



# Nomenclature report for killer-cell immunoglobulin-like receptors (KIR) in macaque species: new genes/alleles, renaming recombinant entities and IPD-NHKIR updates

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## Abstract

The Killer-cell Immunoglobulin-like Receptors (KIR) are encoded by a diverse group of genes, which are characterized by allelic polymorphism, gene duplications, and recombinations, which may generate recombinant entities. The number of reported macaque *KIR* sequences is steadily increasing, and these data illustrate a gene system that may match or exceed the complexity of the human *KIR* cluster. This report lists the names of quality controlled and annotated *KIR* genes/alleles with all the relevant references for two different macaque species: rhesus and cynomolgus macaques. Numerous recombinant *KIR* genes in these species necessitate a revision of some of the earlier-published nomenclature guidelines. In addition, this report summarizes the latest information on the Immuno Polymorphism Database (IPD)-NHKIR Database, which contains annotated *KIR* sequences from four non-human primate species.

**Keywords** Killer-cell immunoglobulin-like receptors · Nomenclature · Macaque species · Rhesus · Cynomolgus · Recombinants

## Introduction

Over the last two decades, the number of human Killer-cell Immunoglobulin-like Receptor (KIR) sequences and haplotypes has increased substantially. These data shed light on a plastic gene cluster of higher primates that is characterized by allelic polymorphism and variable gene content, and that

involves complex recombinations and high levels of alternative splicing (Trowsdale et al. 2001; Hsu et al. 2002; Parham 2004; Hammond et al. 2016; Bruijnesteijn et al. 2018a, b; Bruijnesteijn et al. 2018a, b). The system of nomenclature for human *KIR* genes (Marsh et al. 2003) accounts for the number of domains (2D or 3D), as well as for the activating (S) or inhibitory (L) signalling potential of the intracellular

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tail. In addition, the *KIR* genes and alleles are differentiated by numbers. For example, *KIR3DL1\*001* defines the first allele of a gene encoding a receptor that has three extracellular domains and a long cytoplasmic tail. For non-human primate species (NHP) such as macaques, chimpanzees, and orangutans, the human *KIR* nomenclature rules have been applied, and when these have not been sufficient, species-specific adaptations have been added to the guidelines for the nomenclature (Robinson et al. 2018).

Among the human *KIR* characterized, only a few intragenic recombinations have been reported (Roe et al. 2017; Bruijnesteijn et al. 2018a, b), although the number of such recombinant *KIR* could be underestimated, because family studies have not been a focus of the work, and might be missed by studies that mainly involved unrelated individuals. A recent study of the *KIR* gene transcriptome in families of rhesus (*Macaca mulatta*, *Mamu*) and cynomolgus (*Macaca fascicularis*, *Mafa*) macaques has identified numerous intragenic recombinant *KIR* (Bruijnesteijn et al., unpublished data). In this report on *KIR* nomenclature, we build on the previously reported human and NHP guidelines (Robinson et al. 2018) to focus on macaques, because in these species the number of genes/alleles reported has significantly increased.

## General nomenclature guidelines for macaque *KIR* genes

The naming of macaque *KIR* genes follows the general principles that have been previously described (Marsh et al. 2003; Robinson et al. 2018). In brief, the first digit following the *KIR* abbreviation gives the number of immunoglobulin-like domains (denoted as “D”). In macaques, genes that encode *KIR1D*, *KIR2D*, and *KIR3D* structures are found (Hershberger et al. 2001). Either a long or short cytoplasmic tail, which are characteristic of inhibitory and activating receptors, respectively, is specified with an “L” or an “S” following the D, whereas “P” denotes a pseudogene. Genes considered to be novel but that lack sufficient confirmation—at the genomic DNA level—to define a gene or lineage, are denoted by a “W” for “Workshop”, which follows the designation of the cytoplasmic tail. Different *KIR* genes are distinguished by sequential two-digit numbering. Non-synonymous *KIR* alleles are distinguished by three-digit numbers that are separated from the gene digits by an asterisk. Synonymous polymorphisms in the coding sequence of a *KIR* gene are distinguished by a second set of two digits, which is separated from the non-synonymous three-digit number by a colon (e.g., *Mamu-KIR3DL1\*012:02*). A third set of digits, separated from the synonymous two-digit number by a colon, define substitutions in the introns. Optional suffixes indicating the expression status of alleles can be provided, and these include indicators of no expression, referred to as “Null” alleles (“N”),

low cell surface expression (“L”), soluble and secreted gene products (“S”), and cytoplasmic expression (“C”). The “A” suffix is used when there is doubt as to whether a protein is expressed, whereas “Q” indicates alleles for which the expression is “Questionable” based on the study of previously reported mutations that do affect the level of expression.

## *KIR* genes in the various species of macaque

More than 20 species of macaque have been distinguished (Anandam et al. 2013). At present, characterization of the *KIR* genes has concentrated on rhesus and cynomolgus macaques (Khakoo et al. 2000; Grendell et al. 2001; Hershberger et al. 2001; Rajalingam et al. 2001; Guethlein et al. 2002; Andersen et al. 2004; Sambrook et al. 2005; Guethlein et al. 2007; Bimber et al. 2008; Blokhuis et al. 2009a, b; Blokhuis et al. 2009a, b; Bostik et al. 2009; Abi-Rached et al. 2010; Blokhuis et al. 2010; Chaichompoo et al. 2010; Kruse et al. 2010; Colantonio et al. 2011; Hellmann et al. 2011; Moreland et al. 2011; Bimber and Evans 2015; Prall et al. 2017). Up to now, knowledge regarding the organization of *KIR* genes in macaque is sparse, with only two genomic assemblies of the macaque *KIR* region available (Sambrook et al. 2005; Graves 2019). Consequently, *KIR* genes that are highly similar based on phylogenetic clustering and sequence homology are considered to define a single gene or locus that is common to both species of macaque, and are therefore designated as orthologs and given matching gene names: for example, *Mamu-KIR3DL1* and *Mafa-KIR3DL1*. In contrast, species-specific *KIR* genes are given different numbers in the order in which they are distinguished. To give an example, *KIR3DLW13* has only been detected in cynomolgus macaques (*Mafa-KIR3DLW13*). At the allele level, sequences are numbered in sequence according to the order in which they were defined. This procedure was applied independently to the different macaque species, without taking shared *KIR* alleles into account. In total, 58 and 59 rhesus and cynomolgus macaque *KIR* genes have been defined, and these represent 576 and 334 *KIR* alleles, respectively (Tables 1 and 2).

These guidelines for naming *KIR* sequences will be applied to other macaque species, but will be distinguished by the use of species-specific prefixes (Table 3).

## Nomenclature for recombinant macaque *KIR* genes

Study of rhesus and cynomolgus macaque *KIR* from different geographical origins has identified many recombinant *KIR* that are composed of segments derived from two or more different *KIR* genes, which were confirmed by independent PCRs or segregation analysis. According to the previous

**Table 1** List of rhesus macaque *KIR* genes, their previous names, and the number of reported alleles per gene

KIR gene	Previous designations	Number of reported alleles
<i>Mamu-KIR1D</i>	<i>KIR1D</i>	12
<i>Mamu-KIR2DL04</i>	<i>2DL501NK, 2DL503NK, KIR2DL4, KIR2DL4.1, MmKIR2DL4</i>	49
<i>Mamu-KIR3DL20</i>	<i>KIR3DL20, KIR3DL20_variant_2, KIR3DL06, KIR2DL5</i>	64
<i>Mamu-KIR3DL01</i>	<i>2DL426NK, 3DL34, KIR3DL, KIR3DL-like_1, KIR3DL1, KIR3DL1-like1, KIR3DL12, KIR3DL13, KIR3DL14, KIR3DL15, KIR3DL19, KIR3DL1_variant_2, KIR3DL2, KIR3DL2-old, KIR3DL3, KIR3DL4, KIR3DL5</i>	63
<i>Mamu-KIR3DL02</i>	<i>KIR3DL-like_3, KIR3DL2, KIR3DL21, KIR3DL21-like1</i>	16
<i>Mamu-KIR3DLW03</i>	<i>KIR3DL-4, KIR3DL-5, KIR3DL-like1-BNB, KIR3DL21</i>	15
<i>Mamu-KIR3DL04</i>	<i>KIR3DL11</i>	4
<i>Mamu-KIR3DL05</i>	<i>3DL7b-3DL40, KIR3DL, KIR3DL-3, KIR3DL16, KIR3DL7, KIR3DL7-like2, KIR3DL07</i>	33
<i>Mamu-KIR3DL06</i>	<i>KIR3DL6</i>	8
<i>Mamu-KIR3DL07</i>	<i>2DL420, KIR3DL, KIR3DL18, KIR3DL7, KIR3DL7-like1, KIR3DL7-like3, KIR3DL03</i>	67
<i>Mamu-KIR3DL08</i>	<i>KIR3DL, KIR3DL-like_2, KIR3DL17, KIR3DL8, KIRDL8, Mamu-KIR3DL04, Mamu-KIR3DL4</i>	27
<i>Mamu-KIR3DL10</i>	<i>3DL10-2DL501, 3DL3NK, KIR3DL, KIR3DL10, KIR3DL9, Mamu-KIR3DL05</i>	6
<i>Mamu-KIR3DL11</i>	<i>KIR3DL, KIR3DL-1, KIR3DL-6, KIR3DL-7, KIR3DL11</i>	19
<i>Mamu-KIR3DLW12</i>	Newly identified in Chinese rhesus macaques	2
<i>Mamu-KIR3DLW14</i>	Newly identified in Indian and Chinese rhesus macaques	3
<i>Mamu-KIR3DLW17</i>	Newly identified in Burmese and Chinese rhesus macaques	3
<i>Mamu-KIR3DLW18</i>	Newly identified in Burmese rhesus macaques	2
<i>Mamu-KIR3DLW25</i>	Newly identified in Burmese rhesus macaques	1
<i>Mamu-KIR3DLW31</i>	Renamed <i>Mamu-KIR3DL02</i> fusion alleles	4
<i>Mamu-KIR3DLW32</i>	Renamed <i>Mamu-KIR3DL02</i> fusion alleles, <i>Mamu-KIR3DL10A/3DL02</i>	2
<i>Mamu-KIR3DLW33</i>	Renamed <i>Mamu-KIR3DL02</i> fusion allele, <i>Mamu-KIR3DL10B/3DL02</i>	1
<i>Mamu-KIR3DLW34</i>	Renamed <i>Mamu-KIR3DLW03</i> fusion alleles	9
<i>Mamu-KIR3DLW35</i>	Renamed <i>Mamu-KIR3DLW03</i> fusion allele	1
<i>Mamu-KIR3DLW36</i>	Renamed <i>Mamu-KIR3DL05</i> fusion alleles	3
<i>Mamu-KIR3DLW37</i>	Renamed <i>Mamu-KIR3DL05</i> alleles	2
<i>Mamu-KIR3DLW38</i>	Renamed <i>Mamu-KIR3DL07</i> fusion allele	1
<i>Mamu-KIR3DLW39</i>	Renamed <i>Mamu-KIR3DL07</i> fusion allele	1
<i>Mamu-KIR3DLW40</i>	Renamed <i>Mamu-KIR3DL07</i> fusion allele	1
<i>Mamu-KIR3DLW41</i>	Renamed <i>Mamu-KIR3DL07</i> fusion allele	1
<i>Mamu-KIR3DLW42</i>	Renamed <i>Mamu-KIR3DL07</i> fusion allele	1
<i>Mamu-KIR3DLW43</i>	Renamed <i>Mamu-KIR3DL08</i> fusion alleles	3
<i>Mamu-KIR3DLW44</i>	Renamed <i>Mamu-KIR3DL08</i> fusion allele	1
<i>Mamu-KIR3DLW45</i>	Renamed <i>Mamu-KIR3DL10</i> fusion alleles	7
<i>Mamu-KIR3DLW46</i>	Renamed <i>Mamu-KIR3DS04</i> fusion allele	1
<i>Mamu-KIR3DS01</i>	<i>KIR3DH-7, KIR3DH1, KIR3DH5, Mamu-KIR3DS01-JHB-HEFGH</i>	10
<i>Mamu-KIR3DS02</i>	<i>3DH2, 3DH42, KIR3DH-like_5, KIR3DH-like_6, KIR3DH10, KIR3DH12, KIR3DH13, KIR3DH14, KIR3DH15, KIR3DH16, KIR3DH2</i>	32
<i>Mamu-KIR3DS03</i>	<i>KIR3DH3, KIR3DH8, KIR3DH9</i>	6
<i>Mamu-KIR3DS04</i>	<i>KIR3DH-1, KIR3DH4, KIR3DH6</i>	11
<i>Mamu-KIR3DS05</i>	<i>KIR3DH1, KIR3DM-1, KIR3DM1, KIR3DM6, KIR_Partial_Sequence_1</i>	10
<i>Mamu-KIR3DS06</i>	<i>KIR3DH-4, KIR3DH-like8, KIR3DH-like_7, KIR3DH18</i>	22
<i>Mamu-KIR3DSW07</i>	<i>KIR3DH-5, KIR3DH7, Mamu-KIR3DS07-JHB-HO</i>	5
<i>Mamu-KIR3DSW08</i>	<i>KIR3DH-2, KIR3DH-3, KIR3DH-4, KIR3DH-5, KIR3DH-like_1, KIR3DH-like_2, KIR3DH-like_3, KIR3DH-like_4, KIR3DH21</i>	7
<i>Mamu-KIR3DSW09</i>	<i>KIR3DH-8, KIR3DH20, KIR3DH5, KIR3DH5-like1, mmKIR3DH-1</i>	8
<i>Mamu-KIR3DSW10</i>	Newly identified in Burmese rhesus macaques	1
<i>Mamu-KIR3DSW16</i>	Newly identified in Burmese rhesus macaques	1

**Table 1** (continued)

KIR gene	Previous designations	Number of reported alleles
<i>Mamu-KIR3DSW18</i>	Newly identified in Burmese rhesus macaques	1
<i>Mamu-KIR3DSW20</i>	Newly identified in Burmese rhesus macaques	1
<i>Mamu-KIR3DSW21</i>	Newly identified in Burmese and Chinese rhesus macaques	4
<i>Mamu-KIR3DSW32</i>	Newly identified in Chinese rhesus macaques	1
<i>Mamu-KIR3DSW34</i>	Newly identified in Burmese rhesus macaques	1
<i>Mamu-KIR3DSW35</i>	Renamed <i>Mamu-KIR3DS02</i> fusion alleles	2
<i>Mamu-KIR3DSW36</i>	Renamed <i>Mamu-KIR3DS04</i> allele	1
<i>Mamu-KIR3DSW37</i>	Renamed <i>Mamu-KIR3DS04</i> allele	1
<i>Mamu-KIR3DSW38</i>	Renamed <i>Mamu-KIR3DS06</i> fusion allele	1
<i>Mamu-KIR3DSW39</i>	Renamed <i>Mamu-KIR3DSW08</i> alleles	13
<i>Mamu-KIR3DSW40</i>	Renamed <i>Mamu-KIR3DSW09</i> fusion allele	1
<i>Mamu-KIR3DSW41</i>	Renamed <i>Mamu-KIR3DSW09</i> fusion alleles	2
<i>Mamu-KIRDX1</i>	<i>KIR3DL0</i>	1
Total		576

nomenclature guidelines (Robinson et al. 2018), the recombinant rhesus macaque *KIR* were named after alleles of the gene that contributed the longest gene segment. From experience we have learned that this criterion can result in confusing allele names. For example, *Mamu-KIR3DS04\*011* (acc. nr. LR694568) comprises the first 5 exons of *Mamu-KIR3DS04*, joined to exons encoding the transmembrane region and cytoplasmic tail that are similar to those of *Mamu-KIR3DL07*. Because the activating gene parent makes the larger contribution, this recombinant was originally named as an allele of *Mamu-KIR3DS04*, although the cytoplasmic tail derived from *Mamu-KIR3DL07* predicts that the receptor has an inhibitory signalling function. To prevent confusion, such hybrid *KIR* genes have been renamed, and are indicated by the workshop status (Table 4). In the future, newly discovered recombinant sequences will be assigned sequential gene (workshop) numbers. Previous designations of renamed alleles and genes will be retained and marked as deleted.

An exception is made for recombinant *KIR* genes in the centromeric region and that involve the macaque framework gene *KIR3DL20*. The physical location of these recombinant genes has been established (Sambrook et al. 2005), which contrasts with those of the recombinant lineage II *KIR* genes. Recombinant sequences derived from the centromeric region are still assigned as *KIR3DL20* alleles, but are shown to be “Recombinant” with a novel suffix “R” subsequent to the allele designation. For example, *Mamu-KIR3DL20\*030R* (acc. nr. LR694489) and *Mamu-KIR3DL20\*044R* (acc. nr. LR694507) are recombinants that consist of the first seven exons of *Mamu-*

*KIR3DL20*, and of the intracellular domains of *Mamu-KIR2DL04* and *Mamu-KIR1D*, respectively.

Most recombinant *KIR* genes of cynomolgus macaques have been assigned novel workshop numbers (Bruijnesteijn et al., unpublished data). Three additional *KIR* sequence groups have been renamed based on their recombinant nature (Table 5).

## Renaming other macaque *KIR* genes

Several rhesus and cynomolgus macaque *KIR* sequences that were not obvious recombinants have been renamed based on sequence comparison and phylogenetic analysis (Tables 4 and 5). For example, 13 *Mamu-KIR3DSW08* alleles are readily distinguished from the other *KIR3DSW08* alleles, and have been renamed as alleles of *Mamu-KIR3DSW39* (Table 4).

We should stress that *Mamu-KIR3DL07* and *Mamu-KIR3DL11* alleles group phylogenetically into three and two clusters, respectively, and that some *KIR* haplotypes contain several copies of these genes (Blokhuis et al. 2010; Bruijnesteijn et al. 2018a, b). Although an argument can be made for giving these paralogous genes unique gene names, sequence comparison has yet to indicate distinctive functions, and for this reason these genes have not been renamed.

## The IPD-NHKIR Database

Knowledge regarding the *KIR* repertoire in various NHP species has increased steadily over the past decade, escalating the need

**Table 2** List of cynomolgus macaque *KIR* genes, their previous names, and the number of reported alleles per gene

KIR gene	Previous designations	Number of reported alleles
<i>Mafa-KIR1D</i>	<i>KIR1D</i>	35
<i>Mafa-KIR2DL04</i>	<i>KIR2DL04</i>	41
<i>Mafa-KIR3DL20</i>	–	36
<i>Mafa-KIR3DL01</i>	<i>KIR3DL1</i>	17
<i>Mafa-KIR3DLW03</i>	–	4
<i>Mafa-KIR3DL05</i>	–	5
<i>Mafa-KIR3DL06</i>	–	1
<i>Mafa-KIR3DL07</i>	–	21
<i>Mafa-KIR3DL11</i>	–	18
<i>Mafa-KIR3DLW12</i>	Alleles of <i>Mafa-KIR3DL2</i> , <i>Mafa-KIR2DL02</i>	15
<i>Mafa-KIR3DLW13</i>	Alleles of <i>Mafa-KIR3DL11</i> Alleles of <i>Mafa-KIR3DL11</i>	10
<i>Mafa-KIR3DLW14</i>	Alleles of <i>Mafa-KIR3DL11</i>	8
<i>Mafa-KIR3DLW15</i>	Alleles of <i>Mafa-KIR3DL07</i>	4
<i>Mafa-KIR3DLW16</i>	Alleles of <i>Mafa-KIR3DL07</i>	4
<i>Mafa-KIR3DLW17</i>	–	3
<i>Mafa-KIR3DLW18</i>	–	1
<i>Mafa-KIR3DLW19</i>	Alleles of <i>Mafa-KIR3DL21</i> (EU419080.11)	2
<i>Mafa-KIR3DLW21</i>	–	1
<i>Mafa-KIR3DLW22</i>	–	1
<i>Mafa-KIR3DLW23</i>	–	1
<i>Mafa-KIR3DLW24</i>	Alleles of <i>Mafa-KIR3DL21</i> (EU419100.1)	1
<i>Mafa-KIR3DLW25</i>	Alleles of <i>Mafa-KIR3DL2</i>	4
<i>Mafa-KIR3DLW26</i>	Alleles of <i>Mafa-KIR3DL02</i>	1
<i>Mafa-KIR3DLW27</i>	–	1
<i>Mafa-KIR3DLW28</i>	<i>Mafa-KIR3DL07a</i>	1
<i>Mafa-KIR3DLW29</i>	–	1
<i>Mafa-KIR3DLW30</i>	–	1
<i>Mafa-KIR3DLW47</i>	<i>Mafa-KIR3DL05*001</i>	1
<i>Mafa-KIR3DLW48</i>	Alleles of <i>Mafa-KIR3DL05</i>	2
<i>Mafa-KIR3DS02</i>	–	2
<i>Mafa-KIR3DS04</i>	–	1
<i>Mafa-KIR3DS06</i>	–	3
<i>Mafa-KIR3DSW07</i>	–	3
<i>Mafa-KIR3DSW08</i>	–	3
<i>Mafa-KIR3DSW09</i>	<i>Mafa-KIR3DSW11*004</i>	1
<i>Mafa-KIR3DSW10</i>	Alleles of <i>Mafa-KIR3DS</i>	5
<i>Mafa-KIR3DSW11</i>	–	5
<i>Mafa-KIR3DSW12</i>	Alleles of <i>Mafa-KIR3DS</i>	11
<i>Mafa-KIR3DSW13</i>	Alleles of <i>Mafa-KIR3DS</i>	2
<i>Mafa-KIR3DSW14</i>	–	2
<i>Mafa-KIR3DSW15</i>	–	9
<i>Mafa-KIR3DSW16</i>	–	3
<i>Mafa-KIR3DSW17</i>	Alleles of <i>Mafa-KIR3DS</i> , <i>Mafa-KIR3DH</i>	4
<i>Mafa-KIR3DSW18</i>	–	2
<i>Mafa-KIR3DSW19</i>	–	2
<i>Mafa-KIR3DSW20</i>	Alleles of <i>Mafa-KIR3DS</i>	4
<i>Mafa-KIR3DSW21</i>	Alleles of <i>Mafa-KIR3DS</i>	7
<i>Mafa-KIR3DSW22</i>	<i>Mafa-KIR3DL07b</i>	3
<i>Mafa-KIR3DSW23</i>	–	1

**Table 2** (continued)

KIR gene	Previous designations	Number of reported alleles
<i>Mafa-KIR3DSW24</i>	Alleles of <i>Mafa-KIR3DS</i>	5
<i>Mafa-KIR3DSW25</i>	Allele of <i>Mafa-KIR3DS</i>	1
<i>Mafa-KIR3DSW26</i>	–	1
<i>Mafa-KIR3DSW27</i>	Allele of <i>Mafa-KIR3DS</i>	2
<i>Mafa-KIR3DSW28</i>	Allele of <i>Mafa-KIR3DS</i>	1
<i>Mafa-KIR3DSW29</i>	–	1
<i>Mafa-KIR3DSW30</i>	–	3
<i>Mafa-KIR3DSW31</i>	–	2
<i>Mafa-KIR3DSW33</i>	–	1
<i>Mafa-KIR3DSW39</i>	Alleles of <i>Mafa-KIR3DSW08</i>	3
<i>Total</i>		334

for a centralized database with annotated sequences and a standard nomenclature. In July 2018, the IPD-NHKIR Database (<https://www.ebi.ac.uk/ipd/nhkir/>) was launched, and is now part of the Immuno Polymorphism Database (IPD) platform (<https://www.ebi.ac.uk/ipd/>) (Maccari et al. 2017). The database provides a centralized repository for non-human KIR (NHKIR) sequences, and currently archives data for four different NHP species as well as for cattle. The NHP species represented in the database are chimpanzee (*Pan troglodytes*, *Patr*), Sumatran orangutan (*Pongo abelii*, *Poab*), Bornean orangutan (*Pongo pygmaeus*, *Popy*), and rhesus monkey (*Macaca mulatta*, *Mamu*). For these four species, 266 annotated alleles representing various *KIR* genes are archived (Table 6), and comprise data submitted or published by several different research groups (Khakoo et al. 2000; Grendell et al. 2001; Hershberger et al. 2001; Rajalingam et al. 2001; Guethlein et al. 2002; Andersen et al. 2004; Sambrook et al. 2005; Guethlein et al. 2007; Blokhuis et al. 2009a, b; Bostik et al. 2009; Abi-Rached et al. 2010; Blokhuis et al. 2010; Chaichompoo et al. 2010; Kruse et al. 2010; Colantonio et al. 2011; Hellmann et al. 2011; Moreland et al. 2011). The *KIR* genes identified in cynomolgus macaques

(Bimber et al. 2008; Prall et al. 2017) (Bruijnesteijn et al., unpublished data) have now been named, meaning that the *KIR* data from a fifth non-human primate species should soon be available. The current version of the IPD-NHKIR Database can host genomic sequences, and contains a multiple sequence alignment tool (Maccari et al. 2017). This tool allows for single gene alignments (nucleotide or protein) as well as inter- and intra-species gene alignments from all groups within the IPD-NHKIR Database. For each allele, a nomenclature table is accessible with additional information (for example: previous designations, GenBank/ENA/DDBJ accession number, and publications).

The curators of the IPD-NHKIR Database are responsible for assembling, categorizing, and providing official designations for newly identified alleles. For the NHP part of the IPD-NHKIR Database, the research group of Prof. Dr. R.E. Bontrop (Rijswijk, The Netherlands) is responsible for curation of the *KIR* sequences of macaque species, and for these species currently only full-length sequences are accepted for annotation, whereas curation for all other non-human primate species is the responsibility of Dr. L. A. Guethlein and Prof. Dr. P. Parham (Stanford, USA). Sequences/alleles can be submitted using the online submission tool, which is available from the IPD-NHKIR Database homepage (<https://www.ebi.ac.uk/ipd/nhkir/>). Submitted sequences must meet the criteria described above and have a GenBank/ENA/DDBJ accession number. In addition to newly identified *KIR* sequences, we urge and encourage all scientists working in the field of non-human primate *KIR* to submit all the sequences determined in their cohorts that are identical to published *KIR* alleles. This latter approach will provide an additional and valuable quality control tool for the database of archived *KIR* sequences. Although at present, only one *KIR* sequence at a time can be submitted, we are currently developing a bulk submission tool. The IPD-NHKIR Database provides a data release twice a year, which updates the website with all novel NHP *KIR* sequences that have become public, and relates them to the previously deposited sequences.

**Table 3** Official names of macaque species. The abbreviation of the scientific name is used as suffix for the KIR designation

Species name		
Common	Scientific	KIR designation
Stump-tailed macaque	<i>Macaca arctoides</i>	<i>Maar</i>
Crab-eating macaque*	<i>Macaca fascicularis</i>	<i>Mafa</i>
Japanese macaque	<i>Macaca fuscata</i>	<i>Mafu</i>
Rhesus macaque	<i>Macaca mulatta</i>	<i>Mamu</i>
Southern pig-tailed macaque	<i>Macaca nemestrina</i>	<i>Mane</i>
Lion-tailed macaque	<i>Macaca silenus</i>	<i>Masi</i>
Milne-Edwards's macaque	<i>Macaca thibetana</i>	<i>Math</i>

\*Other common names of this species are long-tailed and cynomolgus macaque

**Table 4** Renamed genes and alleles in rhesus macaques. The previous names are indicated, and the different gene segments are listed for sequences that are the result of fusion events

Previous designation		New designation		Recombination segments			Accession number	Reference
Gene	Allele	Gene	Allele	Segment 1	Segment 2			
<i>Mamu-KIR3DL02</i>	<i>Mamu-KIR3DL02*005</i>	<i>Mamu-KIR3DLW31</i>	<i>Mamu-KIR3DLW31*001</i>	<i>Mamu-KIR3DL02</i>	<i>Mamu-KIR3DL01</i>	EU419054	Moreland et al., BMC Genomics 2001	
	<i>Mamu-KIR3DL02*006</i>		<i>Mamu-KIR3DLW31*002</i>			EU688989	Moreland et al., BMC Genomics 2001	
	<i>Mamu-KIR3DL02*010</i>		<i>Mamu-KIR3DLW31*003</i>			LS997661	D. O'Connor 24-10-2017	
	<i>Mamu-KIR3DL02*011</i>		<i>Mamu-KIR3DLW31*004</i>			LS997662	D. O'Connor 24-10-2017	
	<i>Mamu-KIR3DL02*016</i>		<i>Mamu-KIR3DLW32*001</i>		<i>Mamu-KIR3DL02</i>	LR694230	Bruijesteijn et al., unpublished data	
	<i>Mamu-KIR3DL10A/3DL02</i>		<i>Mamu-KIR3DLW32*002</i>			LT907840	Bruijesteijn et al., Journal of Immunology 2018	
	<i>Mamu-KIR3DL10B/3DL02</i>		<i>Mamu-KIR3DLW33*001</i>	<i>Mamu-KIR3DL05</i>	<i>Mamu-KIR3DL02</i>	LT907841	Bruijesteijn et al., Journal of Immunology 2018	
<i>Mamu-KIR3DLW03</i>	<i>Mamu-KIR3DLW03*001</i>	<i>Mamu-KIR3DLW34</i>	<i>Mamu-KIR3DLW34*001</i>	Unknown donor	<i>Mamu-KIR3DLW03</i>	EU419051	Moreland et al., BMC Genomics 2001	
	<i>Mamu-KIR3DLW03*003</i>		<i>Mamu-KIR3DLW34*002</i>			EU419031	Moreland et al., BMC Genomics 2001	
	<i>Mamu-KIR3DLW03*004</i>		<i>Mamu-KIR3DLW34*003</i>			FN424253	Kruse et al., Immunogenetics 2010	
	<i>Mamu-KIR3DLW03*005</i>		<i>Mamu-KIR3DLW34*004</i>			FN424256	Kruse et al., Immunogenetics 2010	
	<i>Mamu-KIR3DLW03*009</i>		<i>Mamu-KIR3DLW34*005</i>			LS997651	Bruijesteijn et al., unpublished data	
	<i>Mamu-KIR3DLW03*014</i>		<i>Mamu-KIR3DLW34*006</i>			LR694237	Bruijesteijn et al., unpublished data	
	<i>Mamu-KIR3DLW03*016</i>		<i>Mamu-KIR3DLW34*007</i>			LR694239	Bruijesteijn et al., unpublished data	
	<i>Mamu-KIR3DLW03*017</i>		<i>Mamu-KIR3DLW34*008</i>			LR694240	Bruijesteijn et al., unpublished data	
	<i>Mamu-KIR3DLW03*018</i>		<i>Mamu-KIR3DLW34*009</i>			LR694241	Bruijesteijn et al., unpublished data	
	<i>Mamu-KIR3DLW03*023</i>		<i>Mamu-KIR3DLW35*001</i>	Unknown donor	<i>Mamu-KIR3DLW03</i>	LR694248	Bruijesteijn et al., unpublished data	
		<i>Mamu-KIR3DL05*001</i>	<i>Mamu-KIR3DLW36</i>	<i>Mamu-KIR3DLW36*001</i>	<i>Mamu-KIR3DL08</i>	<i>Mamu-KIR3DL05</i>	EU419045	Moreland et al., BMC Genomics 2001
		<i>Mamu-KIR3DL05*011</i>		<i>Mamu-KIR3DLW36*002</i>			FJ562121	Bostik et al., J Immunology 2009
	<i>Mamu-KIR3DL05*017</i>		<i>Mamu-KIR3DLW36*003</i>			LS997639	D. O'Connor 24-10-2017	
	<i>Mamu-KIR3DL05*005</i>	<i>Mamu-KIR3DLW37</i>	<i>Mamu-KIR3DLW37*001</i>	–	–	EU419069	Moreland et al., BMC Genomics 2001	
	<i>Mamu-KIR3DL05*009</i>		<i>Mamu-KIR3DLW37*002</i>	–	–	GU112310	Blokhuys et al., Immunogenetics 2010	
<i>Mamu-KIR3DL07</i>	<i>Mamu-KIR3DL07*042</i>	<i>Mamu-KIR3DLW38</i>	<i>Mamu-KIR3DLW38*001</i>	<i>Mamu-KIR3DL07</i>	<i>Mamu-KIR3DL08</i>	LR694456	Bruijesteijn et al., unpublished data	
	<i>Mamu-KIR3DL07*045</i>	<i>Mamu-KIR3DLW39</i>	<i>Mamu-KIR3DLW39*001</i>	<i>Mamu-KIR3DL05</i>	<i>Mamu-KIR3DL07</i>	LR694459	Bruijesteijn et al., unpublished data	
	<i>Mamu-KIR3DL07*056</i>	<i>Mamu-KIR3DLW40</i>	<i>Mamu-KIR3DLW40*001</i>	<i>Mamu-KIR3DSW08</i>	<i>Mamu-KIR3DL07</i>	LR694470	Bruijesteijn et al., unpublished data	
	<i>Mamu-KIR3DL07*064</i>	<i>Mamu-KIR3DLW41</i>	<i>Mamu-KIR3DLW41*001</i>	<i>Mamu-KIR3DL05</i>	<i>Mamu-KIR3DL07</i>	LR694479	Bruijesteijn et al., unpublished data	

Table 4 (continued)

Mamu-KIR3DL07*065	Mamu-KIR3DLW42	Mamu-KIR3DLW42*001	Unknown donor	Mamu-KIR3DL07	LR694480	Bruijesteijn et al., unpublished data
Mamu-KIR3DL08	Mamu-KIR3DLW43	Mamu-KIR3DLW43*001	Mamu-KIR3DL02	Mamu-KIR3DL08	LT907838	Bruijesteijn et al., unpublished data
Mamu-KIR3DL08*018Mamu-KIR3DL02/3DL08A Mamu-KIR3DL08*018Mamu-KIR3DL02/3DL08A						Journal of Immunology 2018
Mamu-KIR3DL08*019Mamu-KIR3DL02/3DL08BMamu-KIR3DL08*019Mamu-KIR3DL02/3DL08B					LT907839	Bruijesteijn et al., Journal of Immunology 2018
Mamu-KIR3DL08*020	Mamu-KIR3DLW43*003				LR694519	Bruijesteijn et al., unpublished data
Mamu-KIR3DL08*021	Mamu-KIR3DLW44	Mamu-KIR3DLW44*001	Mamu-KIR3DL01	Mamu-KIR3DL08	LR694520	Bruijesteijn et al., unpublished data
Mamu-KIR3DL10*001	Mamu-KIR3DLW45	Mamu-KIR3DLW45*001	Mamu-KIR3DL05	Mamu-KIR3DL10	AY728183	Sambrook et al., Genome Res 2005
Mamu-KIR3DL10*003	Mamu-KIR3DLW45*002				EU419038	Moreland et al., BMC Genomics 2001
Mamu-KIR3DL10*004	Mamu-KIR3DLW45*003				EU419039	Moreland et al., BMC Genomics 2001
Mamu-KIR3DL10*005:01	Mamu-KIR3DLW45*004:01				GU014294	Colantonio et al., PLoS Pathogen 2011
Mamu-KIR3DL10*005:02	Mamu-KIR3DLW45*004:02				GU112295	Blokhuys et al., Immunogenetics 2010
Mamu-KIR3DL10*005:03	Mamu-KIR3DLW45*004:03				LR694529	Bruijesteijn et al., unpublished data
Mamu-KIR3DL10*006	Mamu-KIR3DLW45*005				FJ562113	Bostik et al., J Immunology 2009
Mamu-KIR3DL20*030	Mamu-KIR3DL20*030R		Mamu-KIR3DL20	Mamu-KIR2DL04	LR694489	Bruijesteijn et al., unpublished data
Mamu-KIR3DL20*044	Mamu-KIR3DL20*044R		Mamu-KIR3DL20	Mamu-KIR1D	LR694507	Bruijesteijn et al., unpublished data
Mamu-KIR3DS02*012	Mamu-KIR3DSW35	Mamu-KIR3DSW35*001	Mamu-KIR3DS02	Mamu-KIR3DSW09	JN613291	Hellmann et al., PLoS Pathogen 2011
Mamu-KIR3DS04*008	Mamu-KIR3DSW36	Mamu-KIR3DSW36*001			LR694564	Bruijesteijn et al., unpublished data
Mamu-KIR3DS04*011	Mamu-KIR3DLW46	Mamu-KIR3DLW46*001	Mamu-KIR3DS04	Mamu-KIR3DL07	KY660361	Ries et al., PLoS Pathogens 2017
Mamu-KIR3DS04*012	Mamu-KIR3DSW37	Mamu-KIR3DSW37*001			LR694568	Bruijesteijn et al., unpublished data
Mamu-KIR3DS06*019	Mamu-KIR3DSW38	Mamu-KIR3DSW38*001	Mamu-KIR3DSW07	Mamu-KIR3DS06	LR694573	Bruijesteijn et al., unpublished data
Mamu-KIR3DSW08*005	Mamu-KIR3DSW39	Mamu-KIR3DSW39*001			EU702467	Bruijesteijn et al., unpublished data
Mamu-KIR3DSW08*006	Mamu-KIR3DSW39*002				FN424254	Blokhuys et al., Mol Immunology 2009
Mamu-KIR3DSW08*007	Mamu-KIR3DSW39*003				FN424255	Kruse et al., Immunogenetics 2010
Mamu-KIR3DSW08*008	Mamu-KIR3DSW39*004				GU112325	Immunogenetics 2010
Mamu-KIR3DSW08*010:01	Mamu-KIR3DSW39*005:01				JN613297	Hellmann et al., PLoS Pathogen 2011
Mamu-KIR3DSW08*010:02	Mamu-KIR3DSW39*005:02				LT907836	Bruijesteijn et al., unpublished data
Mamu-KIR3DSW08*012	Mamu-KIR3DSW39*006				GU564159	Bruijesteijn et al., unpublished data



**Table 4** (continued)

<i>Mamu-KIR3DSW08*015</i>		<i>Mamu-KIR3DSW39*007</i>	–	LR694578	Chaichompoop et al., Cell. Immunol 2010
<i>Mamu-KIR3DSW08*016</i>		<i>Mamu-KIR3DSW39*008</i>	–	LR694579	Bruijnesteijn et al., unpublished data
<i>Mamu-KIR3DSW08*017</i>		<i>Mamu-KIR3DSW39*009</i>	–	LR694580	Bruijnesteijn et al., unpublished data
<i>Mamu-KIR3DSW08*018:01</i>		<i>Mamu-KIR3DSW39*010:01</i>	–	LR694581	Bruijnesteijn et al., unpublished data
<i>Mamu-KIR3DSW08*018:02</i>		<i>Mamu-KIR3DSW39*010:02</i>	–	LR694582	Bruijnesteijn et al., unpublished data
<i>Mamu-KIR3DSW08*014</i>		<i>Mamu-KIR3DSW39*011</i>	–	LR694577	Bruijnesteijn et al., unpublished data
<i>Mamu-KIR3DSW09</i>	<i>Mamu-KIR3DSW40</i>	<i>Mamu-KIR3DSW40*001</i>	<i>Mamu-KIR3DSW09</i>	EU702466, G-U112273	Blokhuys et al., Mol Immunology 2009, Immunogenetics 2010
<i>Mamu-KIR3DSW09*005</i>	<i>Mamu-KIR3DSW41</i>	<i>Mamu-KIR3DSW41*001</i>	<i>Mamu-KIR3DSW08</i>	FN424249	Kruse et al., Immunogenetics 2010
<i>Mamu-KIR3DSW09*011</i>		<i>Mamu-KIR3DSW41*002</i>	<i>Mamu-KIR3DSW08</i>	LR694585	Bruijnesteijn et al., unpublished data

**Table 5** Renamed genes and alleles in cynomolgus macaques. The previous names are indicated, and the different gene segments are listed for sequences that are the result of fusion events

Previous designation	New designation		Recombination segments			Reference
	Allele	Gene	Allele	Segment 1	Segment 2	
<i>Mafa-KIR3DL05</i>	<i>Mafa-KIR3DL05*001</i>	<i>Mafa-KIR3DLW47</i>	<i>Mafa-KIR3DLW47*001</i>	Unknown donor	<i>Mafa-KIR3DL05</i>	Bruijnesteijn et al., unpublished data
	<i>Mafa-KIR3DL05*002</i>	<i>Mafa-KIR3DLW48</i>	<i>Mafa-KIR3DLW48*001</i>	<i>Mafa-KIR3DL01</i>	<i>Mafa-KIR3DL05</i>	Bruijnesteijn et al., unpublished data
	<i>Mafa-KIR3DL05*003</i>		<i>Mafa-KIR3DLW48*002</i>			Bruijnesteijn et al., unpublished data
<i>Mafa-KIR3DSW08</i>	<i>Mafa-KIR3DSW08*001</i>	<i>Mafa-KIR3DSW39</i>	<i>Mafa-KIR3DSW39*001</i>	–	<i>Mafa-KIR3DSW39*001</i>	Bruijnesteijn et al., unpublished data
	<i>Mafa-KIR3DSW08*002</i>		<i>Mafa-KIR3DSW39*002</i>	–	<i>Mafa-KIR3DSW39*002</i>	Bruijnesteijn et al., unpublished data
	<i>Mafa-KIR3DSW08*003</i>		<i>Mafa-KIR3DSW39*003</i>	–	<i>Mafa-KIR3DSW39*003</i>	Bruijnesteijn et al., unpublished data
<i>Mafa-KIR3DSW11</i>	<i>Mafa-KIR3DSW11*001</i>	<i>Mafa-KIR3DSW09</i>	<i>Mafa-KIR3DSW09*001</i>	–	<i>Mafa-KIR3DSW09*001</i>	Bruijnesteijn et al., unpublished data

**Table 6** Overview of the number of alleles and genes represented in the non-human primate part of the IPD-NHK (August 2019). The species included are chimpanzee (*Patr*), Sumatran orangutan (*Poab*), Bornean orangutan (*Popy*), and rhesus macaque (*Mamu*)

Gene name	Species			
	<i>Patr</i>	<i>Poab</i>	<i>Popy</i>	<i>Mamu</i>
<i>KIR1D</i>				2
<i>KIR2DL4/KIR2DL04*</i>	3			24
<i>KIR2DL5</i>	5	1		
<i>KIR2DL6</i>	3			
<i>KIR2DL7</i>	1			
<i>KIR2DL8</i>	3			
<i>KIR2DL9</i>	3			
<i>KIR2DL10</i>		1		
<i>KIR2DL11</i>		1		
<i>KIR2DL12</i>		1		
<i>KIR2DS4</i>	2			
<i>KIR2DS10</i>		1	1	
<i>KIR2DS13</i>		1	1	
<i>KIR2DS14</i>		2		
<i>KIR3DL1/KIR3DL01</i>	6	9	3	28
<i>KIR3DL02</i>				9
<i>KIR3DL3</i>	4	1		
<i>KIR3DL4/KIR3DL04</i>	3			4
<i>KIR3DL5/KIR3DL05</i>	3			12
<i>KIR3DL06</i>				2
<i>KIR3DL07</i>				13
<i>KIR3DL08</i>				12
<i>KIR3DL10</i>				8
<i>KIR3DL11</i>				7
<i>KIR3DL20</i>				15
<i>KIR3DLW03</i>				5
<i>KIR3DLX1</i>	1			1
<i>KIR3DS1/KIR3DS01</i>		1		4
<i>KIR3DS2/KIR3DS02</i>	2			15
<i>KIR3DS03</i>				4
<i>KIR3DS04</i>				6
<i>KIR3DS05</i>				4
<i>KIR3DS6/KIR3DS06</i>	1			7
<i>KIR3DSW07</i>				2
<i>KIR3DSW08</i>				12
<i>KIR3DSW09</i>				6
<i>KIRDP</i>		1		

\**KIR2DL4* present in *Patr*, *Poab*, and *Popy*, and *KIR2DL04* present in *Mamu* represent orthologous genes. In the other cases where two gene names are indicated in the table, these do not represent orthologs, and the first mentioned gene in a row can be observed in *Patr*, *Poab*, or *Popy*, and the other in the *Mamu*

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