interaction energy with respect to the dG6 residue. The average total interaction energy ± average standard deviation is provided. All values are in kcal mol^{-1}.

Supplementary Table 13. Samples included in this study. The list shows all 6,226 samples in this study, with their ID, proportion of high-quality bases sequenced in the 1st sequencing round, case/control status and cohort of origin.

Supplementary Table 14. All protein-altering variants in POT1 found in this study after the first round of sequencing. Coordinates are in the GRCh37 reference genome. Details of the number of samples that were re-sequenced for confirmation and other information are included. Variants confirmed are highlighted in green.

Supplementary Table 15. List of samples that were re-sequenced by Illumina for confirmation. The average coverage of coding *POT1* exons is included. In red, samples with a coverage lower than 10.

Supplementary Table 16. List of samples that were re-sequenced by capillary. Information about the variants re-sequenced and the result of the experiment is included. In green, samples and variants that were confirmed.

Supplementary Table 17. List of samples with variants in known melanoma predisposition genes. Genes *CDK4*, *CDKN2A* and *BAP1* were checked for variants. Only samples that were resequenced by Illumina (Supplementary Table 15) were assessed.

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Supplementary Table 7. Linear model used for adjusting telomere lengths by cohort.

Call:

lm(formula = tel ~ cohort, data = full_data, subset = case == control)

Residuals:

Min	1Q	Median	3Q	Max
-301.52	-107.17	-20.56	46.31	814.11

Coefficients

	Estimate Std.	Error	t value	Pr(>|t|)	
(Intercept)	563.49	24.37	23.12	< 2e-16	***
Cohort: Cambridge	-116.38	32.73	-3.556	0.000542	***
Cohort: WTCCC	-173.1	54.95	-3.15	0.002064	**

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Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 170.6 on 119 degrees of freedom

(37 observations deleted due to missingness)
Multiple R-squared:
0.1252,   Adjusted R-squared: 0.1105

F-statistic: 8.512 on 2 and 119 DF, p-value: 0.0003506

Supplementary Table 8. Change in interactions with K39N. Residues that showed the greatest differences (K39N – WT) across systems in their total interaction energy with respect to the K39N residue. The average total interaction energy ± average standard deviation is provided. All values are in kcal mol^{-1}.

	K39N – WT
Ala6	-7.42 ± 0.01
Lys18	-9.83 ± 0.02
Lys30	-11.88 ± 0.02
Lys33	-25.84 ± 0.11
Pro34	1.05 ± 0.01
Leu37	2.27 ± 0.04
Asp42	25.20 ± 0.02
Asp51	9.96 ± 0.01
Lys56	-13.17 ± 0.01
Glu67	13.36 ± 0.09
Lys74	-10.33 ± 0.05
Asp77	11.35 ± 0.04
Arg80	-9.92 ± 0.01
Arg83	-10.83 ± 0.03
Lys85	-14.64 ± 0.04
Lys90	-20.02 ± 0.04
Lys91	-13.28 ± 0.08
Glu92	13.97 ± 0.08
Glu107	9.75 ± 0.04
Arg117	-10.99 ± 0.05
Lys121	-9.29 ± 0.04
Glu128	7.61 ± 0.01
Asp129	9.00 ± 0.01
Lys131	-7.24 ± 0.01

Glu134	7.64 ± 0.01
Arg137	-8.59 ± 0.03
Lys152	-8.87 ± 0.05
Asp155	8.37 ± 0.03
Asp163	12.76 ± 0.05
Lys171	-13.01 ± 0.17
Glu173	14.63 ± 0.24
Asp175	15.10 ± 0.25
Lys182	-9.87 ± 0.08
Asp185	9.23 ± 0.05
Arg188	-7.60 ± 0.04
Arg195	-9.10 ± 0.04
Asp200	8.91 ± 0.08
Glu204	10.90 ± 0.12
Asp206	8.41 ± 0.06
Arg212	-7.42 ± 0.05
Asp219	10.27 ± 0.08
Asp224	25.66 ± 0.78
Arg231	-17.86 ± 0.34
Lys234	-10.94 ± 0.12
Arg240	-11.45 ± 0.08
Lys247	-11.71 ± 0.06
Glu254	7.68 ± 0.09
Glu262	11.20 ± 0.07
Gly268	-1.31 ± 0.04
Arg273	-18.62 ± 0.17
Arg276	-14.51 ± 0.08
Glu280	9.27 ± 0.06
Asp284	9.78 ± 0.04
Asp286	8.08 ± 0.04

Lys289	-8.51 ± 0.05
Lys290	-7.54 ± 0.03
Asp291	8.09 ± 0.04
Glu293	7.17 ± 0.03
Ala299	6.71 ± 0.03
dT1	9.38 ± 0.14
dT2	32.79 ± 0.71
dA3	47.18 ± 1.32
dG4	27.20 ± 0.46
dG5	17.45 ± 0.28
dG6	18.03 ± 0.38
dT7	15.12 ± 0.29
dT8	17.25 ± 0.41
dA9	19.70 ± 0.82
dG10	12.51 ± 0.59

Supplementary Table 9. Change in interactions with D224N. Residues that showed the greatest differences (D224N – WT) across systems in their total interaction energy with respect to the D224N residue. The average total interaction energy ± average standard deviation is provided. All values are in kcal mol^{-1}.

	D224N – WT
Ala6	6.59 ± 0.02
Lys18	7.97 ± 0.05
Lys30	11.83 ± 0.03
Lys33	23.01 ± 0.11
Leu37	-1.06 ± 0.05
Lys39	26.00 ± 0.79
Asp42	-15.03 ± 0.19
Asp51	-9.06 ± 0.02
Lys56	12.19 ± 0.03
Glu67	-12.81 ± 0.11
Lys74	11.63 ± 0.02
Asp77	-11.84 ± 0.01
Arg80	8.79 ± 0.02
Arg83	8.53 ± 0.04
Lys85	9.92 ± 0.06
Lys90	14.16 ± 0.11
Lys91	10.66 ± 0.06
Glu92	-11.49 ± 0.04
Glu107	-10.35 ± 0.01
Arg117	11.35 ± 0.03
Lys121	8.55 ± 0.05
Glu128	-7.02 ± 0.01

Asp129	-8.20 ± 0.02
Lys131	6.78 ± 0.01
Glu134	-7.63 ± 0.01
Arg137	8.72 ± 0.01
Lys152	11.27 ± 0.02
Asp155	-10.60 ± 0.03
Asp163	-16.07 ± 0.04
Lys171	18.41 ± 0.02
Glu173	-24.24 ± 0.09
Val174	1.31 ± 0.01
Asp175	-32.49 ± 0.33
Ala177	-4.17 ± 0.21
Ser178	1.19 ± 0.05
Lys182	15.15 ± 0.06
Asp185	-12.22 ± 0.02
Arg188	10.21 ± 0.03
Arg195	13.68 ± 0.08
Asp200	-12.76 ± 0.06
Glu204	-14.84 ± 0.01
Asp206	-11.05 ± 0.01
Arg212	9.52 ± 0.02
Asp219	-16.37 ± 0.08
His226	3.76 ± 0.09
Val227	3.45 ± 0.07
His228	3.29 ± 0.14
Val229	1.34 ± 0.01
Ala230	1.42 ± 0.00

Arg231	29.38 ± 0.11
Lys234	12.94 ± 0.03
Arg240	13.76 ± 0.03
Lys247	19.67 ± 0.21
Glu254	-10.82 ± 0.09
Glu262	-19.03 ± 0.12
Leu265	-1.88 ± 0.03
His266	1.46 ± 0.21
Gly267	5.74 ± 0.12
Arg273	30.99 ± 0.18
Arg276	15.50 ± 0.07
Glu280	-10.55 ± 0.01
Asp284	-11.26 ± 0.01
Asp286	-9.21 ± 0.00
Lys289	9.88 ± 0.00
Lys290	8.73 ± 0.01
Asp291	-9.95 ± 0.02
Glu293	-8.66 ± 0.01
Ala299	-8.51 ± 0.02
dT1	-4.29 ± 0.11
dT2	-14.74 ± 0.37
dA3	-18.74 ± 0.52
dG4	-17.86 ± 0.36
dG5	-14.14 ± 0.21
dG6	-17.65 ± 0.27
dT7	-17.94 ± 0.21
dT8	-24.81 ± 0.39

dA9	-28.25 ± 0.53
dG10	-10.10 ± 1.25

Supplementary Table 10. Change in interactions with dG6 for K39N. Residues that showed the greatest differences (K39N – WT) across systems in their total interaction energy with respect to the dG6 residue. The average total interaction energy ± average standard deviation is provided. All values are in kcal mol^{-1}.

	K39N – WT
Lys30	2.41 ± 0.76
Lys33	11.95 ± 3.73
Lys39	18.03 ± 0.38
Lys56	4.10 ± 1.02
Lys74	1.11 ± 0.35
Asp77	-1.26 ± 0.37
Lys91	1.13 ± 0.69
Glu92	4.95 ± 0.75
Asp163	-2.28 ± 0.56
Arg240	2.04 ± 0.43
Thr269	-1.25 ± 0.23
Ser270	1.06 ± 0.75
Tyr271	1.59 ± 0.51
Gly272	1.14 ± 0.18
Arg273	2.47 ± 1.10
Asp284	-1.07 ± 0.25
dA9	-2.43 ± 0.39

Supplementary Table 11. Change in interactions with dG6 for C59Y. Residues that showed the greatest differences (C59Y – WT) across systems in their total interaction energy with respect to the dG6 residue. The average total interaction energy ± average standard deviation is provided. All values are in kcal mol^{-1}.

	C59Y – WT
Lys18	-1.01 ± 0.19
Lys33	8.00 ± 2.67
Asp51	1.28 ± 0.20
Lys56	-10.02 ± 0.80
Lys90	-2.62 ± 0.66
Glu92	5.88 ± 0.76
Asp163	1.31 ± 0.36
Asp224	1.13 ± 0.41
Lys247	-1.43 ± 0.23
Thr269	-1.09 ± 0.27
Ser270	-1.09 ± 0.50
Arg273	-1.88 ± 0.83
Arg276	-1.37 ± 0.25
dA3	-1.31 ± 0.29
dG4	-3.12 ± 0.70
dT8	1.02 ± 0.38
dA9	-1.94 ± 0.40

Supplementary Table 12. Change in interactions with dG6 for D224N. Residues that showed the greatest differences (D224N – WT) across systems in their total interaction energy with respect to the dG6 residue. The average total interaction energy ± average standard deviation is provided. All values are in kcal mol^{-1}.

	D224N – WT
Lys30	1.71 ± 0.94
Lys33	11.17 ± 3.92
Lys39	2.07 ± 3.92
Asp42	-1.02 ± 0.49
Lys56	3.74 ± 1.13
Glu67	-1.26 ± 0.33
Lys74	1.13 ± 0.41
Asp77	-1.21 ± 0.45
Lys90	1.76 ± 0.63
Lys91	2.06 ± 0.85
Glu92	4.17 ± 1.03
Asp163	-1.70 ± 0.77
Asp224	-17.65 ± 0.27
Arg240	1.72 ± 0.54
Tyr271	1.78 ± 0.49
Gly272	1.26 ± 0.18
Arg273	2.96 ± 1.27
dA3	-1.56 ± 0.43
dG4	-5.10 ± 0.99
dT8	1.11 ± 0.33

Supplementary Table 13. Samples included in this study. The list shows all 6,226 samples in this study, with their ID, proportion of high-quality bases sequenced in the 1st sequencing round, case/control status and cohort of origin.

Sample ID	Proportion of bases covered with high quality	Status	Cohort
Ctrl_1	1	Control	WTCCC
Ctrl_2	1	Control	WTCCC
Ctrl_3	1	Control	WTCCC
Ctrl_4	1	Control	WTCCC
Ctrl_5	1	Control	WTCCC
Ctrl_6	1	Control	WTCCC
Ctrl_7	1	Control	WTCCC
Ctrl_8	1	Control	WTCCC
Ctrl_9	1	Control	WTCCC
Ctrl_10	1	Control	WTCCC
Ctrl_11	1	Control	WTCCC
Ctrl_12	1	Control	WTCCC
Ctrl_13	1	Control	WTCCC
Ctrl_14	1	Control	WTCCC
Ctrl_15	1	Control	WTCCC
Ctrl_16	1	Control	WTCCC
Ctrl_17	1	Control	WTCCC
Ctrl_18	1	Control	WTCCC
Ctrl_19	1	Control	WTCCC
Ctrl_20	1	Control	WTCCC
Ctrl_21	1	Control	WTCCC
Ctrl_22	0.992650919	Control	WTCCC
Ctrl_23	1	Control	WTCCC
Ctrl_24	1	Control	WTCCC
Ctrl_25	1	Control	WTCCC
Ctrl_26	1	Control	WTCCC
Ctrl_27	1	Control	WTCCC
Ctrl_28	1	Control	WTCCC
Ctrl_29	1	Control	WTCCC
Ctrl_30	1	Control	WTCCC
Ctrl_31	1	Control	WTCCC
Ctrl_32	1	Control	WTCCC
Ctrl_33	1	Control	WTCCC

Ctrl_34	1	Control	WTCCC
Ctrl_35	1	Control	WTCCC
Ctrl_36	1	Control	WTCCC
Ctrl_37	1	Control	WTCCC
Ctrl_38	1	Control	WTCCC
Ctrl_39	1	Control	WTCCC
Ctrl_40	1	Control	WTCCC
Ctrl_41	1	Control	WTCCC
Ctrl_42	1	Control	WTCCC
Ctrl_43	1	Control	WTCCC
Ctrl_44	1	Control	WTCCC
Ctrl_45	1	Control	WTCCC
Ctrl_46	1	Control	WTCCC
Ctrl_47	1	Control	WTCCC
Ctrl_48	1	Control	WTCCC
Ctrl_49	1	Control	WTCCC
Ctrl_50	1	Control	WTCCC
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Ctrl_62	1	Control	WTCCC
Ctrl_63	1	Control	WTCCC
Ctrl_64	1	Control	WTCCC
Ctrl_65	1	Control	WTCCC
PD30749a	1	Control	WTCCC
Ctrl_66	1	Control	WTCCC
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PD30724a	0.954855643	Case	SEARCH
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Case_2327	1	Case	SEARCH
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Case_2353	0.940682415	Case	SEARCH
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Case_2358	0.985826772	Case	SEARCH
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Case_2360	1	Case	SEARCH
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Case_2362	1	Case	SEARCH
Case_2363	1	Case	SEARCH
Case_2364	1	Case	SEARCH
Case_2365	1	Case	SEARCH
Case_2366	1	Case	SEARCH
Case_2367	0.999475066	Case	SEARCH
Case_2368	1	Case	SEARCH
PD30721a	1	Case	SEARCH
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Case_2374	0.999475066	Case	SEARCH
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Case_2380	0.998950131	Case	SEARCH
Case_2381	1	Case	SEARCH

Case_2382	1	Case	SEARCH
Case_2383	0.940682415	Case	SEARCH
Case_2384	0.999475066	Case	SEARCH
Case_2385	1	Case	SEARCH
Case_2386	1	Case	SEARCH
Case_2387	0.999475066	Case	SEARCH
Case_2388	0.940682415	Case	SEARCH
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Case_2399	1	Case	SEARCH
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Case_2403	0.993175853	Case	SEARCH
Case_2404	0.999475066	Case	SEARCH
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Case_2406	0.999475066	Case	SEARCH
Case_2407	1	Case	SEARCH
Case_2408	0.940682415	Case	SEARCH
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Case_2411	1	Case	SEARCH
Case_2412	1	Case	SEARCH
Case_2413	1	Case	SEARCH
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Case_2418	1	Case	SEARCH
Case_2419	1	Case	SEARCH
Case_2420	1	Case	SEARCH
Case_2421	0.998950131	Case	SEARCH

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PD30700a	0.940682415	Case	SEARCH
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PD30722a	1	Case	SEARCH
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Case_2464	1	Case	SEARCH
Case_2465	1	Case	SEARCH
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PD30701a	0.999475066	Case	SEARCH
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Case_2479	1	Case	SEARCH
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Case_2482	1	Case	SEARCH
Case_2483	1	Case	SEARCH
Case_2484	1	Case	SEARCH
Case_2485	0.998425197	Case	SEARCH
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Case_2487	1	Case	SEARCH
Case_2488	1	Case	SEARCH
Case_2489	1	Case	SEARCH
Case_2490	0.996325459	Case	SEARCH
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Case_2494	1	Case	SEARCH
Case_2495	1	Case	SEARCH
Case_2496	1	Case	SEARCH
Case_2497	0.999475066	Case	SEARCH
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Case_2517	1	Case	SEARCH
Case_2518	1	Case	SEARCH
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Case_2521	1	Case	SEARCH
Case_2522	1	Case	SEARCH
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Case_2547	1	Case	SEARCH
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PD30723a	1	Case	SEARCH
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Case_2558	1	Case	SEARCH
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Case_2614	1	Case	SEARCH
Case_2615	1	Case	SEARCH

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Case_2622	0.998950131	Case	SEARCH
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Case_2624	0.999475066	Case	SEARCH
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Case_2629	1	Case	SEARCH
Case_2630	1	Case	SEARCH
Case_2631	1	Case	SEARCH
Case_2632	1	Case	SEARCH
Case_2633	0.999475066	Case	SEARCH
Case_2634	1	Case	SEARCH
Case_2635	1	Case	SEARCH
Case_2636	1	Case	SEARCH
Case_2637	1	Case	SEARCH
Case_2638	1	Case	SEARCH
Case_2639	1	Case	SEARCH
Case_2640	1	Case	SEARCH
Case_2641	1	Case	SEARCH
Case_2642	1	Case	SEARCH
PD30726a	0.998425197	Case	SEARCH
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Case_2644	1	Case	SEARCH
Case_2645	1	Case	SEARCH
Case_2646	1	Case	SEARCH
Case_2647	1	Case	SEARCH
Case_2648	1	Case	SEARCH
Case_2649	1	Case	SEARCH
Case_2650	0.940682415	Case	SEARCH
Case_2651	1	Case	SEARCH
Case_2652	1	Case	SEARCH
Case_2653	0.999475066	Case	SEARCH
Case_2654	1	Case	SEARCH

Case_2655	1	Case	SEARCH
Case_2656	1	Case	SEARCH
Case_2657	1	Case	SEARCH
Case_2658	0.998950131	Case	SEARCH
Case_2659	0.998950131	Case	SEARCH
Case_2660	1	Case	SEARCH
Case_2661	0.984251969	Case	SEARCH
Case_2662	1	Case	SEARCH
Case_2663	0.999475066	Case	SEARCH
Case_2664	1	Case	SEARCH
Case_2665	1	Case	SEARCH
Case_2666	1	Case	SEARCH
Case_2667	1	Case	SEARCH
Case_2668	1	Case	SEARCH
Case_2669	1	Case	SEARCH
Case_2670	1	Case	SEARCH
Case_2671	1	Case	SEARCH
Case_2672	1	Case	SEARCH
Case_2673	0.999475066	Case	SEARCH
Case_2674	1	Case	SEARCH
Case_2675	1	Case	SEARCH
Case_2676	1	Case	SEARCH
Case_2677	1	Case	SEARCH
Case_2678	1	Case	SEARCH
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PD30710a	1	Case	SEARCH
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Case_2688	1	Case	SEARCH
Case_2689	1	Case	SEARCH
Case_2690	1	Case	SEARCH
Case_2691	0.998425197	Case	SEARCH
Case_2692	1	Case	SEARCH
PD30695a	1	Case	SEARCH

Case_2693	1	Case	SEARCH
Case_2694	1	Case	SEARCH
Case_2695	0.999475066	Case	SEARCH
Case_2696	1	Case	SEARCH
Case_2697	1	Case	SEARCH
Case_2698	1	Case	SEARCH
Case_2699	1	Case	SEARCH
Case_2700	0.998950131	Case	SEARCH
Case_2701	1	Case	SEARCH
Case_2702	0.996325459	Case	SEARCH
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Case_2704	1	Case	SEARCH
Case_2705	1	Case	SEARCH
Case_2706	1	Case	SEARCH
Case_2707	1	Case	SEARCH
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Case_2709	1	Case	SEARCH
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Case_2711	1	Case	SEARCH
Case_2712	1	Case	SEARCH
Case_2713	1	Case	SEARCH
Case_2714	1	Case	SEARCH
Case_2715	0.999475066	Case	SEARCH
Case_2716	0.998950131	Case	SEARCH
Case_2717	0.981627297	Case	SEARCH
Case_2718	1	Case	SEARCH
Case_2719	1	Case	SEARCH
Case_2720	1	Case	SEARCH
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Case_2727	1	Case	SEARCH
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Case_2729	1	Case	SEARCH
Case_2730	1	Case	SEARCH
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Case_2732	1	Case	SEARCH

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Case_2734	1	Case	SEARCH
Case_2735	0.993700787	Case	SEARCH
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Case_2738	1	Case	SEARCH
Case_2739	1	Case	SEARCH
Case_2740	1	Case	SEARCH
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Case_2744	1	Case	SEARCH
Case_2745	1	Case	SEARCH
Case_2746	1	Case	SEARCH
Case_2747	1	Case	SEARCH
Case_2748	0.998950131	Case	SEARCH
Case_2749	1	Case	SEARCH
PD30734a	1	Case	SEARCH
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Case_2764	1	Case	SEARCH
Case_2765	1	Case	SEARCH
Case_2766	1	Case	SEARCH
Case_2767	0.962729659	Case	SEARCH
Case_2768	0.999475066	Case	SEARCH
Case_2769	0.999475066	Case	SEARCH
Case_2770	1	Case	SEARCH
Case_2771	1	Case	SEARCH

Case_2772	1	Case	SEARCH
Case_2773	1	Case	SEARCH
Case_2774	1	Case	SEARCH
Case_2775	1	Case	SEARCH
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Case_2777	1	Case	SEARCH
Case_2778	1	Case	SEARCH
Case_2779	0.98687664	Case	SEARCH
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Case_2781	1	Case	SEARCH
PD30715a	1	Case	SEARCH
Case_2782	1	Case	SEARCH
Case_2783	1	Case	SEARCH
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Case_2787	1	Case	SEARCH
Case_2788	0.994225722	Case	SEARCH
Case_2789	1	Case	SEARCH
PD30730a	1	Case	SEARCH
Case_2790	0.981102362	Case	SEARCH
Case_2791	1	Case	SEARCH
Case_2792	1	Case	SEARCH
Case_2793	1	Case	SEARCH
Case_2794	0.999475066	Case	SEARCH
Case_2795	1	Case	SEARCH
Case_2796	0.999475066	Case	SEARCH
Case_2797	1	Case	SEARCH
Case_2798	1	Case	SEARCH
Case_2799	1	Case	SEARCH
Case_2800	1	Case	SEARCH
Case_2801	1	Case	SEARCH
Case_2802	1	Case	SEARCH

Supplementary Table 15. List of samples that were re-sequenced by Illumina for confirmation. The average coverage of coding *POT1* exons is included. In red, samples with a coverage lower than 10.

Sample	Average coverage
PD30545a	287.8183206
PD30546a	288.3867684
PD30547a	316.0020356
PD30548a	261.8880407
PD30549a	270.092112
PD30550a	276.5094148
PD30551a	233.7791349
PD30552a	280.6137405
PD30553a	213.3725191
PD30554a	222.3903308
PD30555a	251.7562341
PD30556a	274.5073791
PD30557a	232.5338422
PD30558a	258.5124682
PD30559a	238.7760814
PD30560a	272.6096692
PD30561a	222.6605598
PD30562a	219.8117048
PD30563a	199.8819338
PD30564a	205.2101781
PD30565a	207.2946565
PD30566a	162.3760814
PD30567a	179.4575064
PD30568a	242.4076336
PD30569a	221.9236641
PD30570a	192.2992366
PD30571a	203.7043257
PD30572a	200.3638677
PD30573a	240.3857506
PD30574a	176.0834606
PD30575a	171.8956743
PD30576a	283.5114504

PD30577a	39.16132316
PD30578a	197.389313
PD30580a	210.7857506
PD30581a	198.3964377
PD30583a	46.1821883
PD30584a	297.8717557
PD30585a	249.1292621
PD30586a	226.3501272
PD30587a	193.0188295
PD30588a	202.0259542
PD30589a	172.4081425
PD30590a	209.4025445
PD30591a	217.8610687
PD30592a	151.3547074
PD30593a	258.092112
PD30594a	254.4625954
PD30595a	277.8605598
PD30596a	370.070229
PD30597a	255.5842239
PD30598a	282.1699746
PD30599a	621.8208651
PD30600a	327.9231552
PD30602a	388.0508906
PD30603a	353.3725191
PD30605a	138.205598
PD30606a	254.4748092
PD30607a	95.09363868
PD30609a	194.2732824
PD30611a	15.45343511
PD30612a	35.04529262
PD30616a	21.76743003
PD30619a	17.80050891
PD30621a	9.415776081
PD30625a	50.44732824
PD30627a	113.9089059
PD30628a	21.96234097
PD30629a	3.165903308
PD30630a	45.34249364
PD30632a	36.01475827

PD30633a	15.52875318
PD30634a	9.458015267
PD30635a	32.99592875
PD30636a	26.81017812
PD30637a	15.63206107
PD30638a	15.51094148
PD30639a	9.541984733
PD30642a	59.01577608
PD30643a	60.43613232
PD30644a	44.78015267
PD30646a	74.86310433
PD30647a	16.94045802
PD30648a	38.43358779
PD30650a	33.04478372
PD30651a	26.5129771
PD30652a	36.93180662
PD30654a	79.25292621
PD30655a	11.03918575
PD30656a	4.024936387
PD30657a	17.70585242
PD30659a	14.7216285
PD30660a	12.85496183
PD30661a	20.13231552
PD30662a	194.1725191
PD30663a	27.2783715
PD30664a	220.9577608
PD30665a	197.2371501
PD30668a	16.32315522
PD30682a	15.10025445
PD30683a	72.46412214
PD30684a	7.121119593
PD30689a	10.51501272
PD30693a	42.9740458
PD30695a	194.9338422
PD30697a	83.20101781
PD30698a	73.72315522
PD30699a	179.6483461
PD30700a	206.3348601
PD30701a	139.0452926

PD30702a	170.1180662
PD30705a	167.4447837
PD30707a	167.2417303
PD30708a	124.3145038
PD30710a	156.3195929
PD30711a	18.57201018
PD30712a	180.1597964
PD30713a	206.6977099
PD30714a	200.1389313
PD30715a	250.7633588
PD30716a	184.5175573
PD30717a	198.6508906
PD30718a	217.8335878
PD30719a	262.378117
PD30720a	291.1007634
PD30721a	198.0447837
PD30722a	235.4697201
PD30723a	266.5867684
PD30725a	172.2631043
PD30727a	287.464631
PD30728a	237.1211196
PD30729a	188.5796438
PD30730a	260.6300254
PD30731a	247.113486
PD30732a	199.1058524
PD30733a	261.3852417
PD30735a	362.6697201
PD30736a	349.4178117
PD30737a	269.4223919
PD30738a	332.5206107
PD30739a	393.026972
PD30740a	343.0900763
PD30741a	419.5821883
PD30742a	367.9903308
PD30743a	314.8748092
PD30744a	377.329771
PD30745a	358.3201018
PD30746a	382.1913486
PD30747a	357.1867684

PD30748a	313.3450382
PD30749a	368.9536896
PD30750a	420.6681934
PD30751a	320.8229008
PD30752a	444.4320611
PD30753a	380.2483461
PD30754a	331.4610687
PD30755a	480.23257
PD30756a	442.5760814
PD30757a	376.9058524
PD30758a	444.9033079
PD30759a	429.3709924
PD30760a	359.3750636
PD30761a	419.8956743
PD30762a	417.4147583

Supplementary Table 16. List of samples that were re-sequenced by capillary. Information about the variants re-sequenced and the result of the experiment is included. In green, samples and variants that were confirmed.

Sample	Variant tested	Result
PD30582a	p.Cys307Arg	Not present
PD30601a	p.Arg117His	Present
PD30604a	p.His393Arg	Present
PD30608a	p.Ile22Val	Present
PD30610a	p.Pro601Leu	Not present
PD30624a	p.Glu92Lys, p.Arg83Gly	Not present
PD30681a	p.Val391Ile	Not present
PD30687a	p.Gln376Ter	Not present
PD30692a	p.Trp194Ter	Not present
PD30696a	p.Pro34Ser	Not present
Case_2636	p.Asp617GlufsTer9	Present
Ctrl_1401	p.Asp617GlufsTer9	Present
Ctrl_3151	p.Asp617GlufsTer9	Present
Case_1755	p.Gln358SerfsTer13	Present
Ctrl_2641	p.Glu204Ter	Not present
Ctrl_2500	p.Asp200Asn	Not present
Case_2329	p.Asp185Glu	Not present
Ctrl_2165	p.Asp185Glu	Not present
Case_1223	p.Asp175Ter	Not present

Supplementary Table 17. List of samples with variants in known melanoma predisposition genes. Genes *CDK4*, *CDKN2A* and *BAP1* were checked for variants. Only samples that were resequenced by Illumina (Supplementary Table 15) were assessed.

Sample	***POT1* variant**	**Variant in pathogenic gene**
PD30744a	p.Gln376Arg	*CDKN2A* Ala148Thr
PD30549a	p.Gly404Val	*CDKN2A* Ala148Thr
PD30730a	p.Gly404Val & p.Tyr419Cys	*CDKN2A* Ala60Thr

Abstract in local language: Spanish

Resumen

Algunas variantes genéticas en el gen *POT1* ('protection of telomeres 1', traducido como 'protección de telómeros 1') han sido asociadas al riesgo a desarrollar varios tipos tumorales, incluyendo melanoma, glioma, leucemia y cardioangiosarcoma. En este trabajo, secuenciamos todos los exones codificantes del gen *POT1* en 2,928 casos y 3,298 controles de ascendencia europea, e identificamos 43 variantes que alteran la secuencia protéica. Probamos la capacidad de unión proteína-ADN telomérico de todas las proteínas con variantes de cambio de amino ácido o codón de paro, e identificamos nueve variantes que debilitan la formación de este complejo. También definimos el papel de algunas variantes en la regulación de longitud telomérica, y en la formación del complejo por medio de simulaciones de dinámica molecular. De esta manera, determinamos que las variantes en *POT1* contribuyen de manera limitada al desarrollo de melanoma en la población en general, ya que solamente aproximadamente el 0.5% de los casos de melanoma fueron portadores de variantes patogénicas en este gen. Este gen podría ser evaluado en individuos con una fuerte historia familiar de melanoma y/o múltiples neoplasias.