

IMGT, the international ImMunoGeneTics database (<http://imgt.cines.fr:8104>) created in 1989 (Université Montpellier II, CNRS, Montpellier, France) [1], provides, for the first time, a standardized description of the complete human immunoglobulin (Ig) germline repertoire based on the IMGT Scientific chart rules [2, 3] and on the IMGT-ONTOLOGY concepts [4].

The human immunoglobulins are the products of three unlinked sets of genes:

1. The immunoglobulin heavy (*IGH*),
2. The immunoglobulin κ (*IGK*), and
3. The immunoglobulin λ (*IGL*) genes,

localized on chromosome 14 (14q32.33), 2 (2p12) and 22 (22q11.2), respectively. The *IGH*, *IGK*, and

clature and other previously used nomenclatures is given in Table 2.

IGH Genes

The *IGH* locus at 14q32.33 spans 1250 kilobases (kb) (see Figure 1) [5]. It consists of 123–129 *IGHV* genes, depending on the haplotypes (see Table 1A), 27 *IGHD* segments belonging to 7 subgroups (see Table 2A), 9 *IGHJ* segments, and 11 *IGHC* genes [5–8]. Eighty-two to 88 *IGHV* genes belong to 7 subgroups, whereas 41 pseudogenes, not assigned to subgroups, define 3 clans. The most 5' *IGHV* genes occupy a position very close to the chromosome 14q telomere whereas the *IGHC* genes are in a more centromeric position. The potential genomic *IGH* repertoire is more limited since it comprises 39–46 functional *IGHV* genes, belonging to 6 or 7 subgroups, depending on the haplotypes (see Table 1A), 23 *IGHD*, 6 *IGHJ*, and 9 *IGHC* genes [5–9].

Thirty-five *IGH* genes have been found outside the main locus in other chromosomal localizations. These genes, designated as orphans cannot contribute to the synthesis of the immunoglobulin chains, even if they have an ORF. Nine *IGHV* orphans and 10 *IGHD* orphans have been described on chromosome 15 (15q11.2) and 16 *IGHV* orphans on chromosome 16 (16p11.2). In addition, one processed gene, *IGHEP2* is localized on chromosome 9 (9p24.2-p24.1). The total number of human *IGH* genes is 170 to 176 (206 to 212 genes, if the orphans and the processed gene are included) of which 77 to 84 genes are functional [9].

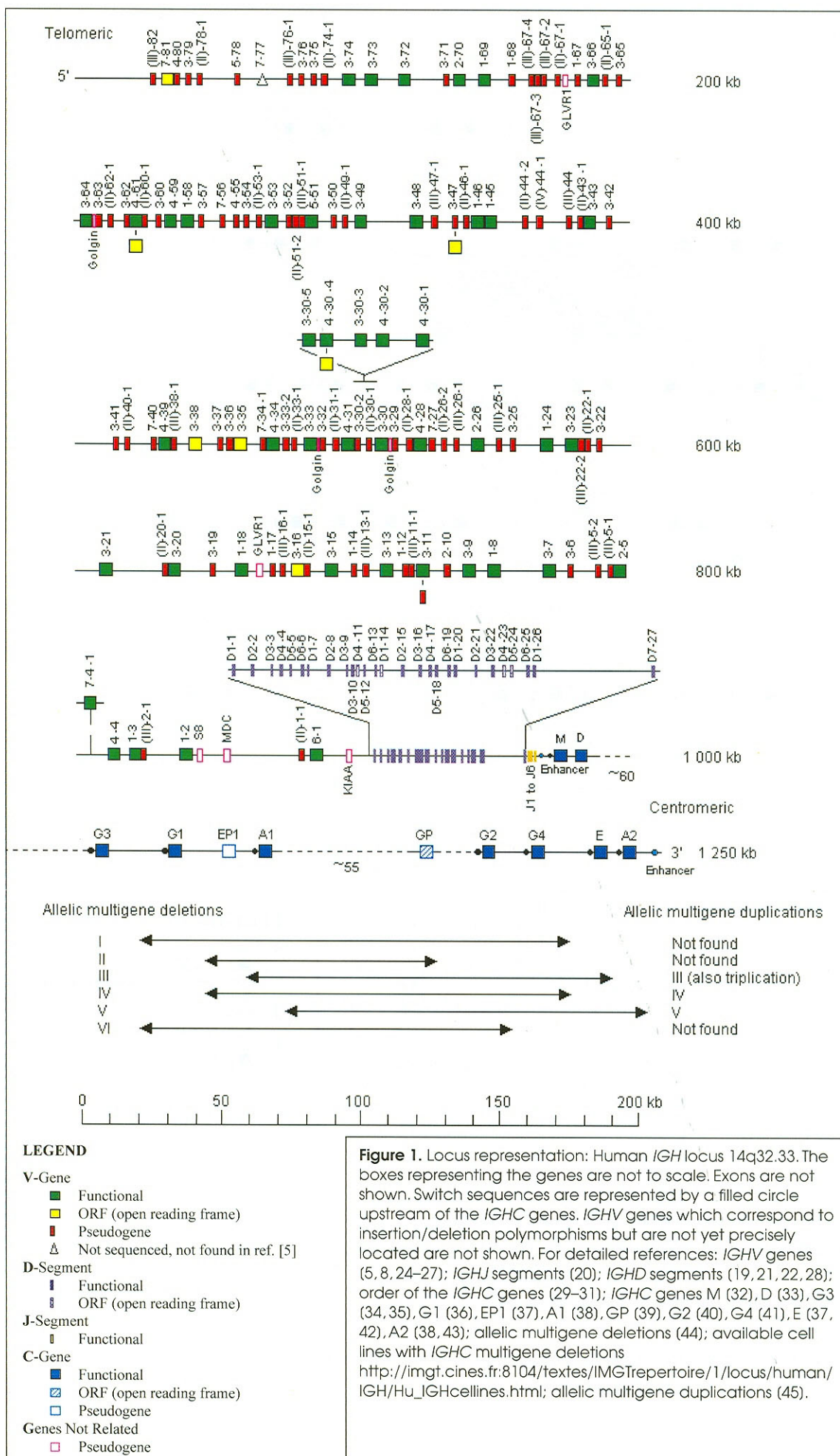
IGK Genes

The *IGK* locus at 2p12 spans 1820 kb (see Figure 2) [10]. It consists of 76 *IGKV* genes belonging to 7 subgroups (see Tables 1B and 2B) [8–11], 5 *IGKJ* segments, and a unique *IGKC* gene. The 76 *IGKV* genes are organized in two clusters separated by 800 kb. The *IGKV* distal cluster (the most 5' from *IGKC* and in the most centromeric position) spans 400 kb and comprises 36 genes. The *IGKV* proximal cluster (in 3' of the locus, closer to the *IGKC* gene, and in the most telomeric position) spans 600 kb and comprises 40 genes. The potential genomic *IGK* repertoire comprises 34–37 functional *IGKV* genes belonging to 5 subgroups, the 5 *IGKJ* segments, and the unique *IGKC* gene. One rare *IGKV* haplotype has been described which contains only the proximal cluster. This haplotype comprises the 40 proximal *IGKV* genes belonging to 7 subgroups, of which 18–20 are functional and belong to 5 subgroups. 28 *IGKV* orphans have been identified and sequenced: 3 on the short arm of chromosome 2 but outside of the main *IGK* locus, 13 on the long arm of chromosome 2, 6 on chromosome 22, one on chromosome 1, 1 on chromosome 15, and 4 outside of chromosome 2 [9–11].

Locus Maps and Genomic Repertoire of the Human Ig Genes

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IGL loci are represented in Figures 1, 2, and 3, respectively. An overview of the potential germline variable repertoire, for each locus, is given in Table 1. In that table, the number of functional genes, ORF (Open Reading Frame) or pseudogenes, and the total number of variable genes per subgroup are indicated. The gene functionality is described according to the IMGT Scientific chart [3]. The aim of the IMGT nomenclature for the immunoglobulin genes is to provide immunologists and geneticists with a unique nomenclature per locus which will allow extraction and comparison of data for the complex B- and T-cell antigen receptor molecules, whatever the species. The IMGT nomenclature for the immunoglobulin- and T-cell receptor genes follows the Human Gene Mapping Nomenclature rules. An exhaustive and standardized list of human immunoglobulin gene names is available from the IMGT repertoire at the IMGT Marie-Paule page (<http://imgt.cines.fr:8104>). All the human immunoglobulin genes have been officially entered in GDB (the Genome Database, <http://www.gdb.org>), the repository of the human gene names. In order to facilitate data comparison from various publications, correspondence between the IMGT nomen-



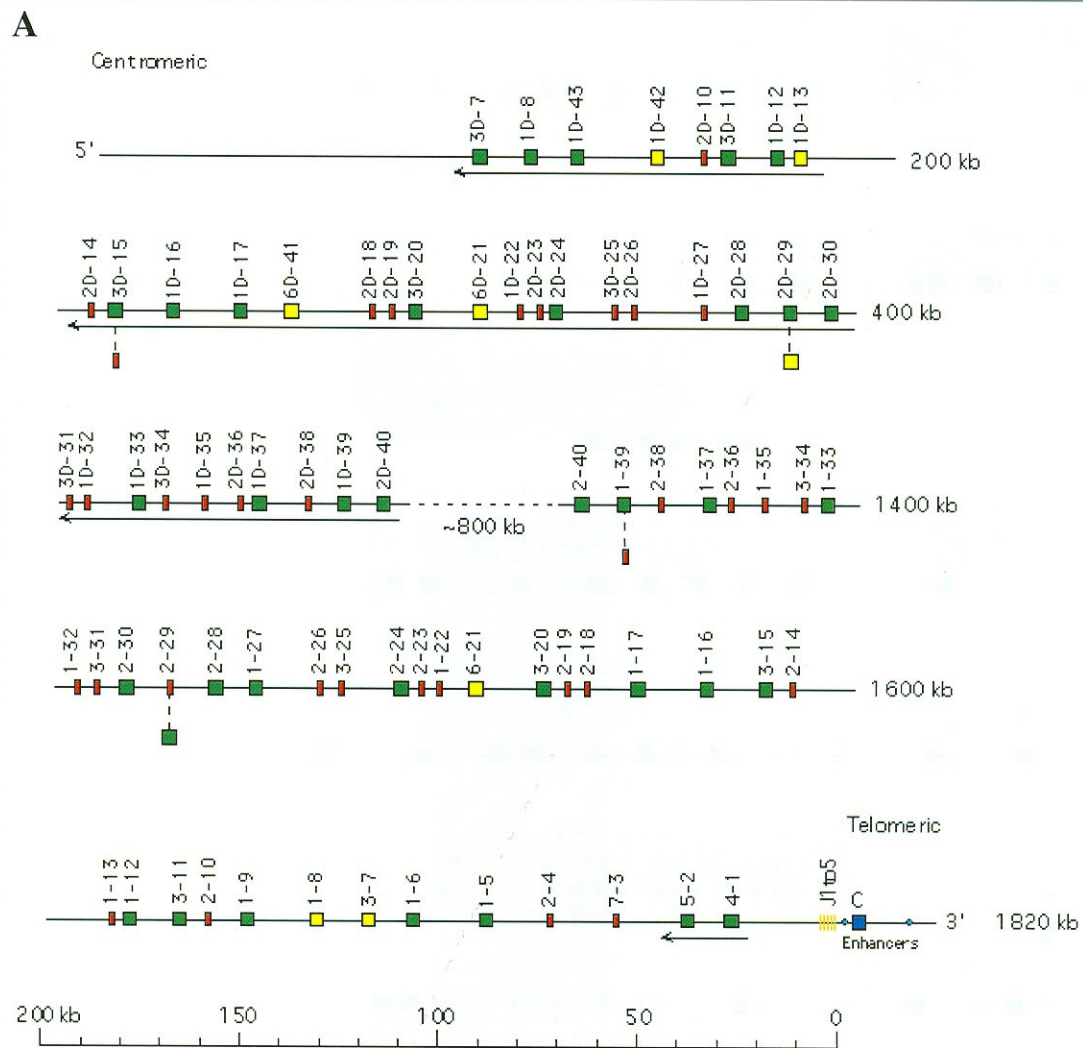
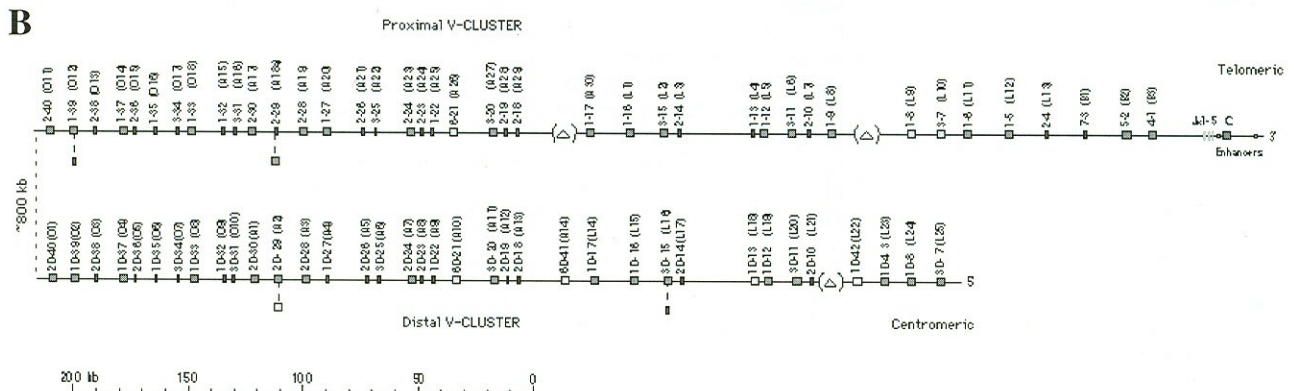
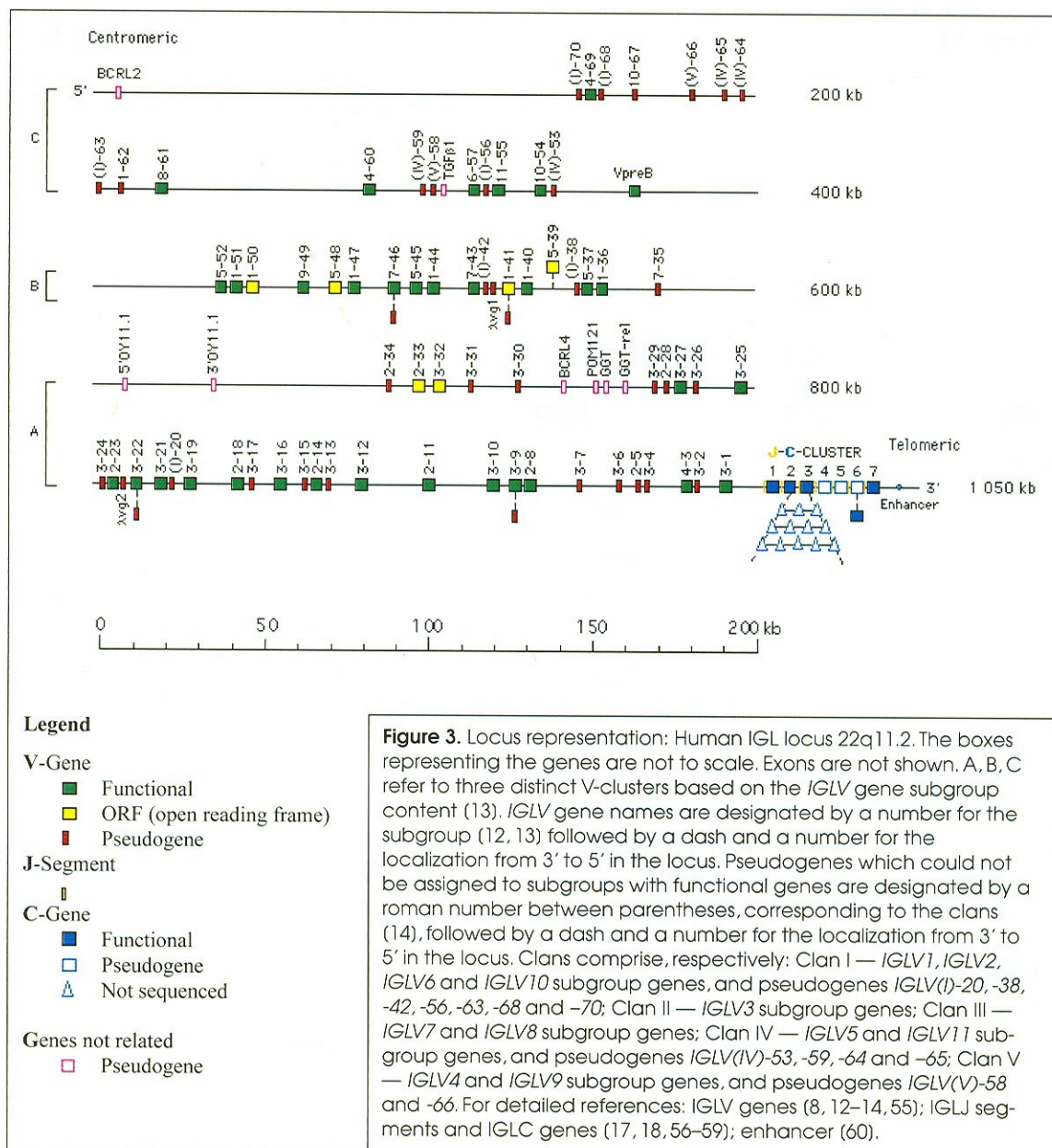


Figure 2. Locus representation: Human IGK 2p12. **A** The boxes representing the genes are not to scale. Exons are not shown. The *IGKV* genes of the proximal V-cluster are designated by a number for the subgroup, followed by a dash and a number for the localization from 3' to 5' in the locus. The *IGKV* genes of the distal duplicated V-cluster are designated by the same numbers as the corresponding genes in the proximal V-cluster, with the letter D added. Arrows show the *IGKV* genes whose polarity is opposite to that of the J-C-cluster. **B** Alternative representation of the human IGK locus, taking into account the polymorphic duplication in the locus (see references from Zachau's group below). Small triangles indicate parts which are absent in the proximal or distal V-cluster when considering the duplication in the human IGK locus. In parentheses: *IGKV* gene designations according to Zachau's group (10, 46). For references: *IGKV* genes (8, 47-50); *IGKJ* segments (51); *IGKC* gene (52); enhancers (53, 54).

LEGEND

- V-Gene**
- Functional
 - ORF (open reading frame)
 - Pseudogene
- J-Segment**
- Functional
- C-Gene**
- Functional





IGL Genes

The *IGL* locus at 22q11.2 spans 1050 kb (see Figure 3) [12–14]. It consists of 70–71 *IGLV* genes, localized on 900 kb (see Tables 1C and 2C) [9, 15], and 7–11 *IGLC* genes depending on the haplotypes, each one preceded by one *IGLJ* segment. Fifty-six to 57 *IGLV* genes belong to 11 subgroups, whereas 14 pseudogenes, not assigned to subgroups, define 3 clans. The most 5' *IGLV* genes occupy the most centromeric position, whereas the *IGLC* genes, in 3' of the locus, are the most telomeric genes in the *IGL* locus. Two *IGLV* orphans have been identified on chromosome 8q11.2 and one of them belonging to subgroup 8 has been sequenced [9]. The recent sequencing of the chromosome 22q localized the *IGL* locus at 6 megabases from the centromere, and showed that chromosome 22q comprises 35 megabases [16]. Two *IGLC* orphans and two *IGLV*

orphans have been characterized on 22q, outside the major *IGL* locus [9, 16].

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Table 1A. Number of germline variable genes and potential repertoire: Human *IGHV* at 14q32.33

Subgroup	Functional	ORF	Pseudogene	Total
<i>IGHV1</i>	9	—	5	14
<i>IGHV2</i>	3	—	1	4
<i>IGHV3</i>	18–20** (+1)*	3 (+1)*	24 (+2)*	47–49**
<i>IGHV4</i>	7–10**	— (*)	2	9–12**
<i>IGHV5</i>	1	—	1	2
<i>IGHV6</i>	1	—	—	1
<i>IGHV7</i>	0–1**	1	4	5–6**
<i>IGHV(II)</i>	—	—	22	22
<i>IGHV(III)</i>	—	—	18	18
<i>IGHV(IV)</i>	—	—	1	1
Total	39–45 (+1)*	4 (+1)*	78 (+2)*	123–129**

Notes

*ORF or pseudogene (*IGHV3–47*); functional or pseudogene (*IGHV3–11*). (*) Note that although some sequences of *IGHV4–30–4* and *IGHV4–61* have been described as ORF, these two genes are considered as functional in this table.

**Allelic polymorphism by insertion/deletion: 50 kb insertion of 5 genes (3–30–5, 4–30–4, 3–30–3, 4–30–2, 4–30–1) in 45% of caucasians; *IGHV7–4–1*.

II, III, IV (in parentheses) refer to the clans for the pseudogenes which could not be assigned to subgroups with functional genes. All these pseudogenes have truncations. Clans comprise, respectively: Clan I — *IGHV1*, *IGHV5*, and *IGHV7* subgroup genes; Clan II — *IGHV2*, *IGHV4*, and *IGHV6* subgroup genes, and pseudogenes *IGHV(II)*; Clan III — *IGHV3* subgroup genes, and pseudogenes *IGHV(III)*; Clan IV — one pseudogene *IGHV(IV)–44*.

There are 123–129 *IGHV* genes on 900 kilobases: 82–88 *IGHV* genes belonging to 7 subgroups and 41 pseudogenes belonging to 3 clans:

- 39–45 functional
- 4 ORF (open reading frame)
- 78 pseudogenes
- 1 ORF or pseudogene
- 1 functional or pseudogene

Criteria of functionality are described in the IMGT Scientific Chart (3). The potential repertoire is 39–46 functional *IGHV* genes belonging to 6 or 7 subgroups (5, 6).

Table 1B. Number of germline variable genes and potential repertoire: Human *IGKV* at 2p12

Subgroup	Functional	ORF	Pseudogene	Total
Distal and proximal V-clusters (for the haplotypes with both clusters)				
<i>IGKV1</i>	17 (+1)*	3	8 (+1)*	29
<i>IGKV2</i>	9 (+1)*	—	17 (+1)*	27
<i>IGKV3</i>	6 (+1)*	1	6 (+1)*	14
<i>IGKV4</i>	1	—	—	1
<i>IGKV5</i>	1	—	—	1
<i>IGKV6</i>	—	3	—	3
<i>IGKV7</i>	—	—	1	1
Total	34(+3)*	7	32(+3)*	76
Proximal V-cluster (for the haplotypes without the distal V-cluster)				
<i>IGKV1</i>	9(+1)*	1	4 (+1)*	15
<i>IGKV2</i>	4 (+1)*	—	9 (+1)*	14
<i>IGKV3</i>	3	1	3	7
<i>IGKV4</i>	1	—	—	1
<i>IGKV5</i>	1	—	—	1
<i>IGKV6</i>	—	1	—	1
<i>IGKV7</i>	—	—	1	1
Total	18(+2)**	3	17(+2)**	40

Notes

*Functional or pseudogene (*IGKV1–39*, *IGKV2–29*, *IGKV3D–15*).

Distal and proximal V-clusters (for the haplotypes with both clusters): There are 76 *IGKV* genes belonging to 7 subgroups, on 1800 kilobases:

- 34 functional
- 7 ORF (open reading frame)
- 32 pseudogenes
- 3 functional or pseudogenes

The potential repertoire is 34–37 functional *IGKV* genes belonging to 5 subgroups.

Proximal V-cluster for the haplotypes without the distal V-cluster: There are 40 *IGKV* genes belonging to 7 subgroups, on 600 kilobases:

- 18 functional
- 3 ORF (open reading frame)
- 17 pseudogenes
- 2 functional or pseudogenes

The potential repertoire is 18–20 functional *IGKV* genes belonging to 5 subgroups. See reference (11).

Table 1C. Number of germline variable genes and potential repertoire: Human *IGLV* at 22q11.2

Subgroup	Functional	ORF	Pseudogene	Total
<i>IGLV1</i> (B)	5	1 (+1)*	(+1)*	7
(C)	—	—	1	1
<i>IGLV2</i> (A)	5	1	3	9
<i>IGLV3</i> (A)	8 (+2)*	1	12 (+2)*	23
<i>IGLV4</i> (A)	1	—	—	1
(C)	2	—	—	2
<i>IGLV5</i> (B)	3	1–2**	—	4–5
<i>IGLV6</i> (C)	1	—	—	1
<i>IGLV7</i> (B)	1 (+1)*	—	1 (+1)*	3
<i>IGLV8</i> (C)	1	—	—	1
<i>IGLV9</i> (B)	1	—	—	1
<i>IGLV10</i> (C)	1	—	1	2
<i>IGLV11</i> (C)	1	—	—	1
<i>IGLV(I)</i> (A)	—	—	1	1
(B)	—	—	2	2
(C)	—	—	4	4
<i>IGLV(IV)</i> (C)	—	—	5	5
<i>IGLV(V)</i> (C)	—	—	2	2
Total	30 (+3)*	4–5 (+1)*	32 (+4)*	70–71

Notes

*ORF or pseudogene (*IGLV1–41*); *Functional or pseudogene (*IGLV3–9*, *IGLV3–22*, *IGLV7–46*).

**Allelic polymorphism by insertion/deletion: *IGLV5–39* (12).

A, B, C (in parentheses) refer to three distinct V-clusters based on the *IGLV* gene subgroup content (13). I, IV, V (in parentheses) refer to the clans (14) for the pseudogenes which could not be assigned to subgroups with functional genes.

There are 69–70 *IGLV* genes on 900 kilobases: 56–57 *IGLV* genes belonging to 11 subgroups and 13 pseudogenes belonging to 3 clans:

- 30 functional
- 4–5 ORF (open reading frame)
- 31 pseudogenes
- 3 functional or pseudogenes
- 1 ORF or pseudogene

The potential repertoire is 30–33 functional *IGLV* genes belonging to 11 subgroups. See references (13–15).

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Table 2A. Correspondence between the different nomenclatures: Human *IGHD* (7)

IMGT <i>IGHD</i> name	Other designations from the literature	
1–1		M4 (5)
2–2	D4 (19)	LR4 (5)
3–3	23/7 (21)	XP4 (22)
4–4		A4 (22)
5–5		K4 (22)
6–6		N4 (22)
1–7		M1 (22)
2–8	D1 (19)	LR1 (22)
3–9	21/0.5 (21)	XP1 (22)
3–10	21/7 (21)	XP'1 (22)
4–11		A1 (22)
5–12		K1 (22)
6–1		N1 (22)
1–14		M2 (22)
2–15	D2 (19)	LR2 (5)
3–16	21/10 (21)	XP2 (5)
4–17		A2 (5)
5–18		K2 (5)
6–19		N2 (5)
1–20		M3 (5)
2–21	D3 (19)	LR3 (5)
3–22	21/9 (21)	XP3 (5)
4–23		A3 (5)
5–24		K3 (5)
6–25		N3 (5)
1–26		M'3 (5)
7–27	DHQ52 (20)	

Notes

IGHD segments are designated by a number for the subgroup followed by a dash and a number for the localization from 5' to 3' in the locus (28).

Table 2B. Correspondence between the different nomenclatures: Human *IGKV*

Proximal V-cluster, from 3' (top of left column) to 5' (bottom of left column)		Distal V-cluster, from 3' (bottom of right column) to 5' (top of right column)	
IMGT <i>IGKV</i> gene name	Zachau's group (10)	IMGT <i>IGKV</i> gene name	Zachau's group (10)
4-1	B3		
5-2	B2		
7-3	B1		
2-4	L13		
1-5	L12, L12a		
1-6	L11		
3-7	L10, L10a	3D-7	L25
1-8	L9	1D-8	L24, L24a
		1D-43	L23, L23a
		1D-42	L22
1-9	L8		
2-10	L7		2D-10 L21
3-11	6, L6a	3D-11	L20
1-12	L5	1D-12	L19
1-13	L4	1D-13	L18
2-14	L3	2D-14	L17
3-15	L2	3D-15	L16, L16a, L16b, L16c
1-16	L1	1D-16	L15, L15a
1-17	A30	1D-17	L14
		6D-41	A14
2-18	A29	2D-18	A13
2-19	A28	2D-19	A12
3-20	A27, A27a	3D-20	A11, A11a
6-21	A26	6D-21	A10
1-22	A25	1D-22	A9
2-23	A24	2D-23	A8
2-24	A23	2D-24	A7
3-25	A22	3D-25	A6
2-26	A21	2D-26	A5
1-27	A20	1D-27	A4, A4a
2-28	A19	2D-28	A3
2-29	A18a, A18b	2D-29	A2a, A2c
2-30	A17	2D-30	A1
3-31	A16, A16a	3D-31	O10
1-32	A15, A15a	1D-32	O9
1-33	O18, O18a	1D-33	O8
3-34	O17	3D-34	O7
1-35	O16	1D-35	O6
2-36	O15	2D-36	O5
1-37	O14	1D-37	O4
2-38	O13	2D-38	O3
1-39	O12, O12a	1D-39	O2
2-40	O11, O11a	2D-40	O1

Notes

The *IGKV* genes of the proximal V-cluster are designated by a number for the subgroup, followed by a dash and a number for the localization from 3' to 5' in the locus. The *IGKV* genes of the distal duplicated V-cluster are designated by the same numbers as the corresponding genes in the proximal V-cluster, with the letter D added. Homologous genes in the proximal and distal V-cluster are on the same line. Cells are empty when no homologous gene is found in the other cluster.

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Table 2C. Correspondence between the different nomenclatures: Human *IGLV*

IMGT <i>IGLV</i> gene name	Fripiat et al. (12), Williams et al. (13)	Kawasaki et al. (14)
3-1	3r	2-1
3-2	3q	2-2P
4-3	4c	5-1
3-4		2-3P
2-5	2a1	1-1P
3-6	3a2	2-4P
3-7	3n	2-5P
2-8	2c	1-2
3-9	3j	2-6
3-10	3p	2-7
2-11	2e	1-3
3-12	3i	2-8
3-13	3f	2-9P
2-14	2a2	1-4
3-15		2-10P
3-16	3a	2-11
3-17	3g	2-12P
2-18	2d	1-5
3-19	3l	2-13
(I)-20		1-6P
3-21	3h	2-14
3-22	3e	2-15
2-23	2b2	1-7
3-24	3d	2-16P
3-25	3m	2-17
3-26	3b	2-18P
3-27		2-19
2-28	2b1	1-8P
3-29	3c	2-20P
3-30	3o	2-21P
3-31	3k	2-22P
3-32	3i1	2-23P
2-33	2f	1-9
2-34		1-10P
7-35	7c	3-1P
1-36	1a	1-11
5-37	5e	4-1
(I)-38		1-12P
5-39	5a	
1-40	1e	1-13
1-41	1d	1-14P
(I)-42	V lambda A	1-15P
7-43	7a	3-2

Table 2C – continued

IMGT <i>IGLV</i> gene name	Fripiat et al. (12), Williams et al. (13)	Kawasaki et al. (14)
1-44	1c	1-16
5-45	5c	4-2
7-46	7b	3-3
1-47	1g	1-17
5-48	5d	4-3
9-49	9a	5-2
1-50	1f	1-18
1-51	1b	1-19
5-52	5b	4-4
(IV)-53		4-5P
10-54	10a	1-20
11-55		4-6
(I)-56		1-21P
6-57	6a	1-22
(V)-58		5-3P
(IV)-59		4-7P
4-60	4a	5-4
8-61	8a	3-4
1-62		1-23P
(I)-63		1-24P
(IV)-64		4-8P
(IV)-65		4-9P
(V)-66		5-5P
10-67	10b	1-25P
(I)-68		1-26P
4-69	4b	5-6
(I)-70		1-27P

Notes

IGLV genes are designated by a number for the subgroup (12, 13) followed by a dash and a number for the localization from 3' to 5' in the locus. Pseudogenes which could not be assigned to subgroups with functional genes are designated by a roman number between parentheses, corresponding to the clans (14), followed by a dash and a number for the localization from 3' to 5' in the locus. Clans comprise, respectively: Clan I — *IGLV1*, *IGLV2*, *IGLV6*, and *IGLV10* subgroup genes, and pseudogenes *IGLV(I)-20*, -38, -42, -56, -63, -68, and -70; Clan II — *IGLV3* subgroup genes; Clan III — *IGLV7* and *IGLV8* subgroup genes; Clan IV — *IGLV5* and *IGLV11* subgroup genes, and pseudogenes *IGLV(IV)-53*, -59, -64, -65, and -66-1; Clan V — *IGLV4* and *IGLV9* subgroup genes, and pseudogenes *IGLV(V)-58* and -66.

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Internet Resources

- IMGT, the international ImMunoGeneTics database [1], <http://imgt.cines.fr:8104>
- IMGT/LIGM-DB: Contains the germline and rearranged sequences of the immunoglobulin and T-cell receptor genes of human and other vertebrates (35,000 sequences of 81 species in December 1999).
- “IMGT Scientific Chart”: Describes the standardized rules for the description and classification of the immunoglobulin and T-cell receptor genes and alleles [2, 3] based on the IMGT-ONTOLOGY concepts[4].
- “IMGT Repertoire”: Provides the locus representations, germline gene tables, potential germline repertoires, correspondence between gene nomenclatures, protein displays, alignments of alleles and tables of alleles for all the human IGH, IGK, and IGL genes. 2D graphical representations designated as Colliers de Perles are provided for the variable genes.