

1 **Population matched (PM) germline allelic variants of**
2 **immunoglobulin (*IG*) loci: New pmIG database to better**
3 **understand *IG* repertoire and selection processes in disease**
4 **and vaccination**

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23 **Running Title: pmIG germline allelic database**

24 Abstract

25 At the population level, immunoglobulin (*IG*) loci harbor inter-individual allelic variants in the
26 many different germline *IG* variable (*V*), Diversity (*D*) and Joining (*J*) genes of the *IG* heavy
27 (*IGH*), *IG* kappa (*IGK*) and *IG* lambda (*IGL*) loci, which together form the genetic basis of the
28 highly diverse antigen-specific B-cell receptors. These inter-individual allelic variants can be
29 shared between or be specific to human populations. The current *IG* databases IMGT, VBASE2
30 and IgPdb hold information about germline alleles, most of which are partial sequences, obtained
31 from a mixture of human (B-cell) samples, many with sequence errors and/or acquired (non-
32 germline) *IG* variations, induced by somatic hypermutation (SHM) during antigen-specific B-cell
33 responses. We systematically identified true germline alleles (without SHM) from 26 different
34 human populations around the world, profiled by the “1000 Genomes data”. Our resource is
35 uniquely enriched with complete *IG* allele sequences and their frequencies across human
36 populations. We identified 409 *IGHV*, 179 *IGKV*, and 199 *IGLV* germline alleles *supported by at*
37 *least seven haplotypes* (= minimum of four individuals), after removal of potential false-positives,
38 based on using other genomic databases, i.e. ENSEMBL, TopMed, ExAC, ProjectMine.
39 Remarkably, the positions of the identified variant nucleotides of the different alleles are not at
40 random (as observed in case of SHM), but show striking patterns, restricted to limited nucleotide
41 positions, the same as found in other *IG* data bases, suggesting over-time evolutionary selection
42 processes. The identification of these specific patterns provides extra evidence that the identified
43 variant nucleotides are not sequencing errors, but genuine allelic variants. The diversity of
44 germline allelic variants in *IGH* and *IGL* loci is the highest in Africans, while the *IGK* locus is
45 most diverse in Europeans. We also report on the presence of recombination signal sequences
46 (RSS) in *V* pseudogenes, explaining their usage in *V(D)J* rearrangements. We propose that this
47 new set of genuine germline *IG* sequences can serve as a new population-matched *IG* (pmIG)
48 database for better understanding B-cell repertoire and B-cell receptor selection processes in
49 disease and vaccination within and between different human populations. The database in format
50 of fasta is available via GitHub (<https://github.com/InduKhatri/pmIG>).

51 **Keywords:** *IG* loci, allelic variants, germline, human populations, diversity, population-matched
52 *IG* (pmIG) database.

53 Contribution to the Field Statement

54 We present a catalogue of immunoglobulin (*IG*) germline-alleles of unprecedented completeness
55 and accuracy from 26 different human populations belonging to five different large ethnicities
56 (Source: 1000 Genomes). We identified the population distribution of several known germline
57 alleles and identified multiple new alleles, especially in African populations, indicative of high
58 allelic diversity of *IG* genes in Africa. Strikingly, the identified variant nucleotides of the different
59 alleles are not at random, but show striking patterns, restricted to limited nucleotide positions, the
60 same as found in other *IG* databases, suggesting over-time evolutionary selection processes.
61 Furthermore, we identified recombination signal sequences in pseudogenes (previously not
62 known). We provide an overview of *IG* germline alleles shared with and between known databases
63 and also point to potential sources of non-germline variation and incompleteness of the existing
64 *IG* databases. More importantly, we believe that this information can serve as a novel population-
65 matched *IG* (pmIG) database, highly valuable for the research community in supporting the
66 dissection and understanding of differences in effectiveness of antibody-based immune responses
67 in infectious diseases, other (immune) diseases and vaccination within and between human
68 populations. Such knowledge might be used in developing population-specific vaccination
69 strategies e.g. for currently ongoing SARS-CoV2 pandemic.

70 Introduction

71 The complex mechanism of antibody production from immunoglobulin (*IG*) genes is key to the
72 development of the broad repertoire of the antigen-specific B-cell receptors of the adaptive
73 immune system (1–5). These Ig proteins (antibodies) are assembled in B cells from two pairs of
74 polypeptide chains, the so-called Ig heavy (IgH) and Ig light (Igκ or Igλ) chains that are assembled
75 from different genes present in the *IG* loci, termed variable (*V*), diversity (*D*), joining (*J*) and
76 constant (*C*) (**Figure 1A**). The *IG* heavy chain locus (*IGH*) on chromosome 14q32.3 consists of
77 multiple different functional genes: ~44 *V*, ~27 *D*, ~6 *J* and ~9 *C* genes (**Figure 1B**). During
78 recombination, one of each *V*, *D* and *J* genes recombine to a *V-D-J* exon to code for the antigen-
79 binding domain of the IgH chain (**Figure 1A**). The rearrangements in both *IG* light chain loci
80 (kappa: *IGK*, on chromosome 2p11.2; lambda: *IGL*, on chromosome 22q11.2) take place in an
81 analogical way with direct rearrangement between *V* and *J* genes, as *D* genes are absent. This
82 process itself can produce up to three million different antibodies (6). Additionally, most of the *IG*
83 genes harbor inter-individual germline allelic variants, which can be shared between or be specific
84 to human populations (7–9). Consequently, different individuals can produce different antibodies
85 (derived from different allelic variants), implying that at the population level the diversity of
86 antibodies is even more extensive than at the individual level.

87 The *V(D)J* recombination process is guided via short highly conserved DNA stretches, called
88 “recombination signal sequences” (RSS), present at each recombination site of the *IG* gene
89 segments, i.e. downstream to *V*, upstream to *J*, and at both sites of *D* (RSS panel in **Figure 1B**)
90 (6,10–12). Each RSS comprises a palindromic heptamer (7bp: CACAGTG), a spacer (12 or 23 bp)
91 and a nonamer (9bp: ACAAAAACC), which are signals for recognition and binding by
92 recombination proteins (5). The heptamer juxtaposes the site of DNA cleavage (13), the spacer
93 length restricts recombination according to the 12-23 recombination rule (5), and the nonamer
94 provides the binding site for the RAG1 recombination protein (14,15).

95 The B-cell receptor (BCR) remains the same during the developmental stages of B cells from bone
96 marrow (BM) to naive mature B cells (**Figure 1C**). However, upon antigen recognition, generally
97 taking place in germinal centers (GC) during interaction with T cells, B cells proliferate and modify
98 the antigen-binding domain of their BCR via somatic hypermutation (SHM), randomly occurring
99 in the *V(D)J* exon region. B-cells with SHM that induce better antigen-binding of their antibodies

100 will be positively selected and contribute to improved B-cell responses such as in vaccination.
101 Thus, *IG* genes sequenced from antigen-experienced B cells, most likely carry SHMs; if used for
102 databases, such sequences might unwantedly result in false identification of allelic variants. The
103 identification of new germline alleles from B-cell repertoire transcriptomics data have changed the
104 perspective of the field (16,17), but they may at any stage also suffer from sequencing errors.

105 Variations in individual germline genes can result in inter-individual differences in immune
106 response (18–21). Consequently, reliable information on true germline allelic variants is important
107 to understand such inter-individual differences. Several *IG* databases, such as IMGT (22–27),
108 IgPdb (<http://cgi.cse.unsw.edu.au/~ihmmune/IgPdb/>), and VBASE2 (28), report germline
109 variations, present in different individuals. The sources of these three databases differ and each of
110 them comprises specific errors depending on the origin of the included *IG* sequences. In **Figure**
111 **1C**, the sources of the three different databases are aligned with the B-cell differentiation &
112 maturation pathway, including the GC and post-GC stages, where SHMs take place or have taken
113 place. IMGT is the most widely used database, because of its early availability, longstanding
114 experience and the most complete structure, but is at least in part derived from mature post-GC B-
115 cells (25,25,26). IgPdb does not comprise complete *IG* gene sequences, owing to short read
116 sequencing technologies. VBASE2 has better strategies for identification of true germline alleles,
117 but all the alleles are partial in sequence; this database is drawn from genome databases, namely
118 the EMBL nucleotide sequence database, Ensembl, and supported by evidence from the rearranged
119 repertoires.

120 Completeness and accuracy of germline sequences will greatly influence downstream analyses in
121 repertoire sequencing (Rep-Seq), as unreported *IG* allelic variants can appear as recurrent SHMs
122 and skew estimated segment distributions and/or estimated mutation frequencies in clinically
123 relevant decision processes e.g. infection response, vaccination studies (17,29–31) and prognosis
124 in chronic lymphocytic leukemia (32). Accordingly, the open germline receptor database
125 (OGRDB) aims to stringently assess and classify the germline alleles (33,34). OGRDB's endeavor
126 does not include *IG* alleles called from high-throughput whole genome mapping studies, as
127 OGRDB believes that the inferred sequences may contain false positives and should be supported
128 by rearrangements (34). Nevertheless, whole genome sequencing provides the opportunity to
129 search for allelic variants, which might be shared or be unique to human populations. With the
130 application of stringent parameters on whole genome studies, a new transitional resource can be

131 created which will have accurate germline alleles with population information for each allele on
132 top of complete *IG* genes similar to IMGT, as well as a proper classification of alleles like
133 VBASE2.

134 The “1,000 Genomes (G1K)” dataset, derived from cell samples of 2,504 individuals, has been
135 used to call alleles (9). Yu *et al* developed a method named alleleminder to determine alleles for the
136 *IG* and *TR* loci from the G1K data creating the Lym1k database. The Lym1k database has provided
137 a base to use G1K data, but the information provided may not be relevant for the research
138 community because the reliability of the new alleles identified is not provided. Moreover, they did
139 not retain population information, which is critical to develop a rich resource (9). Furthermore, Yu
140 *et al* also did not include all relevant components of each *IG* locus namely *D*, *J*, *C* genes and RSS,
141 which is a strong feature of the IMGT database. To obtain an accurate set of alleles with enriched
142 information, we have profiled all alleles for the *V*, *D*, *J*, *C* regions as well as the RSS regions for
143 all three *IG* loci from the G1K whole-genome sequencing (WGS) data, and the reliability and
144 population information of each allele is mentioned meticulously in a database called pmIG

145 Using the G1K resource, or using short read data, to profile alleles for the *IG* loci raises potential
146 pitfalls (35–37). The repetitive and complex nature of *IG* loci makes it difficult regions to identify
147 germline alleles from short read sequencing data in these regions. The level of haplotype diversity
148 of *IG* loci is another limitation (37). The main complexity with analyzing the G1K data lies in the
149 sample origin from the Epstein-Barr virus (EBV) transfected B-cell lines (**Figure 1C**). As ~75%
150 of the genomes (1,941 genomes) in G1K are derived from EBV-transformed B-cell cultures, we
151 framed a set of rules to obtain high-fidelity alleles (detailed in Methods) that prevent them from
152 being the result of sequencing errors or SHM. We have manually interfered with the resource to
153 obtain highly accurate alleles, submitted them to GenBank and made them also available via
154 GitHub with population information and confidence levels to provide access for the community.
155 The compiled resource comprises of *IG* germline allelic variants that cover a wide range of
156 ethnicities as investigated for five superpopulations, namely Africans (AFR), Americans (AMR),
157 East Asians (EAS), Europeans (EUR) and South Asians (SAS).

158 **Materials and methods**

159 **Data source**

160 The 1,000 Genomes data (G1K) (May, 2013 release; <http://www.1000genomes.org>; GRCh37
161 assembly) in the form of phased variant cell format (VCF) was used for this study. Phased variants
162 for GRCh38 (a recent release for the 1,000 genomes) are available, however, we used the GRCh37
163 version as the SNP IDs are not yet available for the GRCh38 mapping. These SNP IDs are relevant
164 to perform mapping to other databases and assess false negatives. Both genome assemblies do not
165 comprise of all the *V* genes mentioned in the IMGT database as multiple duplicated genes are not
166 present in all individuals. The full release of the data set was collected from 2,504 cell samples
167 from diverse ethnic groups that have a uniform distribution of individuals across populations. The
168 samples are classified in five superpopulations i.e. Africa, America, East Asia, Europe and South
169 Asia, that are further subdivided into 26 populations (7 African, 4 American, 5 East Asian, 5
170 European and 5 South Asian populations) with a minimum of 61 and a maximum of 113 samples
171 per population (**Table S1**). The VCF format of the data comprises information of both parental
172 and maternal chromosomes for each sample.

173 **Identification of alleles from G1K data**

174 The genes (*V*, *D*, *J* and *C*) from *IG* loci were retrieved from the VCF files for Chromosome 14
175 (*IGH*), Chromosome 2 (*IGK*), and Chromosome 22 (*IGL*). Only SNPs, deletions or insertions were
176 processed from the VCF files. Copy number variations were not considered. Software, such as
177 Plink (<http://zzz.bwh.harvard.edu/plink/>), to retrieve haplotypes from VCF files cannot process
178 multi-allelic SNPs. Therefore, special python scripts were written, while R scripting was used to
179 obtain the 5,008 independent haplotypes from the 2,504 cell samples (all available via GitHub).
180 Identical haplotypes are merged, and the number of times a particular haplotype appears is counted
181 and marked as an allele. The IMGT nomenclature is used to name genes, and alleles extend this
182 name with a numbering, for example the 01 and 02 alleles of the *IGHV1-8* gene are referred to as
183 *IGHV1-8_01*, *IGHV1-8_02*. IMGT alleles are denoted with an asterix, such as *IGHV1-8*01*,
184 *IGHV1-8*02*. The alleles are sorted in descending order such that it the first allele is supported by
185 the maximum number of haplotypes.

187 **Terminology**

188 With the term “*haplotype*” we refer to an operationally distinguishable gene (segment) present on
189 one strand (inherited from a single parent) in one individual. There are two haplotypes, one on
190 each positive and negative strand, with exactly the same or different polymorphisms. With “*allele*”
191 we refer to the profile of variants across one haplotype.

192 “*Mutations*” are genetic mutations that occurred to form different alleles of the gene and “*Somatic*
193 *Hypermutation Mutation (SHM)*” are the mutation that arises in *IGH/IGK/IGL* sequences in post-
194 GC cells.

195 **Mapping the alleles to existing databases**

196 The alleles obtained from the G1K samples are mapped to three different databases namely IMGT,
197 IgPdb and VBASE2 (28) using Muscle (38) and manually checked to ensure accurate mapping.
198 IMGT (www.imgt.org) is the global reference in immunogenetics and immunoinformatics studies
199 and is maintained since 1989. IgPdb (<http://cgi.cse.unsw.edu.au/~ihmmune/IgPdb>) is a repository
200 of suspected allelic variants of human *IG* germline genes. VBASE2 (<http://www.vbase2.org>)
201 presents *V* gene sequences extracted from the EMBL nucleotide sequence database and Ensembl
202 together with links to the respective source sequences. VBASE2 classifies the *V* genes into three
203 different classes: Class-1, genomic and rearranged evidence; Class-2, genomic evidence only; and
204 Class-3, rearranged evidence only (28). This evidence classification of alleles was only performed
205 by VBASE2 database; none of the other databases had such feature, implying that the capability
206 for rearrangement is formally not included in the IMGT and IgPdb databases.

207 **Classifying alleles into confidence levels**

208 The alleles in our study were classified into three major confidence levels (allele set (AS) 1-3) as
209 described below:

210 *AS1 (known)*: G1K alleles with a minimum support of 4 haplotypes and identified in either the
211 IMGT, IgPdb and/or VBASE2 (Class-1) databases. This AS1 allele set obviously has the highest
212 level of confidence as the alleles are observed in the G1K resource as well as in at least one of the
213 three existing databases. This set of alleles also validates G1K as a solid resource since there is
214 substantial overlap with the existing databases.

215 The alleles that did not classify as AS1 were divided into two categories:

216 *AS2 (frequent new alleles)*: G1K alleles with a minimum support of 19 haplotype (minimum of
217 ten individuals). These alleles would represent a set of newly identified alleles that are frequent.

218 *AS3 (rare new alleles)*: G1K alleles that have a haplotype support between 7 and 18 (minimum
219 four individuals). This group of new alleles with less confidence in terms of haplotype support is
220 called rare alleles. Despite the rarity of these alleles, we believe that they are genuine allelic
221 variants, because the chance that 7 identical haplotypes within 5,008 independent haplotypes are
222 caused by sequencing errors is highly unlikely.

223 As alleles can be duplicated or diverged from each other, we further subdivided all alleles into
224 three other categories (**Figure S1**):

225 *Alleles for Group genes*: Alleles for which the genes are marked as duplicated in the *IG* loci. These
226 are *IGHV1-69*, *IGHV1-69D*; *IGHV3-43*, *IGHV 3-43D*; *IGHV3-23*, *IGHV3-23D*; *IGHV3-64*,
227 *IGHV3-64D* and *IGHV2-70*, *IGHV2-70D* pairs.

228 *Alleles for operationally indistinguishable (OI) genes*: As multiple *V* genes are paralogous
229 (39,40), the mapping of short reads to such genes can be erroneous, influencing the subsequently
230 derived alleles. Mutations on the alleles of such genes can thus easily be false positives, even after
231 using stringent parameters. We denote these genes as operationally indistinguishable (OI) genes.
232 As these genes can be recognized based on their similarity (41), we generated a neighbor-joining
233 (NJ) tree for all *V* genes on the *IGH*, *IGK* and *IGL* loci, separately. The genes sharing a clade with
234 a short branch length i.e. 0.02, are called OI genes (**Figure S1**); and the corresponding alleles as
235 OI alleles.

236 *Alleles for self-evident (SE) genes*: Alleles that are *not* annotated as group or OI alleles.

237 The alleles that fall into AS1 category i.e. Known alleles are also termed as group or OI alleles as
238 these resources also contain false positives.

239 **Filtering out false positive alleles**

240 The G1K alleles were scrutinized manually.

241 1. Alleles with stop codons were removed from the final set.
242 2. Alleles with mutations or frameshift mutations absent in any of the following resources were
243 removed: ESP (<https://evs.gs.washington.edu/EVS/>), TOPMed
244 (<https://www.nhlbi.nih.gov/science/trans-omics-precision-medicine-topmed-program>), gnomAD
245 (<https://gnomad.broadinstitute.org/>), and ProjectMine (<https://www.projectmine.com/>).
246 3. All the alleles of group genes or OI genes (e.g. *IGHV1-69D* gene from IMGT and alleles for
247 *IGHV1-69* gene (group genes); alleles for all *IGHA1* and *IGHA2* genes (OI genes)) were aligned.
248 We removed alleles within group genes and OI genes when a mutation of an allele is shared
249 between alleles belonging to different genes within the group (pointing towards a mis-alignment
250 of a read) except when this mutation is present in one of the databases across multiple alleles. For
251 example, an allele of *IGHA1* has a position mutated i.e. A->C exclusively and two alleles from
252 *IGHA2* also has similar mutation at the same aligned position, then all the three alleles were
253 considered as false positives and filtered out.

254 **Identifying mutation patterns in the filtered alleles**

255 To identify the mutation patterns, we performed alignments of all alleles per gene. The alleles were
256 compiled from our database pmIG and the other existing databases i.e. IMGT, IgPdb and
257 VBASE2. In the alignments per gene, the mutating positions are identified for all alleles. In the
258 complete set of alignments per gene, the mutated positions for all alleles of that gene are compared
259 and characterized as *new* (when the mutation is only seen in our resource) or *known* (when the
260 mutation is seen in one of the other resources). We have done this for mutations in the *V* region as
261 well as the leader sequences. The positions added by our resource are mentioned and the pattern
262 of the mutations i.e. conserved (= at fixed positions) or random (= scattered, as caused by SHM)
263 is identified.

264 **Mapping population information to the identified alleles**

265 G1K alleles are annotated with superpopulation information (**Tables S2-S4**) into four categories:
266 1) ALL, present in all superpopulations; 2) AFR, only present in Africans; 3) AFR SHARED,
267 present in African and at least one of the other superpopulations, but not all; and 4) NON-AFR,
268 present in at least one of the superpopulations but not in Africans.

269 **Variants in RSS haplotypes**

270 We retrieved the RSS variants from the 40 bases adjacent to 3' *IGHV* genes and the 5' *IGHJ* genes
271 (having 23-bp spacers), and from the 30 bases adjacent to 5' and 3' *IGHD* genes (having 12-bp
272 spacers). Similarly, variants were retrieved from the 30 bases adjacent to 3' *IGKV* and 5' *IGLJ*
273 genes (having 12-bp spacers) and from the 40 bases adjacent to 5' *IGKJ* and 3' *IGLV* genes (having
274 23-bp spacers). The perfect RSS sequence has a conserved heptamer “CACAGTG”, a conserved
275 nonamer “ACAAAAAACC”, and a specific length of the spacer sequence (23 bp or 12 bp).
276 Mutations in heptamer and nonamer sequences as well as a deviating length of the spacer (less
277 than 23 bp or 12 bp) directly affect the recombination frequency of the linked genes (6,29,42,43).

278 **Phylogenetic trees for alleles**

279 Maximum Likelihood trees were built for the alleles using RAxML (44). The PROTGAMMAJTT
280 model was used to build the trees with 100 bootstraps. The trees were visualized using the iTOL
281 server (45). The trees taxa were colored as per AS classification; the population level annotation
282 is displayed in binary format and the frequency of alleles as text.

283 **Independent validation of the mutation patterns in the pmIG alleles**

284 To validate that the mutations that we detect are caused by somatic hypermutations (SHM), we
285 aligned the alleles to the rearranged *IGH* sequences derived from the transcriptomics data of
286 antigen-experienced B cells i.e. sorted HBsAg⁺ B cells, sampled after primary Hepatitis B
287 vaccination (46). The raw fastq files were obtained from SRA (SRP068400). Paired-end reads
288 were joined using fastq-join (ea-utils) with default settings and filtered for minimum Phred quality
289 of 30 over at least 75 % of bases. IMGT/HighV-Quest (17) was used for sequence annotation and
290 functional *IGH* sequences were retained. We selected 20 B-cell receptor sequences from affinity-
291 matured B-cells after Hepatitis B vaccination for each gene randomly and aligned those
292 sequences to the all alleles (detected by us (pmIG), IMGT, IgPdb and VBASE2) for the respective
293 genes. The mutating positions are marked and the mutation patterns were compared between
294 germline alleles and antigen-experienced *IGH* sequences from HepB study.

295 **Genetic diversity and migration events of population based on *IG* loci**

296 The VCF file of the complete individual locus, i.e. *IGH* (Chr14 [106032614, 107288051,
297 complement]), *IGK* (Chr2 [89890568, 90274235]), [89156874, 89630436, complement]) and *IGL*
298 (Chr22 [22380474, 23265085]), was subjected to a principal component analysis (PCA) using the
299 R Bioconductor package ‘SNPRelate’ (47). We then calculated the pairwise population
300 differentiation, which is based on levels of differentiation in polymorphism frequencies across
301 populations, as quantified by the fixation index (F_{ST}). F_{ST} is proportional to the evolutionary branch
302 length between each pair of populations. F_{ST} distances between populations were visualized with
303 a Neighbor joining tree. We used TreeMix (48) that uses the composite likelihood to build the
304 population trees. Six migration edges are tested for significance using 500 SNPs per block (-k
305 500). As “Out of Africa” is the most accepted theory (49) we used Yoruba population (YRI) of the
306 African superpopulation an outgroup for building the migration trees.

307 **Results**

308 The 1,000 Genomes (G1K) database from 2,504 individuals is a resource covering 26 populations
309 representing five continents (**Table S1**). We identified population-specific alleles in all three *IG*
310 loci (*IGH*, *IGK* and *IGL*), where each allele is supported by at least seven haplotypes (four
311 haplotypes for known alleles). We have collected the alleles identified from G1K to create a
312 population matched *IG* (pmIG) database. These alleles were divided into three allele sets (AS1,
313 AS2, or AS3) based on different confidence levels (see Methods). AS1 are known alleles; AS2 are
314 novel alleles that are frequent in the populations (supported by at least 19 haplotypes); and AS3
315 are novel rare alleles (supported by at least 7 haplotypes and at max by 18 haplotypes) (**Figure**
316 **S1**). The population matched *IG* (pmIG) database further contains meta information about the
317 alleles such as the support of haplotypes for each (sub)population (**Tables S2, S3 and S4**).

318 **The alleles from G1K samples are not affected by SHM from EBV transfected cell-lines**

319 The G1K samples originate from different sources, including EBV-transfected B-cell cultures and
320 blood as well as an unreported source in a few cases. SHMs might be present in mature B-cells
321 immortalized by EBV transfection. It should be noted that such EBV-transfected B-cells are
322 mainly polyclonal, unless cultured for (very) long time (= many months or more) or single cell
323 subcloned; this has not been the case for the G1K samples. Polyclonal B-cell cultures will not
324 likely have dominant SHM-based nucleotide variants detectable (50). Nevertheless, we tested
325 whether more allelic variants are found in samples stemming from an EBV origin. The metadata
326 of the G1K samples reports EBV coverage which was obtained by mapping the sequencing reads
327 to the EBV genome. Using these annotations, we divided the samples into two groups: 1) **Set-1**,
328 the non-EBV samples (563 samples), comprising of samples derived from blood (i.e. samples with
329 EBV coverage <20X) and samples where the source was not reported; and 2) **Set-2**, the EBV
330 samples, containing the remaining samples (1,941 samples). We used filtered *IGHV* alleles for this
331 analysis. Of 410 different *IGHV* alleles, 186 (45%) alleles are supported by samples in Set-1
332 (**Figure 2A**). From the 410 *IGHV* alleles, 145 (35%) are known to existing databases (AS1
333 category, Methods), and 103 (55%) of those are supported by Set-1 samples. There are 196 (47%)
334 frequent novel alleles (AS2 category, Methods) from which 77 (39%) are also supported by Set-1
335 and 119 (61%) by Set-2. These relative frequencies comply with the distribution of the number of

336 samples between the two sets, as Set-1 has about 3 times fewer samples than Set-2. Furthermore,
337 rare alleles are not supported by Set-1 samples (**Figure 2B**).

338 These observations on the novel alleles convince us that the *alleles that we detected in the G1K*
339 *samples are not influenced by SHMs related to EBV-transfection* of mature (post-GC) B-cells,
340 likely because we used the strict requirement of at least seven haplotypes for calling an allele. The
341 Lym1k database by Yu *et al.* seems to have suffered from the contamination by EBV transfection
342 as Yu et al. reported ~3-4,000 alleles for *IGH* and *IGL* loci (9).

343 **Conserved mutation pattern of pmIG alleles differs from SHM-affected *IGH* sequences**

344 Germinal center (GC) reactions result in affinity maturation of the Ig molecules, based on SHM
345 and subsequent selection processes (51). To further substantiate that the alleles identified from the
346 G1K resource with its stringent filtering criteria are correct, we aligned the alleles from all the
347 resources with the *IG* sequences obtained after Hepatitis B (HepB) vaccination in naive individuals
348 (**Methods**). **Figure 2C** shows the mutating positions for selected genes i.e. *IGHV1-69*, *IGHV3-15*
349 and *IGHV3-30* (mutated positions in red).

350 Interestingly, the mutations in the pmIG alleles for these genes are not random and thus follow the
351 above described strictly conserved pattern. In contrast, IMGT alleles for *IGHV1-69* and *IGHV3-*
352 23 are heavily mutated, as well as the IgPdb alleles for *IGHV1-69*. From this, we conclude that the
353 novel alleles that we identify in our database, pmIG, are generally free from SHMs and mostly
354 represents combinations of already known mutating positions with only a few new mutations, if at
355 all (**see also Figure S2**). Moreover, it is highly likely that the existing databases thus suffer from
356 the false-positive alleles as a result of SHMs.

357 **Most known alleles are frequent and present in all ethnicities**

358 The alleles that map to the IMGT database as well as to the other databases were instrumental in
359 identifying two groups of alleles, i.e. known and novel alleles (see Methods). We found that 35%
360 of the *IGHV* alleles mapped to the known alleles (**Table 1**) with 60% of them present in all the
361 superpopulations with support of at least 100 haplotypes (**Figure 3A**). Most of these alleles are
362 shared with the IMGT database, indicating that the IMGT database contains universal alleles. This
363 was similar for the *IGKV* (34%) and *IGLV* (31%) alleles.

364 Out of 29 African *IGHV* alleles that mapped to known alleles (**Figure 3B, 4**), 17% (5) map to
365 IMGT and the majority of them (60%;16) map to IgPdb with a minimum haplotype support of 5
366 (**Figure 3B**). The lower haplotype support of the alleles mapped to IgPdb databases suggests that
367 the IgPdb includes rare alleles, whereas IMGT is comprised of frequent alleles. Similarly, known
368 African alleles in *IGK* and *IGL* loci had a larger overlap with IgPdb and VBASE2 than with IMGT,
369 suggesting that alleles private to specific populations are not present in IMGT. IgPdb and
370 VBASE2, however, do not capture the complete diversity of African ethnicity as they contain
371 ~20% of the total African frequent *IGHV* alleles found from ~600 African individuals in G1K.
372 *IGHV* alleles private to Asian populations are mostly absent in all three existing databases. *IGKV*
373 and *IGLV* alleles private to any population including Africans are not profiled in any of the current
374 resources (**Figures 5, 6**). These findings indicate a biased sampling by the current databases.

375 **Conserved mutation patterns in the filtered alleles as compared to the existing databases**

376 Even after stringent filtering, “novel alleles” might suffer from SHM or sequencing errors (37).
377 As SHMs are introduced randomly and do not have a fixed pattern, we have already eliminated
378 possible false positives by putting a threshold of seven haplotypes (= at least four persons).
379 Furthermore, 118 potential false-positive alleles were eliminated that were arising due to the lack
380 of support in other databases or the same mutating patterns between the members of group and OI
381 genes (**Table S5**). Moreover, when we performed the alignments of the novel alleles with the
382 known alleles present in the pmIG, IMGT, IgPdb and VBASE2 databases, it appeared that the
383 novel alleles revealed highly conserved mutation patterns at fixed nucleotide positions, the same
384 positions as found in the other databases (**Figure S2**). The most spectacular examples from *IGH*
385 locus are that the novel alleles of the *IGHV2-5, 3-15, 3-20, 3-49, 3-64, 3-72, 3-74, 4-39, 6-1* genes
386 that did not gain any new polymorphisms, suggesting that evolutionary pressure and selection play
387 an important role for the remaining locations in these genes (**Figure S2**). A comparable
388 observation was made for the *IGHV1-69* gene, where only one new mutation was found in the
389 CDR1 region, which was specific to Asian populations (1 allele supported by 10 haplotypes)
390 (**Figure S2, Table S2**). The identification of these specific mutation patterns provides extra
391 evidence that the identified variant nucleotides are not sequencing errors, but genuine allelic
392 variants.

393 On the contrary, we found that several alleles for the *IGKV* genes (*VI-5*, *VI-33*, *VI-39*, *V3-11*, *V3-15*, *V3D-20*) in the IgPdb database suffer from possible SHMs as several new mutations across the
394 reported alleles are concentrated towards the end of the *V* gene (near the CDR3 region). Also, the
395 IMGT alleles mentioned to be false positives by Wang et al., 2008 (31), are too heavily mutated
396 (**Figure S2**, alleles with yellow background) to be considered as genuine germline alleles.
397 Accordingly, we did not find these alleles back in our pmIG database.

399 Based on the comparisons of different resources we realized that each *IG* germline database has
400 certain unique features as well as disadvantages (**Table 2**). Our database does not contain alleles
401 from the genes that are duplicated, as they are not present in human chromosome GRCh37
402 assembly. Elegantly, IMGT database has profiled all such genes to its completeness. In contrast to
403 any of the existing databases, we have devised an elegant strategy to exclude SHMs possibly
404 arising in group and OI genes along with the enriched information regarding confidence levels,
405 haplotype and population information.

406 **Novel alleles are ‘maximally two mutations away’ from the known alleles**

407 Frequent new alleles were either a combination of known polymorphisms or gained
408 polymorphisms. Many of the newly detected *IGHV* alleles (AS2/3 category) have no new
409 mutations or only one new previously unreported mutation (**Table 3**), or in other words, the 134
410 novel *IGHV* alleles each contain a new unique combination of already observed (individual)
411 mutations. 7 *IGHV* alleles gained more than three new mutations which belonged to the lower
412 confidence category AS3. These observations were corroborated in the IgPdb and VBASE2
413 database, where novel alleles indeed also had one to ten new mutations as compared to the IMGT
414 alleles (note that frequency of alleles is not reported in both databases) (**Figure S2**).

415 The *IGKV* and *IGLV* alleles did show a slightly different pattern as in *IGHV* alleles, i.e. the 85
416 novel *IGKV* and 102 novel *IGLV* alleles all have at least one new mutation as compared to the ones
417 in known alleles (**Table 3**). However, the position of these new mutations is important, i.e. they
418 can occur in the *V* region or in the leader region (16% *IGHV*, 18% *IGKV* and 25% *IGLV* of total
419 mutating positions). Most of the light chain alleles (9 *IGKV* and 35 *IGLV* alleles) in the current
420 databases are only partial i.e. they do not comprise of leader region. We believe this to be the
421 reason why we observe for the *IGKV* and *IGLV* novel alleles have a new mutation instead of a
422 novel combination of existing mutations.

423 **Population Distribution of the *IGH* alleles**

424 The first allele of each *IGHV* gene (_01), sorted such that it is supported by the maximum number
425 of haplotypes, is known and present across all superpopulations (denoted by the annotation
426 “ALL”). Approximately 100 new *IGHV* alleles (frequent or rare) are unique to the African
427 populations (denoted as “AFR”) while only 29 African *IGHV* alleles are known (**Figure 4A**).
428 Alleles not observed in Africa (“Non-AFR”) or observed in Africa and other superpopulations but
429 not all (“AFR Shared”) occur less (~40% less). Together, this suggests that Africans have a huge
430 diversity that has not been captured so far.

431 *IGHV1-69* (**Figures 4B**), *IGHV2-70*, *IGHV3-53* and *IGHV3-23* (**Figures S3**) genes have the
432 highest allelic diversity in the African superpopulation. *IGHV3-48* alleles are highly diverse in
433 South Asians (**Figure S3**), whereas new alleles in the *IGHV4* family are highly diverse in Africans
434 and East Asian populations (**Figure S4**). Similarly, *IGHV7-81* alleles mostly belong to the African
435 and American superpopulations (**Figure S4**). These differential diversities suggest an
436 environmental adaptability or population drift of these *IGHV* genes.

437 Most of the *IGHD* alleles are present in all populations and only a few are private to (super-
438)populations. Even rare variants are shared among different ethnicities, which hints that the *IGHD*
439 genes are evolutionary conserved across populations. Also, all *IGHJ* alleles are shared between all
440 the ethnicities (**Figure 4A**).

441 The constant genes of the *IG* loci are responsible for the effector functions of the antibodies and
442 have been considered to be more conserved as compared to the *V, D, J* genes. In contrast, we found
443 196 alleles for the nine *IGHC* genes. As *IGHA1,2* and *IGHG1,2,3,4* genes are highly conserved,
444 also visible from the alignment of the alleles within these groups based on their CH1-3 domains
445 (**Figure S6**), we grouped the alleles within these two groups (group alleles, Methods). This resulted
446 in that only 125 alleles were retained, where the majority of the alleles that were filtered out are
447 from the *IGHA1*, *IGHG1*, *IGHG3* and *IGHG4* genes (**Table S2, S5**).

448 To further understand the contrast between the supposedly conserved constant genes and the many
449 alleles found, we converted the nucleotide sequences of the *IGHC* alleles into protein sequences
450 and mapped them to the known allotype sequences. This shows that multiple mutations in the
451 allelic sequences for *IGHC* genes are synonymous and, therefore, the diversity at the protein level
452 is quite low as compared to the nucleotide level (**Table S2, Figure S6**). This suggests a high

453 evolutionary pressure on the *IGH* constant genes to conserve the structural and functional
454 properties of the Ig proteins.

455 Three new allotypes were identified for the IgA1, IgE and IgD proteins, respectively, all specific
456 to African populations (**Figure S6**). The amino acid change in the IgG1 allotypes did not result in
457 a change of either structural properties (aliphatic <-> aromatic) or the charge (neutral <-> negative
458 <-> positive).

459 **Population Distribution of the *IGK* alleles**

460 76 *IGKV* alleles are present in all superpopulations, of which 62 alleles are already known (**Figure**
461 **5A**). Only 10 of the 41 African alleles map to known alleles. A large number of alleles is observed
462 outside Africa (“Non-AFR”), suggesting that the diversity in the *IGK* locus does not only prevail
463 in the African superpopulation (**Figure 5B, S7**). All *IGKJ* alleles are shared between ethnicities
464 except one allele that was unique to Africans. Of the two major *IGKC* alleles, one is present in all
465 superpopulations and one is unique to Africans. A third rare allele is present in Europeans and
466 South Asians.

467 **Population Distribution of the *IGL* alleles**

468 The population distribution of the *IGL* alleles is similar to that of the *IGH* locus. Most of the known
469 *IGLV* alleles are present in all superpopulations. The majority of the new alleles in both the
470 frequent and rare alleles is unique to African populations (**Figure 6A**). Similarly, known *IGLJ*
471 alleles are present in all the superpopulations, whereas rare *IGLJ* alleles are either unique to
472 African populations or are not observed in the African population (“Non-AFR”). The first *IGLC*
473 alleles (_01) are present in all superpopulations, except *IGLC2_01* that is unique to Africans. New
474 rare *IGLC* alleles belong to either the African populations or populations outside Africa (“Non-
475 AFR”). Of the new frequent *IGLC* alleles, only a few are unique to European and South Asian
476 populations, and the majority exists in African populations (**Figure 6B, S8**).

477 **Recombinant Signal Sequence (RSS) variants in *IG* (pseudo)genes influence their
478 recombination frequencies**

479 RSS regulates the recombination process in which the conservation of RSS heptamers and
480 nonamers play a significant role (15,52,53). We did not find variations in conserved heptamers
481 and nonamers of allelic RSSs that may explain population-specific recombination frequency of the

482 respective genes. Also the conservation of RSSs in *IGHV* genes was reported to be related to
483 differences in recombination frequencies (29,54). We found that the heptamers and nonamers in
484 all *IGHV* RSSs are conserved, except the ones related to *IGHV3-16* and *IGHV7-81*. Interestingly,
485 a relatively lower recombination frequency of *IGHV7-81* has been reported before (29).

486 Several *IGHD* genes have mutated heptamer sequences at 3'D-RS and 5'D-RS (**Figure 7, Table**
487 **S6**), which might explain their reported reduced recombination frequencies in healthy individuals
488 (29). All *V* genes in *IGK* and *IGL* locus have conserved heptamers, except the *IGKV1D-13* and
489 *IGKV2D-30* genes in the *IGK* locus (**Table S7**), and the *IGLV5-48*, *IGLV2-33*, *IGLV3-22*, *IGLV3-*
490 *19* and *IGLV2-14* genes in the *IGL* locus (**Table S8**). These genes have mutations in the first three
491 bases of their heptamers, which consequently should result in less efficient (=reduced)
492 recombination frequencies (15,52,53).

493 The RSS spacer length also plays a role in the recombination frequency (11,43,55). We found that
494 the spacer length in RSSs of most *IGHJ* genes is 22bp, except for the *IGHJ3* and *IGHJ4* genes that
495 have a spacer of 23bp. In addition, *IGHJ4* has the most conserved heptamers followed by *IGHJ6*
496 (**Table S6**). These observations could explain why the *IGHJ4* and *IGHJ6* genes have the maximum
497 recombination frequency among *IGHJ* genes (56).

498 We also found conserved RSS heptamers adjacent to fifteen and eight pseudogenes in the heavy
499 and light *IG* loci, respectively (**Table S9**). The location of the RSS in few of these pseudogenes is
500 10-30 bases more distant from the *V* pseudogene boundaries than for regular *IGHV* genes in which
501 the RSS is generally 0-3 bases adjacent to the *V* gene boundary. Also, five *IGLV* functional genes
502 had RSS sequence 10-25 bases downstream to the gene (**Table S8**). We found that only *IGLV3-7*
503 (pseudogene) has a stop codon in between RSS heptamer and *V* gene boundary which could impact
504 the recombination frequency of this gene. The impact of distance between RSS and gene
505 boundaries is not yet known.

506 **Relation of *IG* alleles to variable immune responses in populations**

507 Although we acknowledge that the immune repertoire is individual-specific, the efficiency of the
508 response in different populations can be driven by the germline allelic variants. Therefore, we set
509 out to understanding the diversity in immune responses to infections or diseases by investigating
510 the allele distribution in the *IG* loci. To do so, we annotated alleles with their impact on human

511 health based on their polymorphisms and whether they contain at least one known disease-
512 associated variant (based on a literature search with keyword “*IG* gene name + disease/vaccine”).
513 We then checked the frequencies of the disease alleles across the different ethnicities. Here, we
514 report four examples that show different frequencies across the different (super-)populations.

515 **EXAMPLE-1:** The *IGKC* gene mutation rs232230 (C->G) results in a nonsynonymous variant
516 (V->L) that is a risk factor in both gastric cancer and breast cancer (odds ratio 1.64 and 1.94,
517 respectively) as well as *Helicobacter pylori* infection in gastric cancer and age in breast cancer
518 (57). The IMGT allele *IGKC*04* is equal to the same variant, and we found this allele to be present
519 in 1,066 Haplotypes of the G1K samples. The distribution of the alleles in different populations
520 was not known before, but we found the allele to be evenly distributed across all populations with
521 a median of 38 (Min: 7 – Max: 90) haplotypes (**Figure 8A**).

522 **EXAMPLE-2:** The F->L polymorphism in in the CDR2 region of *IGHV1-69* gene is known to
523 have a potential role in modulating the anti-influenza antibody repertoire (18). We not only
524 detected a high diversity of the *IGHV1-69* gene in the African (super-)populations that bear the
525 amino-acid “Phe: F” polymorphism (10 AFR alleles with F variant whereas only 5 with L variant)
526 but also that the F variant is overrepresented in African (super-)populations (**Figure 8B** grey bars).
527 For Non-African populations, we found that F and L amino-acid mutations occur in equal ratios,
528 except for South Asians where most alleles have the “Leu: L” polymorphism (**Figure 8B** blue
529 bars). These findings are concordant with those of Avnir et al. (18). The understanding of the
530 population distribution of this polymorphism in *IGHV1-69* gene and its role in flu, can have an
531 immediate implication in the implementation of “influenza” vaccines in different
532 superpopulations.

533 **EXAMPLE-3:** The *IGHV3-23*03* IMGT allele is known to be four-fold more effective than
534 *IGHV3-23*01* against *Haemophilus influenza* type b (Hib) (20). Recent studies suggest that
535 meningitis caused by Hib is a common and serious disease in children in China (21,58). We
536 observed that the *IGHV3-23*03* allele is very rare and is present frequently only in the East Asian
537 superpopulations. Only 30 haplotypes support this allele in the East Asian (super-)populations
538 (CDX:4, CHB:2, CHS:5, JPT:10, KHV:9) (30 haplotypes) (**Figure 8C**).

539 **EXAMPLE-4:** The *IGHV4-61*02* IMGT allele is related to higher risk of rheumatic heart disease
540 (RHD) in Oceanic populations where four polymorphisms (rs201076896, rs201691548,
541 rs200931578 and rs202166511) increase the susceptibility (59). In this study, the relationship was
542 drawn only within the Oceanic populations. Therefore, we profiled the alleles carrying these four
543 mutating positions in our population matched database which comprises five different ethnicities.
544 We found nine alleles comprising of these four mutating positions and their frequency was highest
545 in African populations followed by Asian populations (**Figure 8D**). This might suggest that RHD
546 is more frequent in African populations as compared to Asian populations.

547 **Evolutionary dynamics of variation patterns in different populations**

548 The genetic diversity of individual genes does not reflect on the diversity of the complete *IG* loci
549 including coding and non-coding regions. Therefore, we used the SNPs in the complete locus to
550 identify the existing variations between (super-)populations. In **Figure 9A** we found African
551 populations to be unique and highly diverse for *IGH* and *IGL* loci, whereas the *IGK* loci are much
552 more condensed due to some large outlier samples in African and American populations.

553 To completely capture the variability of the locus, we looked at the pairwise population
554 differentiation (F_{ST}) in the *IG* loci. The *IGH* and *IGL* loci again point towards higher diversity in
555 African populations ($F_{ST} \sim 0.20$; **Figure 9B**). Interestingly, we found a different pattern in the *IGK*
556 locus that has highest variability within Europeans ($F_{ST} \sim 0.30$) rather than Africans (**Figure 9B**).
557 The lower diversity of the *IGK* locus in Africans is consistently visible in the population
558 distribution of the alleles (**Figures 4, S6**). This might suggest that the variability in this locus is
559 more recent in evolution, as compared to the *IGH* and *IGL*.

560 Furthermore, the cladogram (**Figure 9B**, marked by dotted circles) reveals a closer relationship
561 between the Peruvian (PEL) population and East Asian populations, especially the Han Chinese
562 in Beijing in China (CHB), and Japanese in Tokyo (JPT) in each *IG* locus, suggestive of a mixture
563 between the Peruvian and East Asian populations. To obtain insight into the migration patterns
564 between populations, we plotted the tree for 26 populations from the G1K resource where
565 horizontal branch lengths are proportional to the amount of genetic drift that has occurred on the
566 branch (**Figure 9C**). Six migration links are plotted with a directed connection between
567 populations wherein orange colored connections depict higher migration rate. We indeed observed

568 the highest migration weights between the Peruvian and East Asian populations in all loci,
569 supporting the mixture hypothesis (**Figure 9C**, marked by dotted circle).

570 **Discussion**

571 We performed an extensive analysis of *IG* germline alleles from 2,504 individuals, representing
572 26 populations, and created a population matched *IG* germline database (pmIG), that comprises a
573 comprehensive overview of haplotypes across five main different ethnicities. We enriched pmIG
574 by including information on rare and frequent germline alleles per population, facilitating
575 identification of genuine germline alleles and excluding SHM. This will be important when
576 studying differences between populations in immune responses as a consequence of germline
577 differences (7,42,60–64).

578 Similar to the Lym1K resource by *Yu et al.*, we have used the 1,000 Genomes dataset to derive all
579 *IG* alleles. But there are important differences. We report information on haplotype support,
580 including a minimal support of seven haplotypes (four haplotypes for known alleles), categorized
581 them into confidence levels, scrutinized each allele manually for their use in repertoire studies,
582 and also profiled population information for each allele. As a result, we report ten times less alleles
583 than the ones reported by Lym1K. It is fair to say that the “alleleminer tool” (used to create Lym1k)
584 has a cutoff option for the minimal haplotype support. However, to identify potential sources of
585 non-germline errors, the processes of B-cell development and SHM-based affinity maturation of
586 antibodies should be understood carefully. For example, the existence of duplicated genes reduces
587 the confidence in associated alleles. Therefore, we adopted a manual curation of alleles and
588 assigned confidence levels to each allele. Currently, alleles are categorized into three different
589 confidence levels based on the observed haplotype support and further grouping based on the
590 duplications of *IG* genes. Additional support from sanger sequencing of the alleles from
591 independent sources, can further increase the confidence level of the pmIG database.

592 One confidence level, the AS1 level, indicates whether the alleles that we detected are previously
593 reported in other databases. Aligning alleles with tools like Muscle (38) is, however, not trivial,
594 but a manual check was also performed to ensure accuracy. We found that the known alleles that
595 we detect (and thus present in existing databases) are mainly present in the European-Caucasian
596 populations, suggesting a population bias in the current IMGT, VBASE2, and IgPdb databases.

597 The largest numbers of novel frequent and rare alleles are identified in African populations of
598 which 70-90% of diversity is not captured by the existing databases. Several studies analyzing
599 genome wide patterns, genetic variations, demographic history and immune responses have also
600 reported higher immune diversity in Africans (39,61,65–70). The sampling of more individuals

601 from multiple African populations can further reveal the genetic diversity in Africa and can thereby
602 substantiate our understanding of allelic diversity in *IG* loci. The recent completion of the African
603 reference genome (69) can put this divergence in a different perspective, particularly when
604 compared with the more narrow diversity of the European reference genomes (71,72).

605 The accuracy of our novel alleles is supported by the highly conserved mutation patterns, restricted
606 to a limited number of nucleotide positions, remarkably the same as found in other *IG* databases.
607 This also allowed us to identify possible false-positive alleles in the IMGT and IgPdb databases.
608 Our findings were consistent with a previous study that indicated that 104 IMGT alleles are false-
609 positives (31). We believe the reliability of our pmIG database is mostly due to the stringent
610 threshold for novel alleles to have been seen in at least 4 individuals (7 haplotypes).

611 Different germline alleles have shown to result in different responses and effectiveness against
612 infections in individuals (18,20,32). The population information of these alleles can provide better
613 understanding of these response differences at the population level. For example, the *IGHV3-*
614 23*03 IMGT allele is known to be four-fold more effective than *IGHV3-23*01* against
615 *Haemophilus influenza* type b (Hib) (20). The *IGHV3-23*03* IMGT allele is supported by only 30
616 haplotypes and frequent in East Asian populations. This allele might a potential therapeutic
617 antibody for meningitis caused by Hib in China (21,58). Similarly, the under-representation of
618 *IGHVI-69* alleles in European populations and their higher copy number in Africans might explain
619 why European populations are more prone to pandemic flu outbreaks as compared to African
620 populations. Together, these examples underpin the significant role of germline alleles in different
621 populations and their protective nature against infection with the consequent potential impact of
622 population-specific therapeutic antibodies. Detailed studies on differences in clinical disease
623 course and final outcome in different regions of the world during pandemic outbreaks, such as the
624 currently ongoing SARS-CoV2 pandemic, might at least in part show a role of the here presented
625 diversity of *IG* gene alleles within and between human populations.

626 VBASE2 and IgPdb do not report pseudogenes or rearrangeable pseudogenes. With the extensive
627 genomic information from the G1K resource, we could identify conserved heptamer sequences
628 adjacent to these pseudogenes. Interestingly, these conserved heptamers were 10-30 bases
629 juxtaposed to the pseudogene boundaries. Also, a similar pattern was observed in a few *IGLV*
630 genes. The pseudogenes are reported to be rearranged in several repertoire analysis studies (29,73),

631 which also relates to our unique above-mentioned finding. This suggests a possible role for the
632 position of RSSs on the recombination frequency of these genes.

633 The high variability in the *IGH* and *IGL* loci in African populations, as compared to Non-African
634 superpopulations, could indicate the migration of human populations out of Africa based on *IG*
635 loci. On the other hand, the *IGK* locus represents higher variability in European populations, as
636 compared to Non-African populations. We did not find many new alleles in the *IGK* locus from
637 G1K, which hints to current databases being biased towards a sampling from mostly European
638 populations. Pairwise differences between alleles in the *IGK* locus show that Non-European
639 populations are closer to each other than to the European population. Although we cannot follow
640 the trend of mutations over time, the migration analysis and the alleles statistics support the
641 variability and environmental adaptation of this locus over time.

642 The IMGT database is the most used database in research because of its completeness. Also, the
643 database hosts several tools to support researchers in analyzing and understanding next generation
644 sequencing data of *IG* loci. With our pmIG database of *IG* alleles, we report identified and curated
645 alleles across 5 superpopulations, containing 26 populations, resulting in 170% more allelic
646 variation. Having a richer source of *IG* alleles improves the interpretation of repertoire sequences.
647 For example, determining whether an observed sequence belongs to a germline allele or is the
648 result of SHM in response to an antigen. Or, whether measured sequences of naive B cells are
649 considered to be the result of a sequencing error, which now is determined based on the presence
650 of the observed allele in databases (74). Alternatively, pmIG can be exploited for applications in
651 immune response dynamic analysis and clonal lineage analysis. Perhaps the most clinically
652 relevant application of pmIG is understanding differences between populations and to help
653 implementation of population-specific vaccination studies.

654

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662 Authors contributions statement

663 Concept and design of the study: IK, MAB, EBvdA, CIT, MJTR, and JJMvD

664 Data acquisition, data analysis and organization of the database: IK

665 Wrote the manuscript and designed the figures: IK, MAB, MJTR, and JJMvD

666 Manuscript revisions and approval of the submitted version: All authors

667 Conflict of Interest Statement

668 J. J. M. van Dongen is the founder of the EuroClonality Consortium and one of the inventors on
669 the EuroClonality-owned patents and EuroFlow-owned patents, which are licensed to
670 Invivoscribe, BD Biosciences or Cytognos; these companies pay royalties to the EuroClonality
671 and EuroFlow Consortia, respectively, which are exclusively used for sustainability of these
672 consortia. J. J. M. van Dongen reports an Educational Services Agreement with BD Biosciences
673 and a Scientific Advisory Agreement with Cytognos to LUMC.

674 The rest of the authors declare that they have no other relevant conflicts of interest.

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- 911

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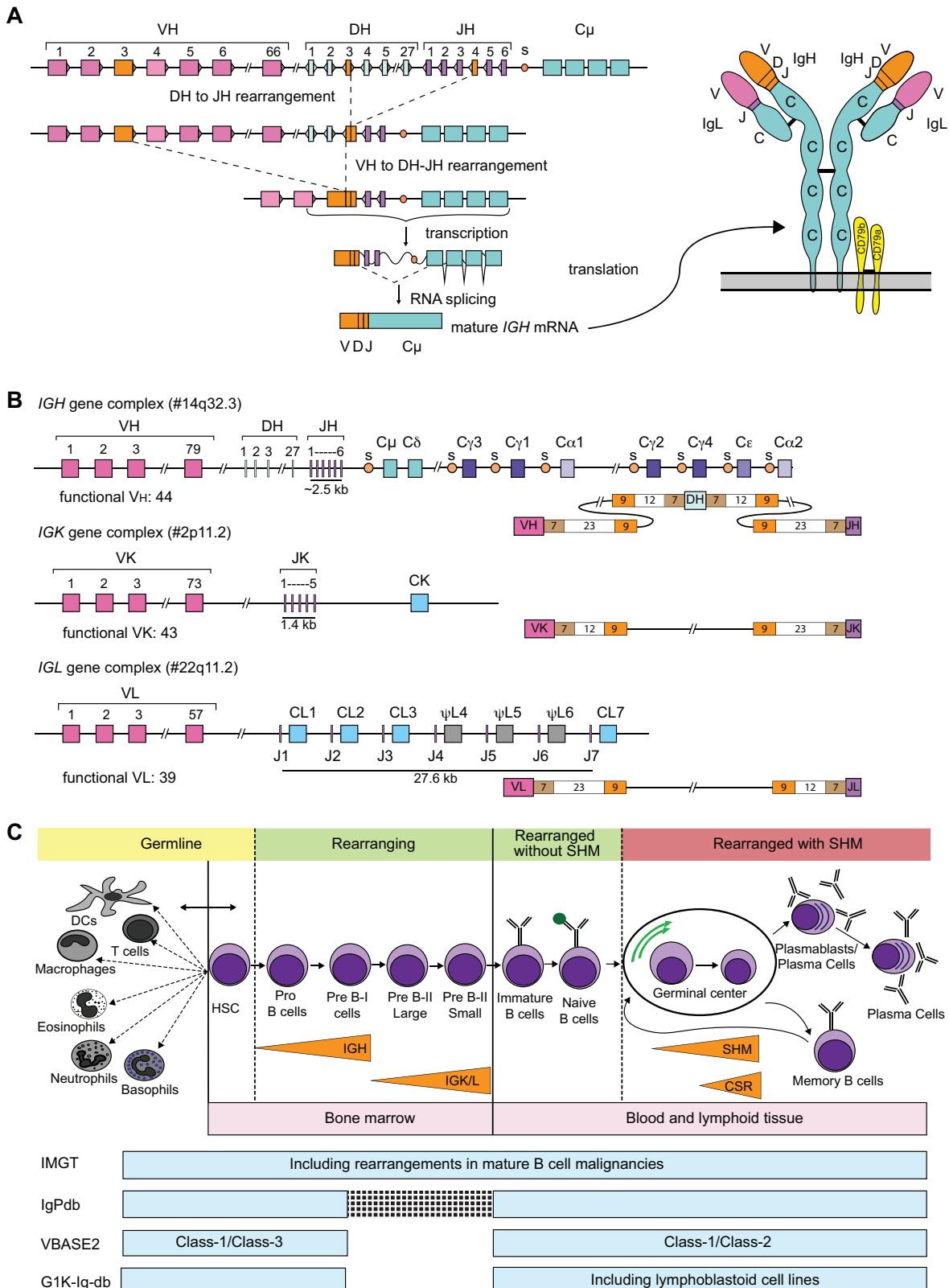
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920 expressed in this document reflect only the author's view. The European Commission is not
921 responsible for any use that may be made of the information it contains.

922 **Availability of data**

923 The full set of alleles (AS1-3) and all R and python scripts used for analysis are available from
924 GitHub (<https://github.com/InduKhatri/pmIG>). The alleles are available in three different files,
925 according to the confidence level. Also, the gapped sequences for the pmIG alleles as per IMGT
926 standards are available to be used as a reference allele set for Rep-Seq data analysis, that can be
927 directly implemented as database in IgBLAST (75).

928 **Figures:**

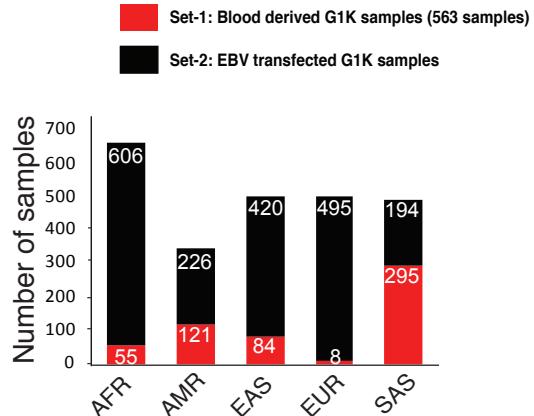
Figure 1



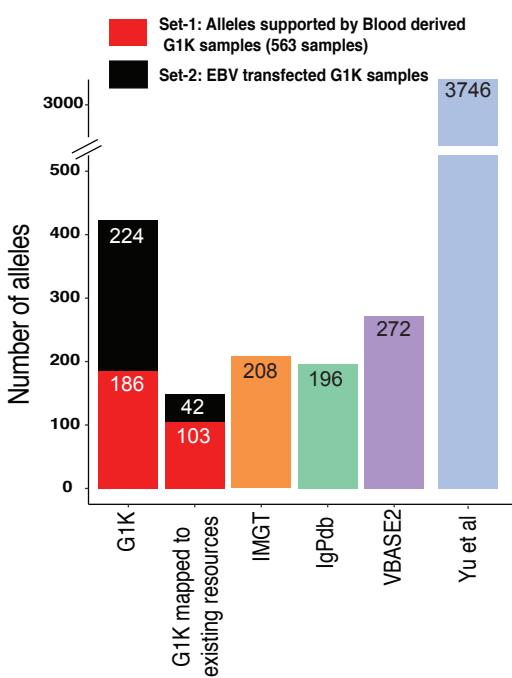
930 **Figure 1: Generation and assessment of diversity in *IG* loci.** **(A)** In the first step of *V(D)J* recombination in the *IGH* locus a *D* gene is coupled to a *J* gene. Subsequently, a *V* gene is coupled to the *DJ* joint. The *VDJ* exon is transcribed and spliced to the *IGHM* exons. An analogical process takes place in the *IG* light chain genes. When a functional IgM protein is transported to the plasma membrane with anchoring molecules CD79a and CD79b, and a functional Ig light chain it forms a complete antibody molecule. **(B)** Schematic overview of the three *IG* loci: *IGH*, *IGK*, *IGL* and the structure of their corresponding Recombination Signal Sequences (RSS). Genomic position of the loci is indicated in brackets. In *IG* loci each rectangle depicts one of the variable (*V*), diversity (*D*), joining (*J*) and constant (*C*) genes, and circles depict switch regions. The number of known functional genes, as listed in the IMGT, is indicated underneath each scheme. RSS structure schemes depict the position of heptamers (7), nonamers (9) and spacers (12/23) relative to *V*, *D* and *J* genes. **(C)** Hematopoietic stem cells in bone marrow, give rise to cells of both myeloid and lymphoid origin. While most of the cell types retain *IG* genes in their germline configuration, precursor B cells rearrange first Ig heavy chain and then Ig light chain genes to form a functional antibody. B cells with the functional B-cell receptor migrate to the periphery where they can recognize antigen. Upon antigen recognition and receiving help from T cells, B cells enter germinal center reaction during which they undergo intensive proliferation, improve affinity for antigen by the introduction of somatic hypermutations (SHM) in rearranged *IG* genes, and may change their effector functions in the process of class-switch recombination (CSR). This results in the formation of memory B cells and antibody-secreting plasma cells. *IG* genes can be sequenced from any B-cell type. However, in (virtually) all cells other than B cells, they will be in their germline configuration. Precursor B cells and naive mature B cells carry rearranged *IG* genes, which can be further modified by the presence of SHM in post-germinal center cells. Light blue block underneath B-cell maturation scheme depicts the sources of *IG* sequencing in the three existing *IG* databases: IMGT (ImMunoGeneTics, <http://www.imgt.org/>), IgPdb (<http://cgi.cse.unsw.edu.au/~ihmmune/IgPdb>), VBASE2 (<http://www.vbase2.org>), and the *IG* gene sequence data from the 1000 genome project (G1K-Ig-db, <http://www.internationalgenome.org>). VBASE2 has classified the alleles in different classes based on their genomic and rearrangement evidence. Class-1 alleles in VBASE2 have evidence from both; Class-2, and Class-3 alleles of VBASE2 are supported either by germline occurrence or rearranged repertoires.

Figure 2

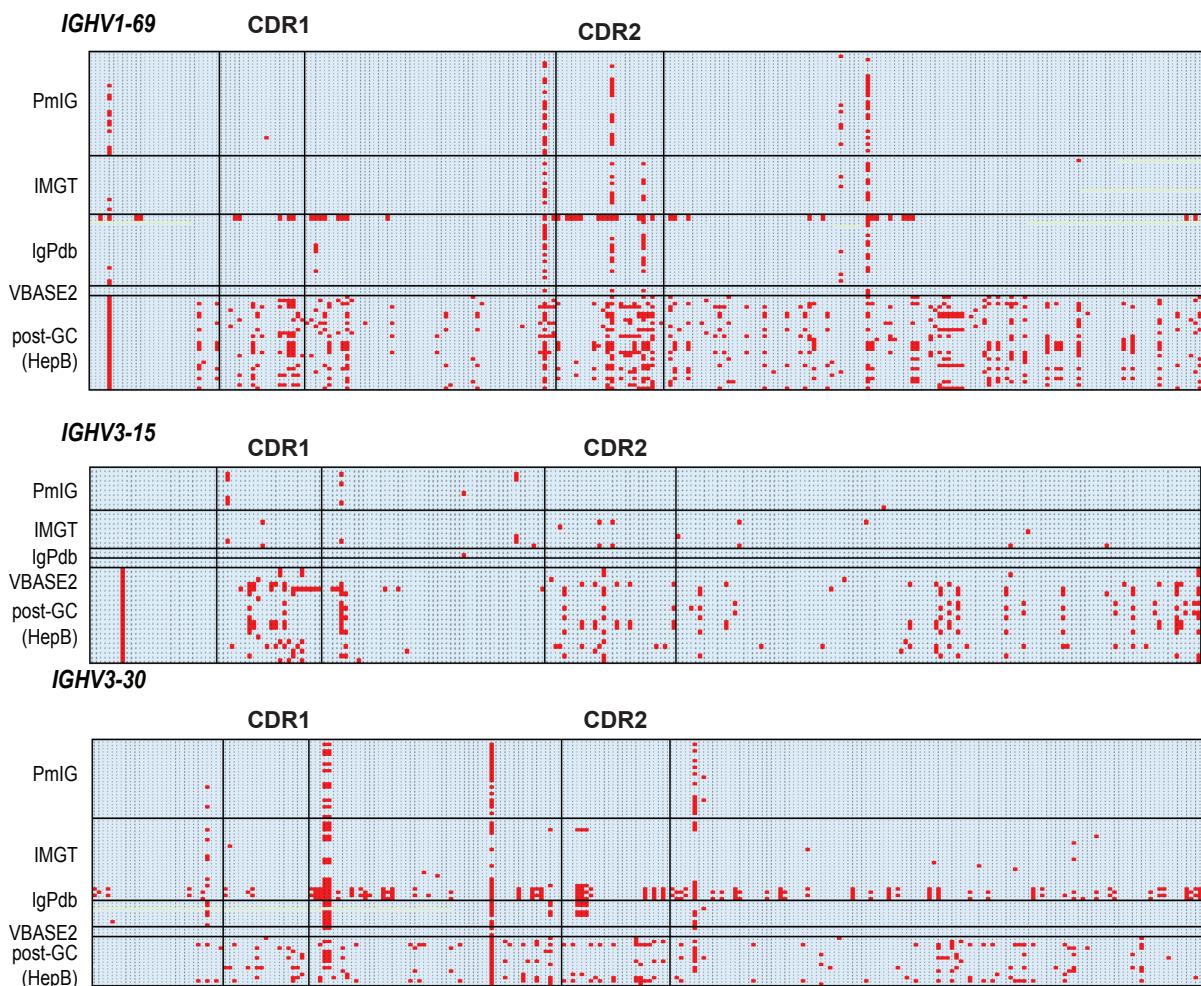
A



B



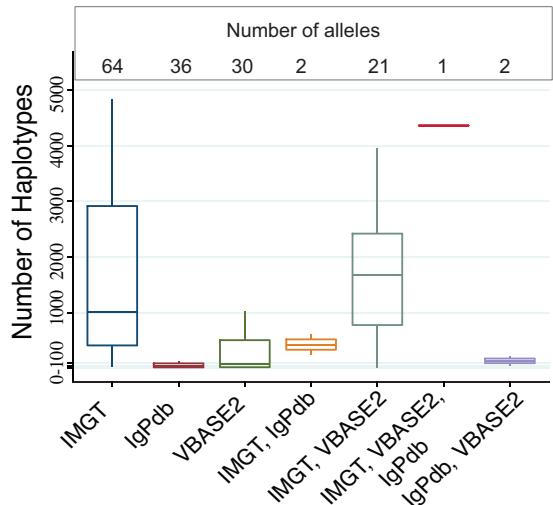
C



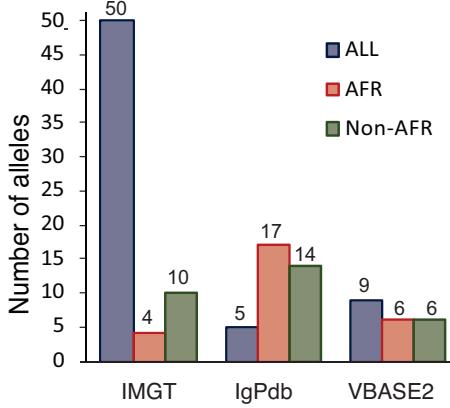
962 **Figure 2: pmIG alleles are free of somatic-hypermutations (SHM). A)** The distribution of
963 samples in Set-1 and Set-2 from each super-population in G1K resource. **B)** The count of *IGHV*
964 alleles in different resources. **C) Mutations mapped to the alleles from pmIG, IMGT, IgPdb965 and VBASE2 databases with the corresponding *IGHV* sequences from the HepB vaccination
966 study for *IGHV1-69* and *IGHV3-30* genes. The blue shade represents the conserved nucleotides
967 and red shades indicate the mutated positions. Strikingly, the positions of the identified variant
968 nucleotides of the *IGHV1-69* and *IGHV3-30* alleles in the pmIG database are not at random, but
969 show restricted patterns, restricted to limited nucleotide positions, the same as found in other *IG*
970 databases. However, several sequences in the IMGT and IgPdb databases show additional variant
971 nucleotides at positions, which are mutated in the post germinal center (GC) B-cells after Hepatitis
972 B vaccination. This comparison indicates that most likely the IMGT and IgPdb databases are
973 contaminated with SHM-mutations, which is supported by the fact that several IMGT and IgPdb
974 sequences seem to have comparable SHM patterns and are therefore most likely derived from the
975 same postGC B-cell populations.**

Figure 3

A



B

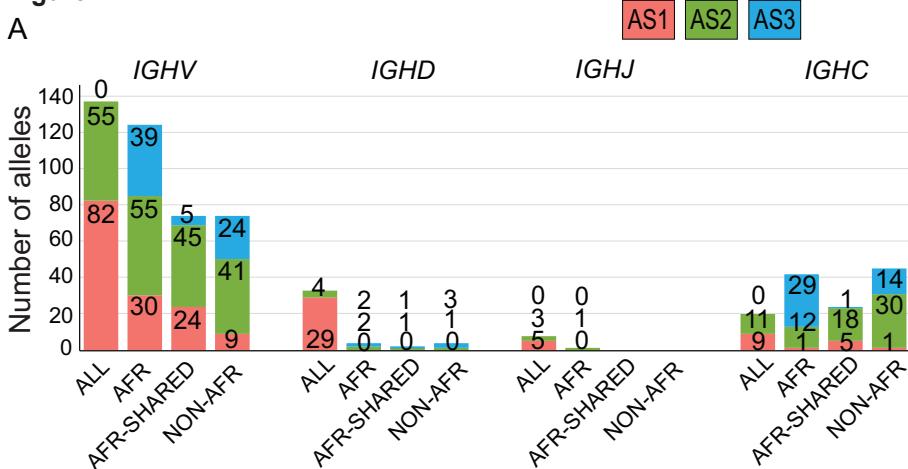


976

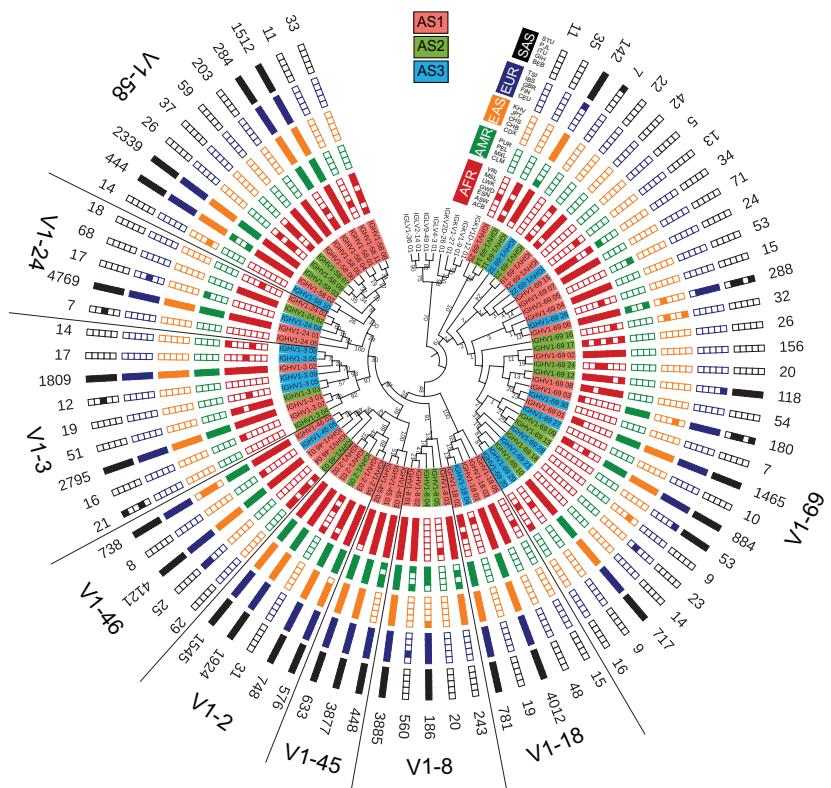
977 **Figure 3: The known alleles are frequent and are present in all the ethnicities. A)** Haplotypes
978 support of the alleles mapped to the existing databases. Each dot is an allele. The alleles mapped
979 to the alleles in multiple resources are also indicated. **B)** The population distribution of the AS1
980 (known) alleles. The alleles shared between IMGT and other resources are considered to be an
981 IMGT alleles. Similarly, alleles are considered to be belonging to IgPdb if mapped to IgPdb and
982 VBASE2 databases. IgPdb and VBASE2 harbor alleles unique to specific populations.

Figure 4

A



B

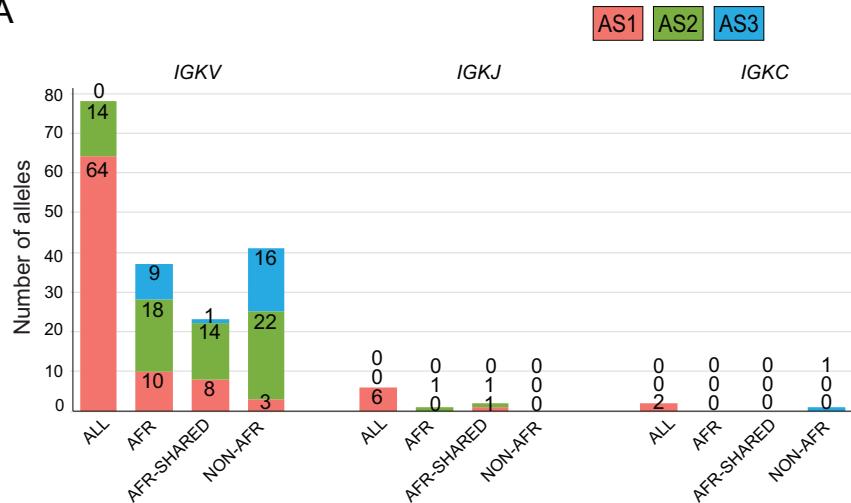


983

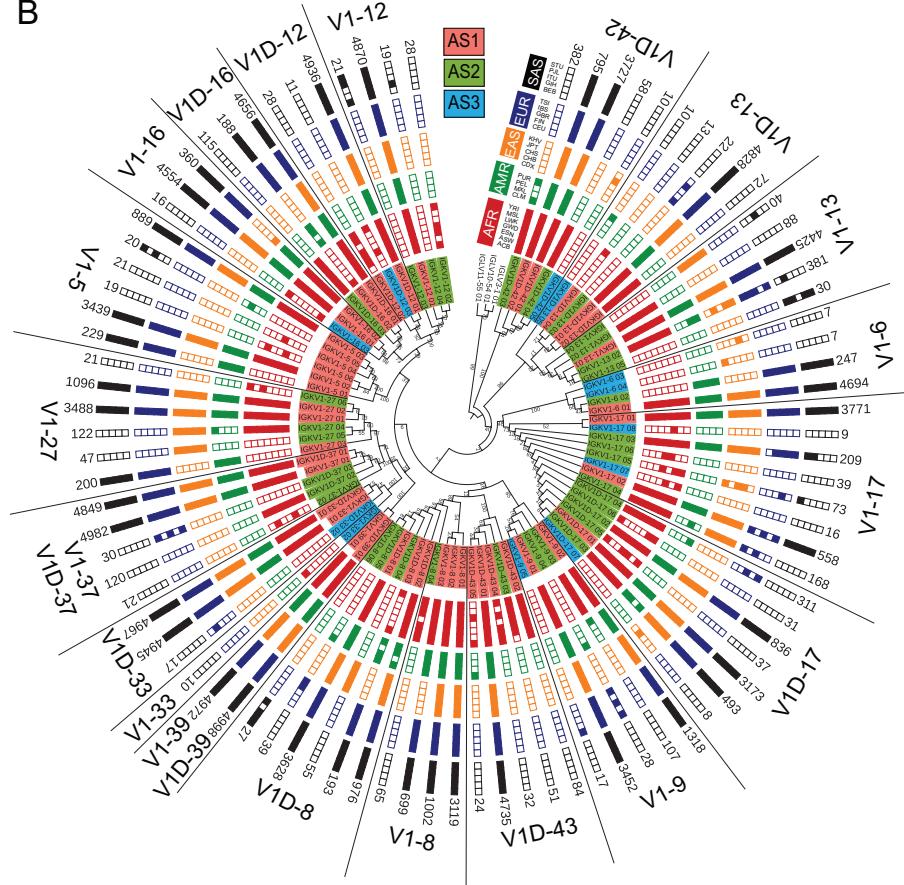
984 **Figure 4: Population distribution of alleles in *IGH* heavy chain locus. A)** The relative
985 superpopulation distribution of *VDJ* genes and *C* genes for *IGH* locus. The population plots are
986 represented for all superpopulations (ALL), Africans only (AFR), Africans shared with one of the
987 other superpopulations (AFR Shared) and ‘Non-AFR where alleles are present in at least one of
988 the populations other than Africans. **B)** Maximum Likelihood tree of the population distribution
989 of *IGHV1* family alleles. The *IGHV1* family genes are indicated in the legends. Red label
990 background indicates AS1 alleles, green AS2 and blue AS3 alleles. The population distribution is
991 plotted in a binary format where each block is a population. Filled block represents the presence
992 of that allele in at least four haplotypes in that population, otherwise the block is unfilled. For the
993 population distribution of other *IGHV* families refer to Figures S3 and S4.

Figure 5

A



B

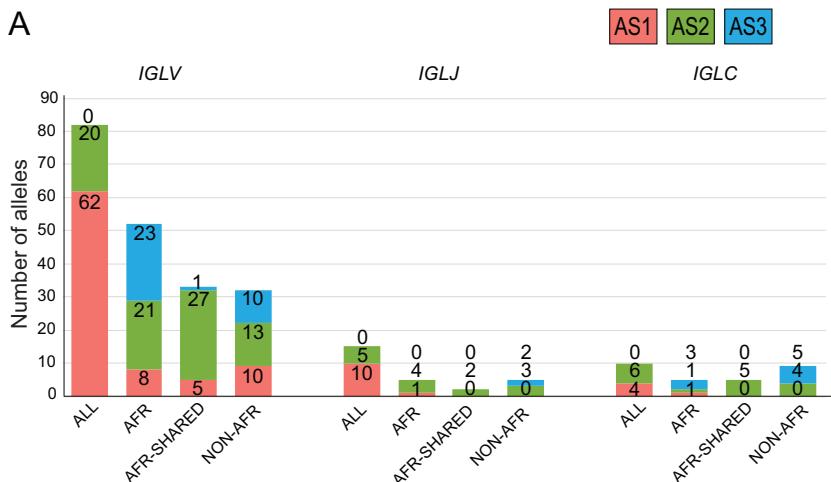


994

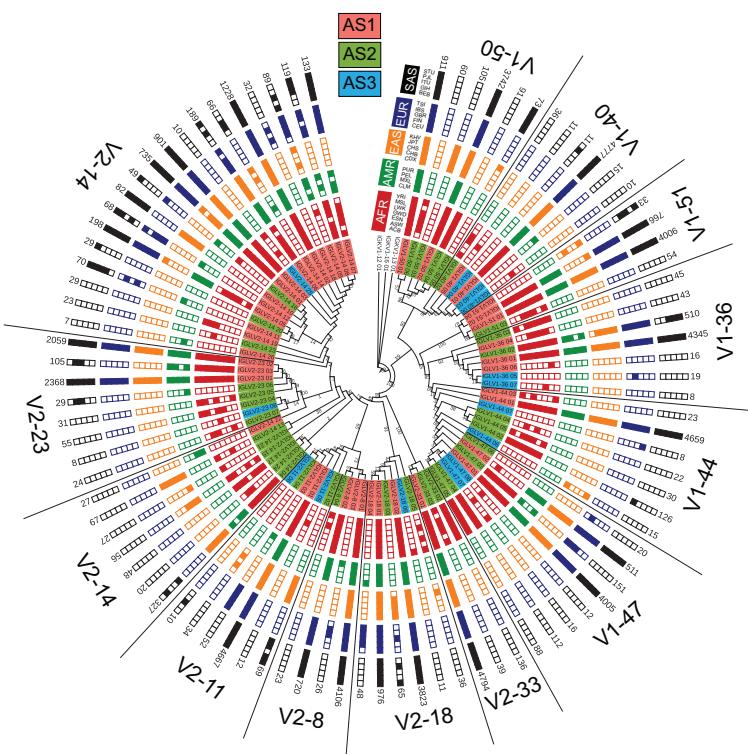
995 **Figure 5: Population distribution of alleles in *IGK* light chain locus. A)** The relative
996 superpopulation distribution of *VJ* genes and *C* genes for *IGK* locus. The population plots are
997 represented for all superpopulations (ALL), Africans only (AFR), Africans shared with one of the
998 other superpopulations (AFR Shared) and ‘Non-AFR where alleles are present in one of the
999 populations other than Africans. **B)** Maximum Likelihood tree of the population distribution of
1000 *IGKV1* family alleles. For the population distribution of other *IGKV* families refer to Figure S7.

Figure 6

A



B

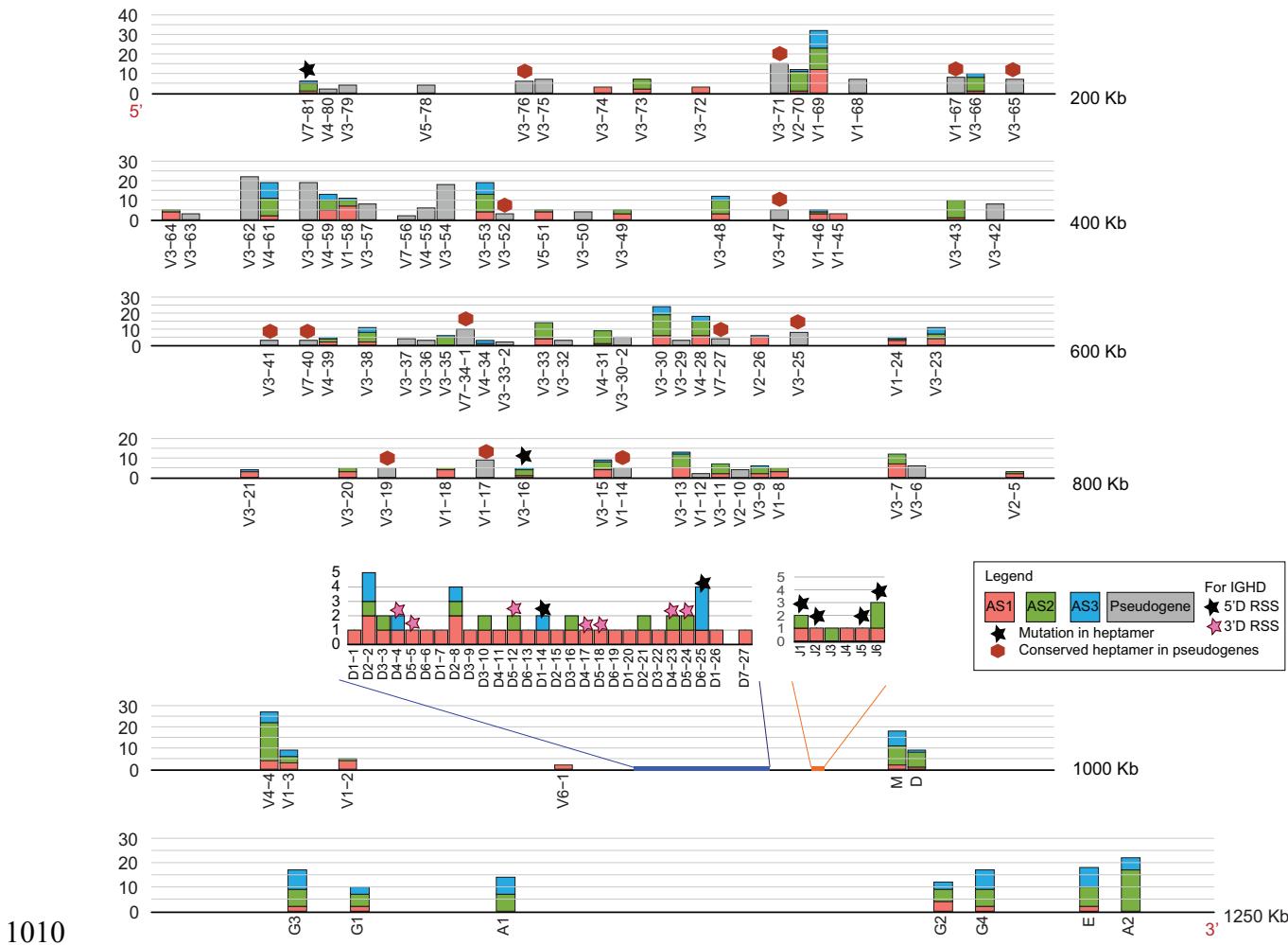


1001

1002 **Figure 6: Population distribution of alleles in *IGL* light chain locus. A)** The relative
1003 superpopulation distribution of *VJ* genes and *C* genes for *IGL* locus. The population plots are
1004 represented for all superpopulations (All), Africans only (AFR), Africans shared with one of the
1005 other superpopulations (AFR Shared) and ‘Non-AFR where alleles are present in one of the
1006 populations other than Africans. **B)** Maximum Likelihood tree of the population distribution of
1007 *IGLVI* and *V2* family alleles. For the population distribution of other *IGLV* families refer to Figure
1008 S8.

1009

Figure 7



1011 **Figure 7: IGH alleles per gene with confidence levels in the locus representation.** The alleles
 1012 are marked on the locus with a confidence level AS1 (red), AS2 (green) and AS3 (blue), where
 1013 the bar height represents the number of alleles. Pseudogenes are represented by grey colored bars.
 1014 The Y-axis on the locus shows the absolute number of alleles. *IGHD* and *IGHJ* are projected
 1015 outwards. A star indicates that the RSS sequence is mutated and it could have effect on the
 1016 recombination frequency of these genes. *D* have stars colored with black and blue which indicates
 1017 the mutation in 5' RSS and 3' RSS, respectively. A red hexagon on the pseudogenes indicates the
 1018 presence of conserved heptamers.

Figure 8

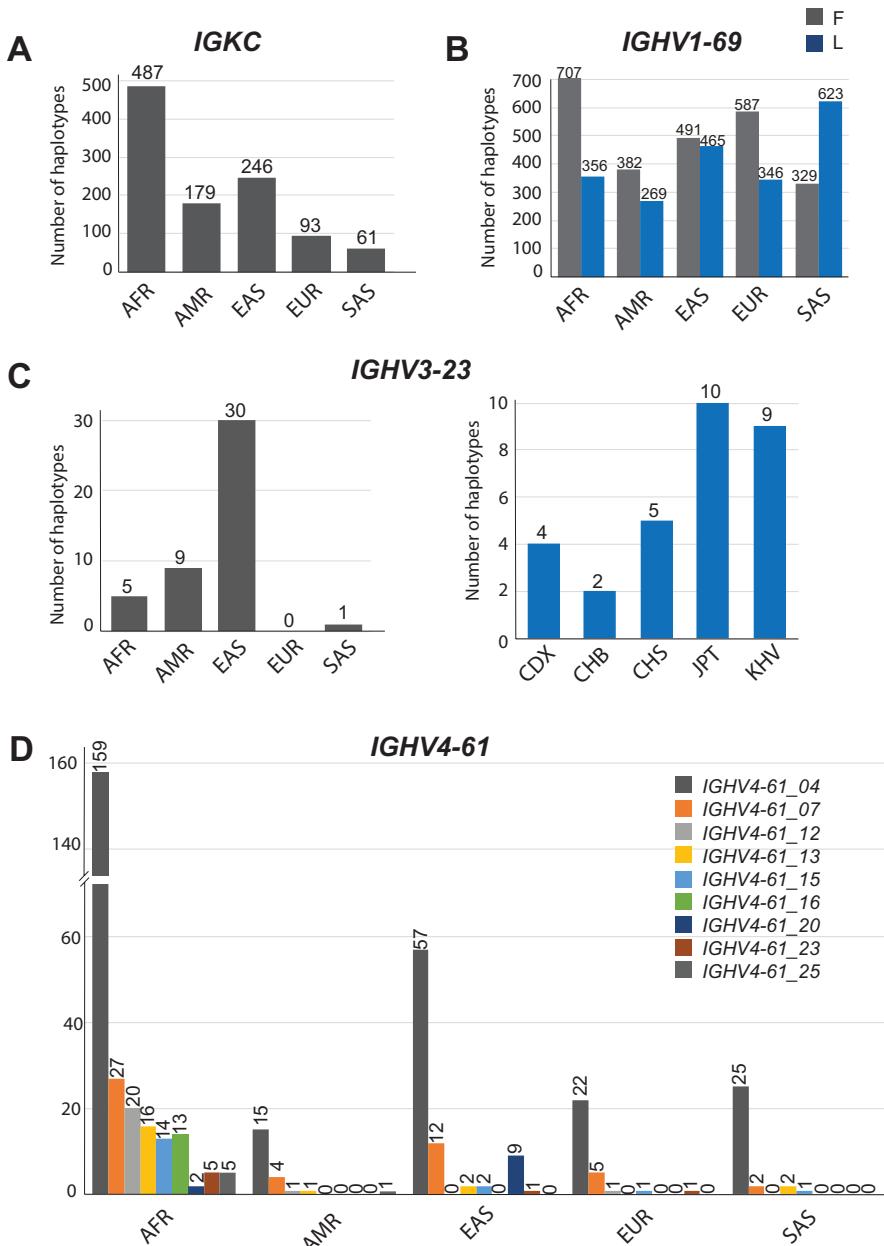
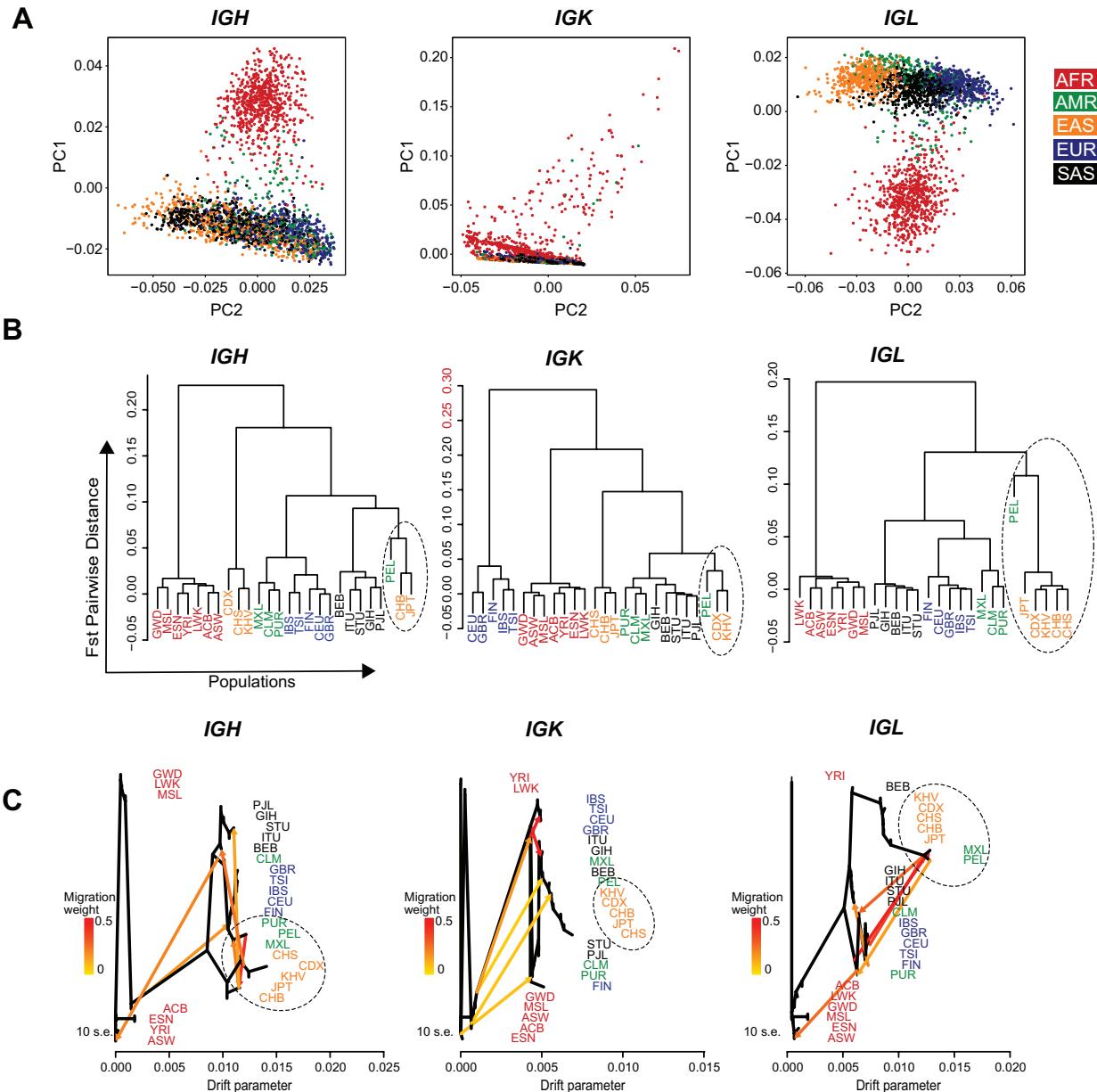


Figure 8: Frequency of *IG* alleles associated with immune responses in populations. **A) *IGKC*:** One allele supported by 1066 haplotypes is distributed in all the superpopulations. **B) *IGHV1-69*:** All the alleles were divided into two groups i.e. one with F “Phe” in CDR2 region and other with “L”. The combined distribution of the two groups is represented in the figure. **C) *IGHV3-23*:** One allele is supported by 45 haplotypes. The plot on the left represents the superpopulation distribution of the allele. The right plot represents the population distribution of the allele in the East Asian population. CDX: Chinese Dai in Xishuangbanna, China; CHB: Han Chinese in Beijing, China; CHS: Han Chinese South; JPT: Japanese in Tokyo, Japan; KHV: Kinh in Ho Chi Minh City, Vietnam **D) *IGHV4-61*:** Nine alleles i.e. *IGHV4-61_04*, *IGHV4-61_07*, *IGHV4-61_12*, *IGHV4-61_13*, *IGHV4-61_15*, *IGHV4-61_16*, *IGHV4-61_20*, *IGHV4-61_23* and *IGHV4-61_25* were found to have the mutations in combination with other mutations. Separate bar plots are drawn for each allele.

Figure 9



1032

1033 **Figure 9: Genetic diversity, population structure and migration events in five**
 1034 **superpopulations for *IG* loci. A)** Separate PCA plot of the heavy and light chains of *IG* locus based
 1035 on the single-nucleotide polymorphisms in the complete locus. Each dot represents a sample and
 1036 each sample is colored based on the superpopulation they belong. In *IGH* and *IGL* locus Africans
 1037 have higher diversity as compared to Non-African superpopulations, while *IGK* has more diversity
 1038 in part of the European population. **B)** Pairwise population distribution calculated by Fst Matrix is
 1039 represented as a cladogram for each locus namely *IGH*, *IGK* and *IGL*. 26 populations are colored
 1040 as per the superpopulations i.e. Africans in red; Americans in green; East Asians in orange;
 1041 Europeans in blue and South Asians in black. **C)** Migration events in *IGH*, *IGK*, and *IGL* locus.
 1042 Six migration events are marked in the ML tree where edge color represents the migration weight;
 1043 red suggest higher migration weight and yellow the lowest.

1044 **Tables**

1045

1046 **Table 1: Number of alleles in different functional gene segments in *IG* loci.** AS1 (Known),
 1047 AS2 (Frequent) and AS3 (Rare) are major confidence levels. AS2 and AS3 alleles are further
 1048 subdivided into SE (self-evident alleles), GA (group alleles) and OI (operationally
 1049 indistinguishable) alleles.

1050 * 5 AS1 alleles were identified as false positives, based on mapping to the paralogs in *IGHG* alleles.

1051

	AS1				AS2				AS3				TOTAL	IMGT	IgPdb	VBASE2
	Sum	SE	GA	OI	Sum	SE	GA	OI	Sum	SE	GA	OI				
<i>IGHV</i>	145	95	31	19	196	91	47	58	68	25	18	25	409	236	196	272
<i>IGHD</i>	29	29	0	0	8	8	0	0	5	5	0	0	42			
<i>IGHJ</i>	5	5	0	0	4	4	0	0	0	0	0	0	9			
<i>IGHC</i>	16*	5	11	0	71	24	47	0	44	16	28	0	125			
<i>IGKV</i>	83	10	73	0	70	5	65	0	26	3	23	0	179	80	23	168
<i>IGKJ</i>	7	7	0	0	2	2	0	0	0	0	0	0	9			
<i>IGKC</i>	2	2	0	0	0	0	0	0	1	1	0	0	3			
<i>IGLV</i>	84	56	0	28	81	59	0	23	34	26	0	8	200			
<i>IGLJ</i>	10	10	0	0	11	11	0	0	6	6	0	0	27	10	0	0
<i>IGLC</i>	5	5	0	0	16	16	0	0	8	8	0	0	29			

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Table 2: Comparison of key features in different databases that profile *IG* germline alleles.

	IMGT	VBASE2	IgPdb	pmIG
Completeness of <i>IGHV</i> alleles	138 Complete and 98 Partial	V-region only	V region only	All complete (including leader)
Completeness of <i>IGKV</i> alleles	71 Complete and 9 Partial	V-region only	V region only	All complete (including leader)
Completeness of <i>IGLV</i> alleles	39 Complete and 35 Partial	V-region only	V region only	All complete (including leader)
Presence of <i>IGHD</i> and <i>IGHJ</i> genes	Present	None	A few	Present
Presence of <i>IGKJ</i> genes	Present	None	A few	Present
Presence of <i>IGLJ</i> genes	Present	None	A few	Present
Presence of constant genes	Present	None	None	Present
RSS	Present	None	None	Present
Completeness in terms of alternate duplicated genes	Complete	No (Not all genes present)	No (Not all genes present)	Complete as per availability from GRCh37 (does not include alternate duplicated genes)
Strategy for exclusion of SHM	Not reported	Not reported	Not reported	Explicitly reported
Confidence Levels	NONE	Class-1, 2, 3	None	Double layer of confidence levels (Confidence levels with information on group genes and OI genes)
Haplotype/Population frequency	None	None	None	Present

1055

1056 **Table 3: Number of alleles with count of new mutating positions as compared to the**
1057 **existing databases.** Complete sequence includes leader sequence and the *V* region for all the *V*
1058 genes/ This is important to realize that 98 *IGHV*, 9 *IGKV* and 35 *IGLV* alleles are partial and do
1059 not contain the leader sequence.

1060

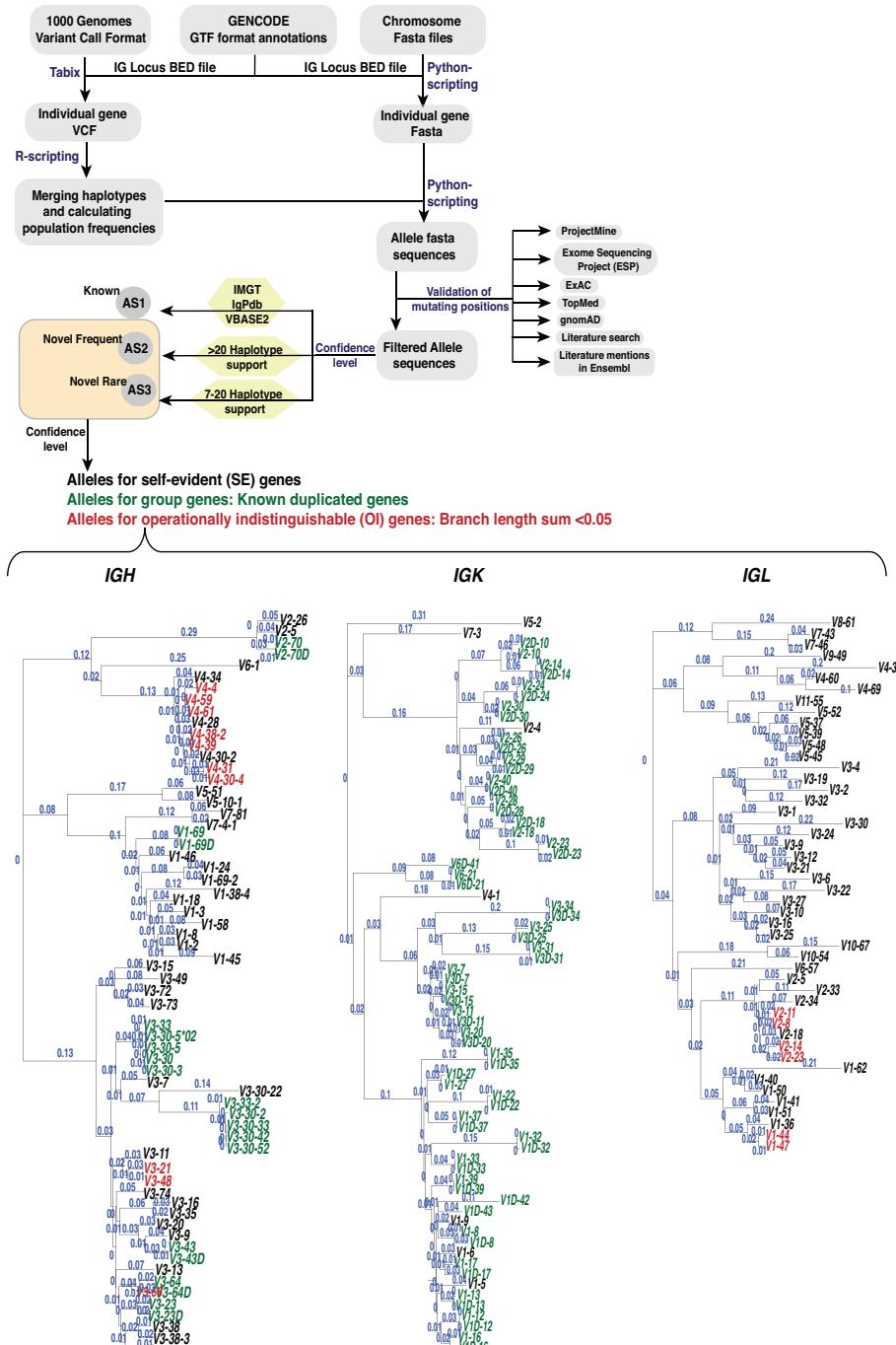
	<i>IGHV</i>		<i>IGKV</i>		<i>IGLV</i>	
Mutation Counts	<i>Complete Sequence</i>	<i>V region only</i>	<i>Complete Sequence</i>	<i>V region only</i>	<i>Complete Sequence</i>	<i>V region only</i>
<i>Zero</i>	279	312	85	95	68	91
<i>One</i>	102	72	85	78	102	93
<i>Two</i>	21	19	7	4	26	14
<i>Three</i>	5	5	1	1	3	2
<i>Four</i>	1	1	1	1	1	0
<i>Five</i>	1	1	0	0	0	0

1061

1062

1063 **Supplementary Figures**

Figure S1



1064

1065 **Figure S1: The pipeline developed to call alleles and assign confidence levels.** The assigned
 1066 confidence levels AS1-3 were identified based on known (AS1) and novel (AS2 and AS3) alleles.
 1067 The novel alleles were further divided into self-evident, group and OI alleles highlighted in black,
 1068 green and red colors, respectively on the NJ trees for *IGHV*, *IGKV* and *IGLV*. All the genes were
 1069 obtained from GRCh37 version of human genomes. The genes absent in the human genome
 1070 assembly were retrieved from the IMGT database.

Figure S2

IGHV1-2

V1-2_01	atggactggacctggaggatcctcttggcagcagccacaggagcccactcccagggtcagctggtcagtctgggctgaggtgaa
V1-2_02	atggactggacctggaggatcctcttggcagcagccacaggagcccactcccagggtcagctggtcagtctgggctgaggtgaa
V1-2_03	atggactggacctggaggatcctcttggcagcagccacaggagcccactcccagggtcagctggtcagtctgggctgaggtgaa
V1-2_04	atggactggacctggaggatcctcttggcagcagccacaggagcccactcccagggtcagctggtcagtctgggctgaggtgaa
V1-2_05	atggactggacctggaggatcctcttggcagcagccacaggagcccactcccagggtcagctggtcagtctgggctgaggtgaa
IGHV1-2*01	atggactggacctggaggatcctcttggcagcagccacaggagcccactcccagggtcagctggtcagtctgggctgaggtgaa
IGHV1-2*02	atggactggacctggaggatcctcttggcagcagccacaggagcccactcccagggtcagctggtcagtctgggctgaggtgaa
IGHV1-2*03	atggactggacctggaggatcctcttggcagcagccacaggagcccactcccagggtcagctggtcagtctgggctgaggtgaa
IGHV1-2*04	atggactggacctggaggatcctcttggcagcagccacaggagcccactcccagggtcagctggtcagtctgggctgaggtgaa
IGHV1-2*06	atggactggacctggaggatcctcttggcagcagccacaggagcccactcccagggtcagctggtcagtctgggctgaggtgaa
IGHV1-2*05	-----caggtcagctggtcagtctgggctgaggtgaa
IP_V1-2*p05	-----
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V_V1-2*01	-----caggtcagctggtcagtctgggctgaggtgaa
V_V1-2*02	-----caggtcagctggtcagtctgggctgaggtgaa
V_V1-2*03	-----caggtcagctggtcagtctgggctgaggtgaa

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V1-2_03	gaaggcctggggcctcagtaaggctccctgcaaggcttcggatacacccctaccggctactatatgcactgggtgcgacaggcccct
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IGHV1-3

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V1-3_02 atggactggacctggaggatccttttggcagccacaggtgtccactcccaggttcagcttgtcagtcggctgaggtgaagaa
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IP_V1-24*p03 -----
V_V1-24*01 -----

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IP_V1-24*p03 -----
V_V1-24*01 -----

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V_V1-24*01 -----

IGHV1-45

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IGHV1-46

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IGHV1-58

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IGHV1-69

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V1D-33_01

V1D-33_02

IGKV1D-33*01

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V2-24_02
IGKV2-24*01
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V2-24_02
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V_V2-24*01

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V2-24_02
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V_V2-24*01

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V2-24_02
IGKV2-24*01
V_V2-24*01

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IGKV2-40*02

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IGKV4-1

V4-1_01
V4-1_02
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V_V4-1*01

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V4-1_01
V4-1_02
IGKV4-1*01
V_V4-1*01

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V4-1_01
V4-1_02
IGKV4-1*01
V_V4-1*01

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V4-1_01
V4-1_02
IGKV4-1*01
V_V4-1*01

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V4-1_01
V4-1_02
IGKV4-1*01
V_V4-1*01

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V4-1_02
IGKV4-1*01
V_V4-1*01

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V4-1_02
IGKV4-1*01
V_V4-1*01

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V6-21_01
IGKV6-21*01
IGKV6-21*02

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V6-21_01
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IGKV6-21*02

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V6D-41_03
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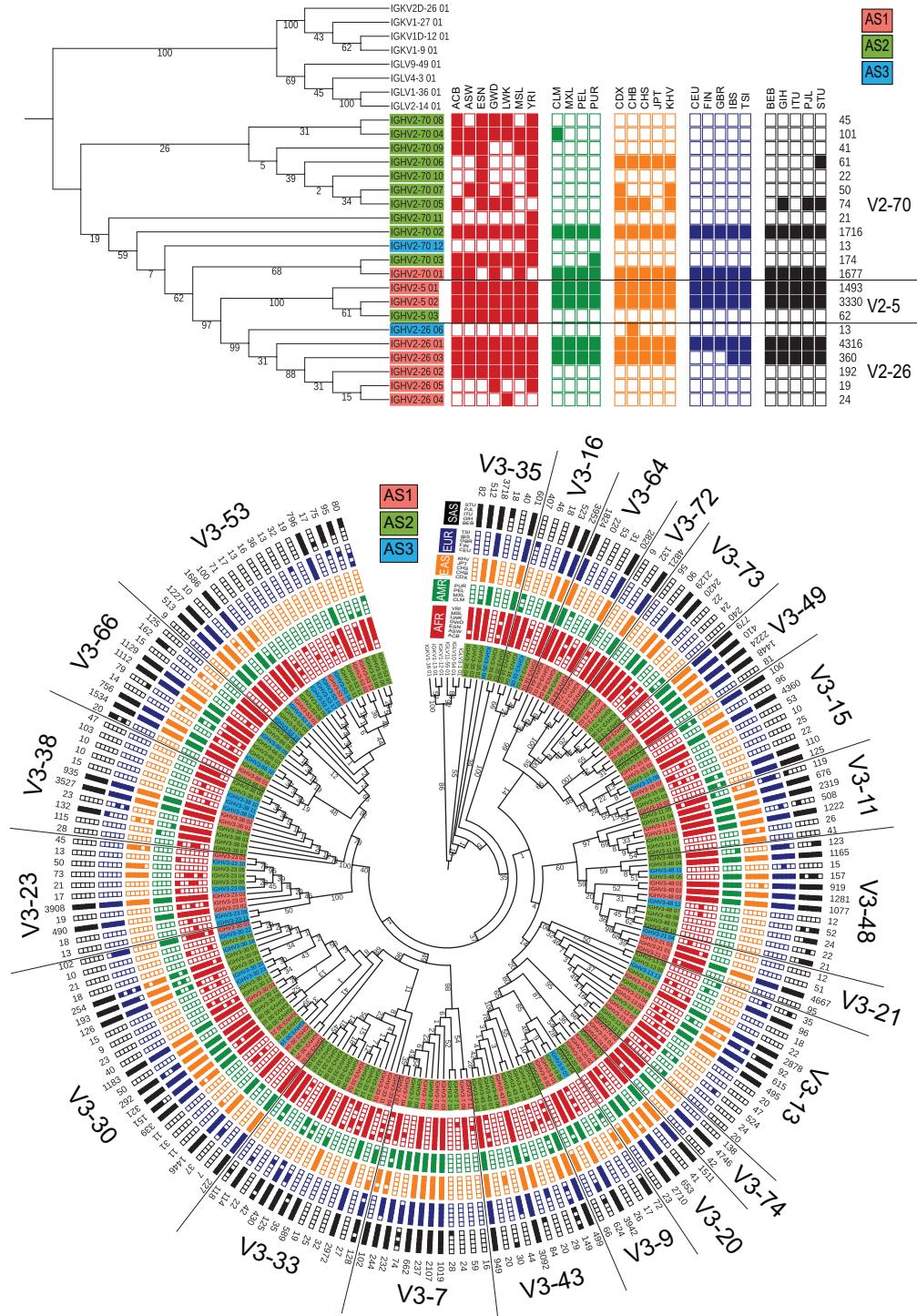
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agtgcataatcacagtgagacagatgaggaagtcgacaaaaaccaaggtttaa
agtgcataat-----
agtgcataat-----
agtgc-----

1071 **Figure S2: Per gene alignment of alleles from pmIG, IMGT, IgPdb and VBASE2 databases**
1072 **for *IGHV*, *IGKV* and *IGLV* locus. The name of pmIG alleles are marked with grey**
1073 **background. Yellow background is used for the 104 IMGT alleles mentioned to be**
1074 **erroneous/false positives by Wang et al, 2008.**

1075

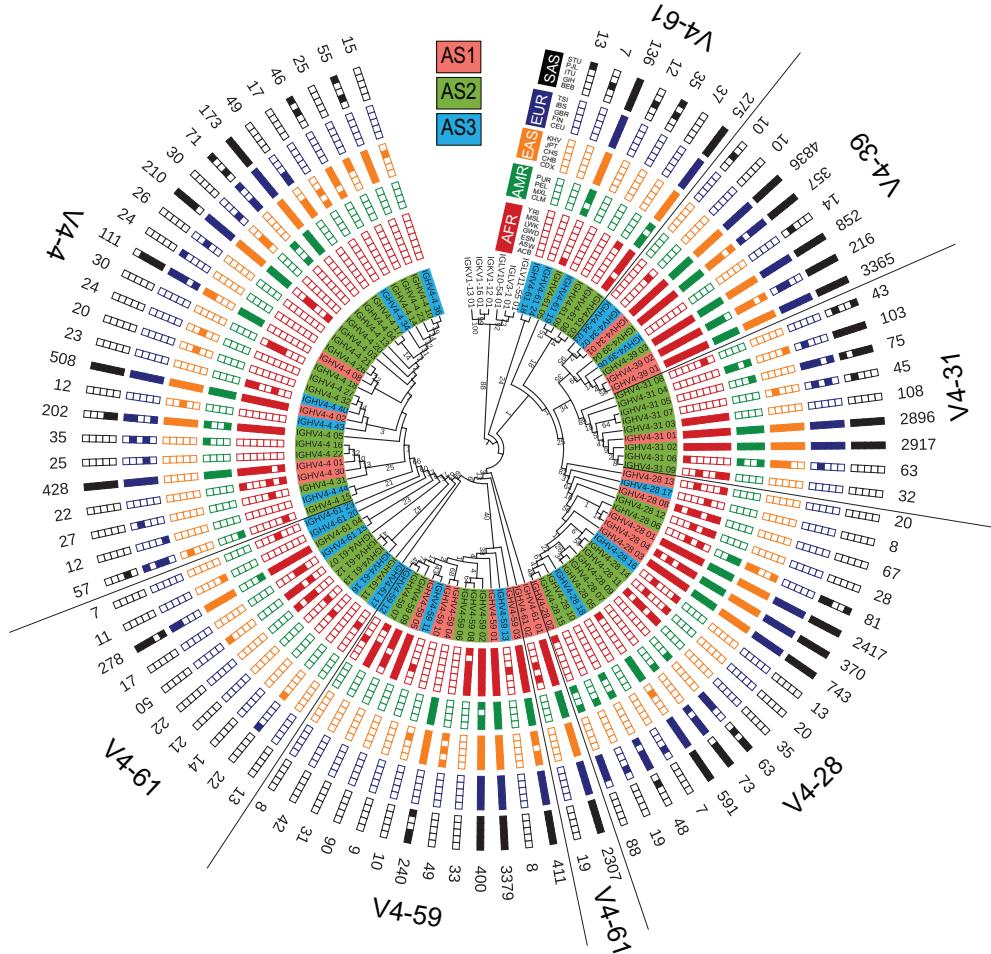
Figure S3



1076

1077 **Figure S3: ML tree of the population distribution of *IGHV2* and *V3* family alleles.**

Figure S4



1078

1079 **Figure S4: ML tree of the population distribution of *IGHV4*, *V5*, *V6* and *V7* family alleles.**

1080

1081

Figure S5

IGHA1 and *IGHA2*

IGHA1_IMGT	gcatccccgaccagcccc	aaggctttccgctgaggctc	tg	cagcacccagcc	agatggg
IGHA1_GRCh37	gcatccccgaccagcccc	aaggctttccgctgaggctc	tg	cagcacccagcc	agatggg
IGHA1_01	gcatccccgaccagcccc	aaggctttccgctgaggctc	tg	cagcacccagcc	agatggg
IGHA1_02	gcatccccgaccagcccc	aaggctttccgctgaggctc	tg	cagcacccagcc	agatggg
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IGHA1_05	gcatccccgaccagcccc	aaggctttccgctgaggctc	tg	cagcacccagcc	agatggg
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IGHA1_07	gcatccccgaccagcccc	aaggctttccgctgaggctc	tg	cagcacccagcc	agatggg
IGHA1_08	gcatccccgaccagcccc	aaggctttccgctgaggctc	tg	cagcacccagcc	agatggg
IGHA1_09	gcatccccgaccagcccc	aaggctttccgctgaggctc	tg	cagcacccagcc	agatggg
IGHA1_10	gcatccccgaccagcccc	aaggctttccgctgaggctc	tg	cagcacccagcc	agatggg
IGHA1_11	gcatccccgaccagcccc	aaggctttccgctgaggctc	tg	cagcacccagcc	agatggg
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IGHA1_21	gcatccccgaccagcccc	gaggctttccgctgaggctc	tg	cagcacccagcc	agatggg
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IGHA2_01	gcatccccgaccagcccc	aaggctttccgctgaggctc	ga	cagcacccccc	aaagatggg
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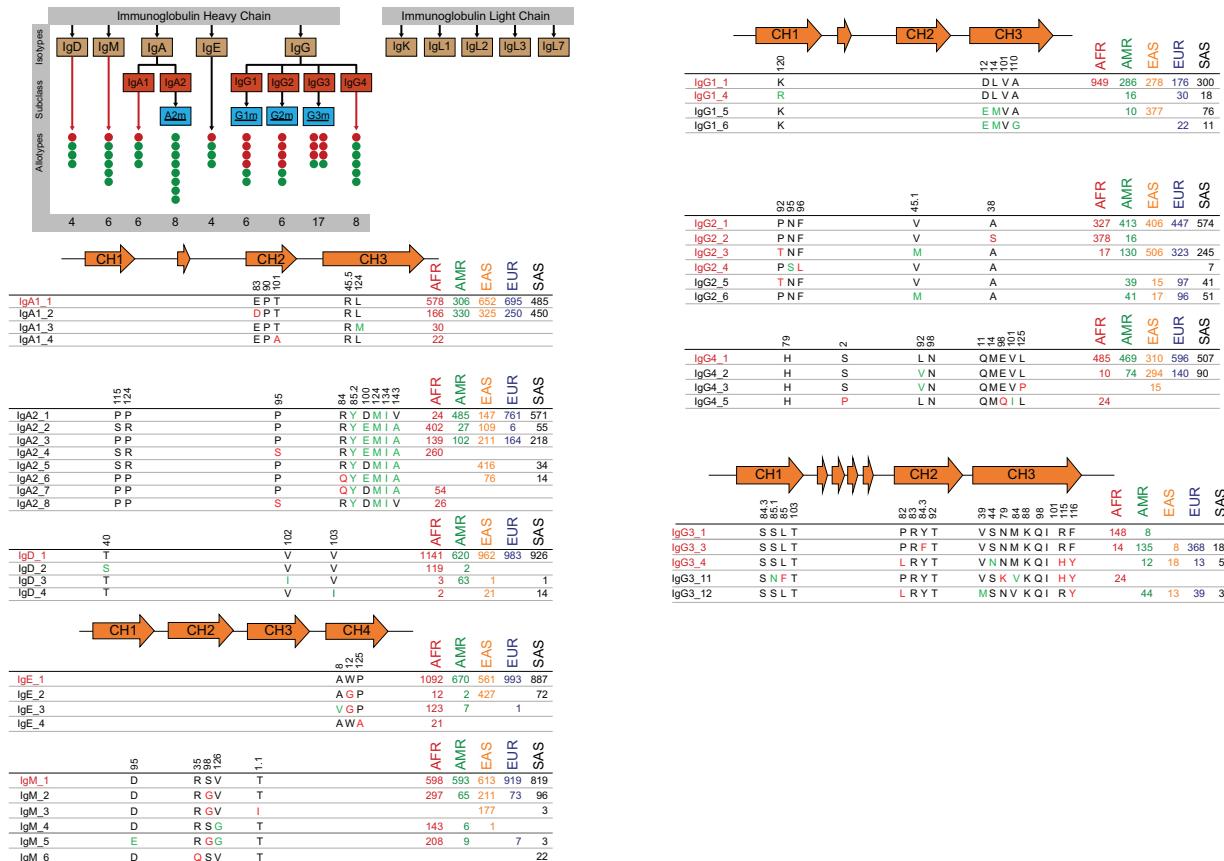
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1082 **Figure S5: Alignment of CH1, CH2 and CH3 domain for *IGHA1*, *IGHA2* group and *IGHG1*,**

1083 *IGHG2*, *IGHG3* and *IGHG4* group.

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Figure S6

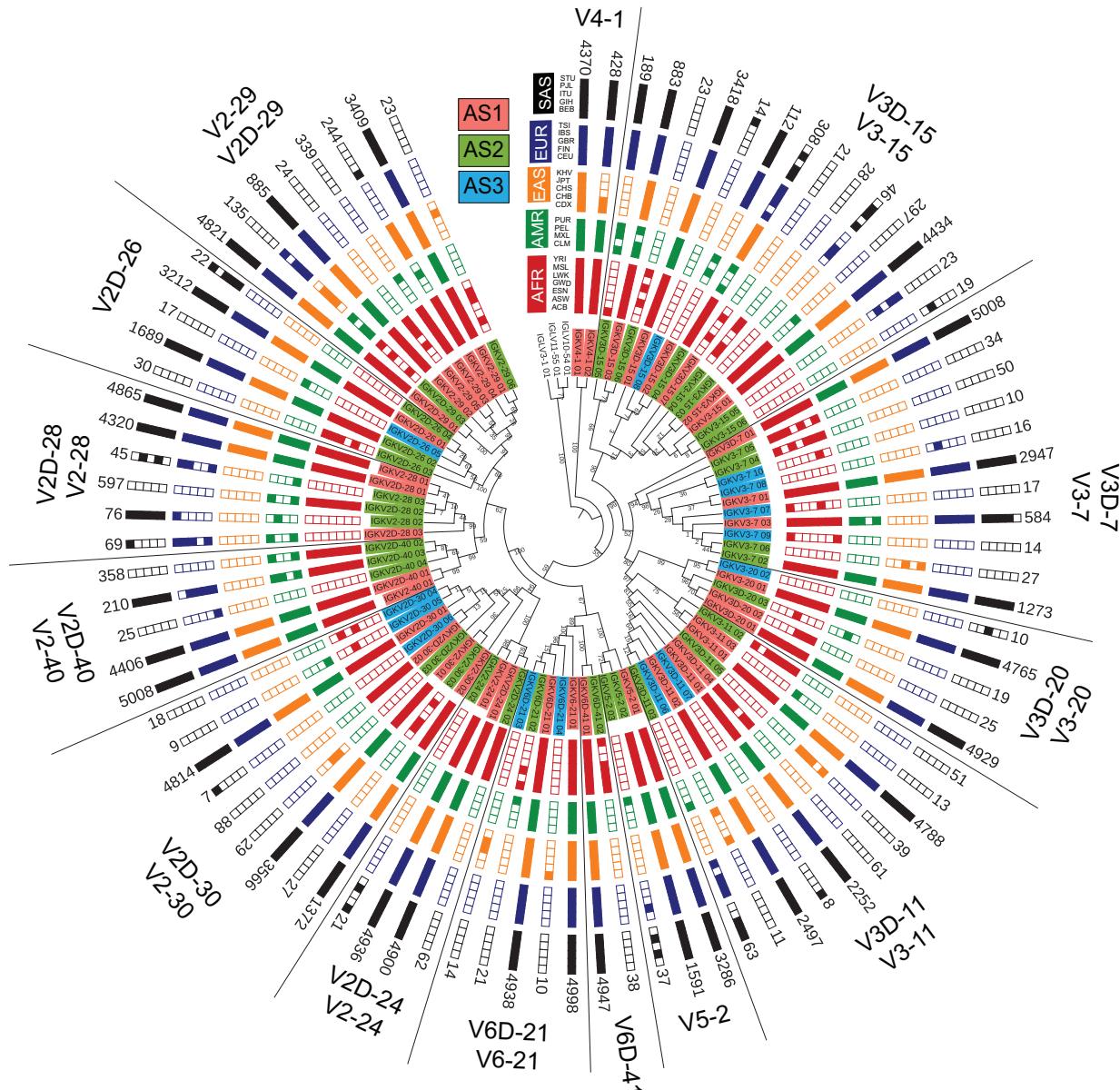


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1086 **Figure S6: Isotypes, Subclasses and allotypes of IGH locus.** The red circles in the nomenclature plot represents the number of allotypes (protein level translation of nucleotide germline alleles) matched with IMGT (similar to AS1) and green circles represents the new allotypes identified from G1K data. All the IGH constant genes are represented here. The three CH domains and one hinge region for IgA1, IgA2 and IgD is shown in 2-D diagram and the mutation existing in each domain is under the respective domain. The IgG3 protein has four hinges and three CH domains. IgM and IgE have four CH domains. The position of the amino-acid mutated is mentioned for the respective domain. The determinants marked in green represents no change in charge or structure whereas red determinant suggests the change in amino-acid properties.

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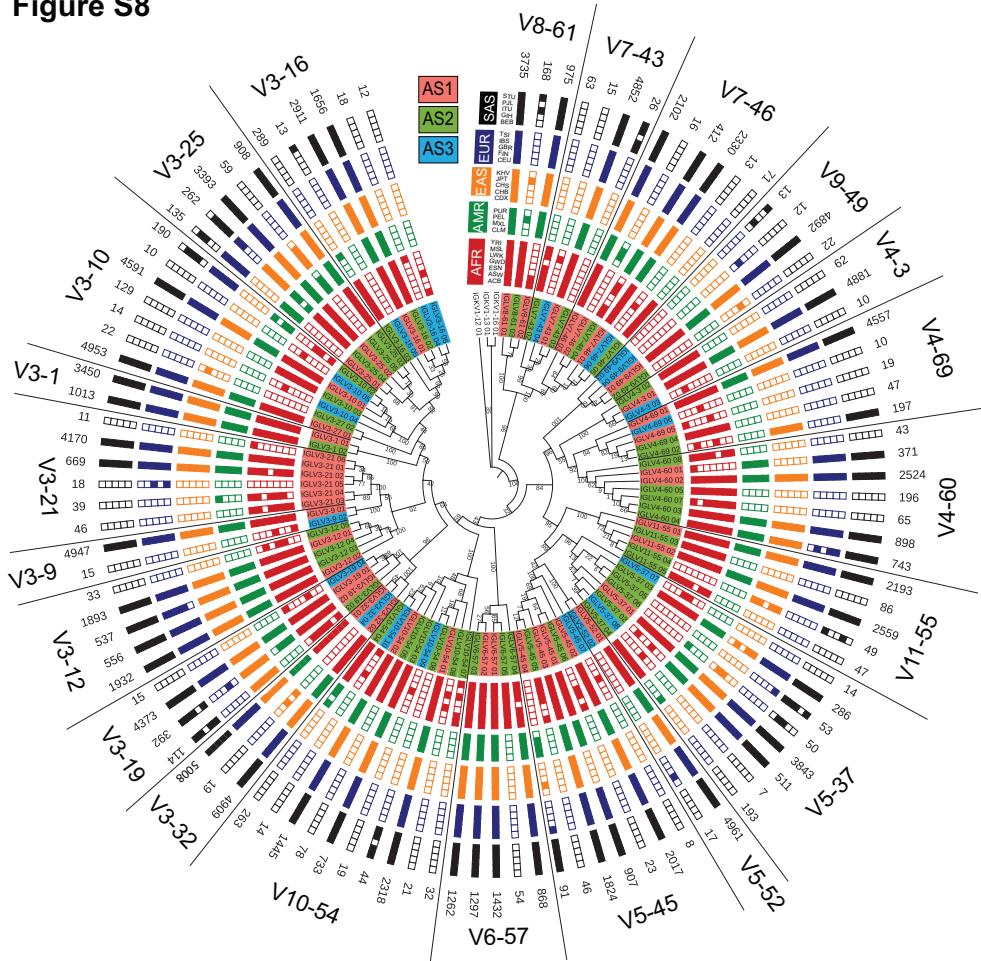
Figure S7



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1096 **Figure S7: ML tree of the population distribution of *IGKV2*, *V3*, *V4*, *V5*, and *V6* family alleles.**

Figure S8



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Figure S8: ML tree of the population distribution of *IGLV3*, *V4*, *V5*, *V6*, *V7*, *V8*, *V9*, *V10* and *V11* family alleles.

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1101 **Supplementary Tables**

1102 **Table S1:** 1000 Genomes population information for 2504 and 563 individuals. Individual
1103 Sample IDs with their source and EBV coverage is mentioned in the table below. The 563
1104 genomes selected are marked with green shade.

1105 **Table S2:** pmIG functional alleles for *IGH* Locus with confidence level information, database
1106 mapping information, full sequence and haplotype support in both population and
1107 superpopulation.

1108 **Table S3:** pmIG functional alleles for *IGK* Locus with confidence level information, database
1109 mapping information, full sequence and haplotype support in both population and
1110 superpopulation.

1111 **Table S4:** pmIG functional alleles for *IGL* Locus with confidence level information, database
1112 mapping information, full sequence and haplotype support in both population and
1113 superpopulation.

1114 **Table S4:** Deleted pmIG functional alleles for *IGH*, *IGK* and *IGL* Locus with confidence level
1115 information, database mapping information, full sequence and haplotype support in both
1116 population and superpopulation.

1117 **Table S5:** *IG* pseudogenes with conserved heptamer of RSS sequence.

1118 **Table S6:** RSS sequences in pmIG functional alleles for *IGH* Locus for each allele.

1119 **Table S7:** RSS sequences in pmIG functional alleles for *IGK* Locus for each allele.

1120 **Table S8:** RSS sequences in pmIG functional alleles for *IGL* Locus for each allele.

Note: For Supplementary Tables visit the GitHub page (<https://github.com/InduKhatri/pmIG>)