Ancient Trans-Species Polymorphism at the Major Histocompatibility Complex in Primates

Alyssa Lyn Fortier[1,2*] **and Jonathan K. Pritchard**[1,2]

***For correspondence:**
afortier@stanford.edu (ALF);
pritch@stanford.edu (JKP)

[1]Department of Biology, Stanford University, Stanford, CA USA; [2]Department of Genetics, Stanford University, Stanford, CA USA

Abstract

Classical genes within the Major Histocompatibility Complex (MHC) are responsible for peptide presentation to T cells, thus playing a central role in immune defense against pathogens. These genes are subject to strong selective pressures including both balancing and directional selection, resulting in exceptional genetic diversity—thousands of alleles per gene in humans. Moreover, some allelic lineages appear to be shared between primate species, a phenomenon known as trans-species polymorphism (TSP) or incomplete lineage sorting, which is rare in the genome overall. However, despite the clinical and evolutionary importance of MHC diversity, we currently lack a full picture of primate MHC evolution. In particular, we do not know to what extent genes and allelic lineages are retained across speciation events. To start addressing this gap, we explore variation *across* genes and species in our companion paper (***Fortier and Pritchard, 2025***) and here we explore variation *within* individual genes. We used Bayesian phylogenetic methods to determine the extent of TSP at 17 MHC genes, including classical and non-classical Class I and Class II genes. We find strong support for ancient TSP in 7 of 10 classical genes, including—remarkably—between humans and old-world monkeys in MHC-DQB1. In addition to the long-term persistence of ancient lineages, we additionally observe rapid evolution at nucleotides encoding the proteins' peptide-binding domains. The most rapidly-evolving amino acid positions are extremely enriched for autoimmune and infectious disease associations. Together, these results suggest complex selective forces—arising from differential peptide binding—that drive short-term allelic turnover within lineages while also maintaining deeply divergent lineages for at least 31 million years in some cases.

Introduction

The Major Histocompatibility Complex (MHC) is a large locus containing many immune genes that is shared among the jawed vertebrates (***Radwan et al., 2020***). In humans, the MHC is also known as the HLA (Human Leukocyte Antigen) region; it spans about 5 megabases (Mb) on chromosome 6 and contains 412 genes (***Figure 1***A) (***MHC, 2022***; ***O'Leary et al., 2016***). Many of these are part of the MHC gene family, a large group of evolutionarily-related genes with varying functions. The "classical" MHC genes are responsible for presenting protein fragments for inspection by T cells. MHC peptide presentation allows T cells to monitor the body for the presence of foreign peptides, which might indicate infection or cancer; this is crucial for vertebrate immune surveillance (***Neefjes et al., 2011***). "Non-classical" MHC genes are essential to the innate immune system, where they perform a variety of niche roles. See the appendices of our companion paper (***Fortier and Pritchard, 2025***)

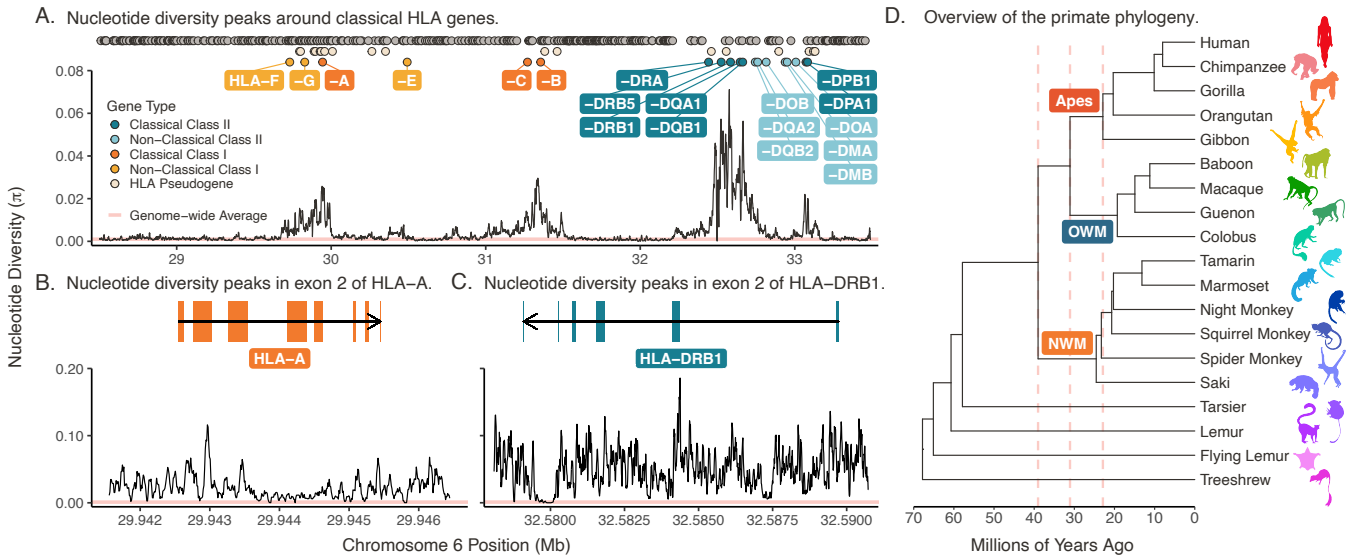

Figure 1. The MHC region in humans (HLA). A) Each point at top represents the location of a gene. The different types of HLA genes are distinguished by different colors, shown in the key at left. The 19 functional HLA genes are labeled with their name (omitting their "HLA" prefix due to space constraints). Gray points represent non-HLA genes and pseudogenes in the region. The black line shows nucleotide diversity (Nei and Li's π) across the region, while the pink horizontal line shows the genome-wide average nucleotide diversity ($\pi \approx 0.001$) (***Sachidanandam et al., 2001***). **B)** Nucleotide diversity around classical Class I gene HLA-A, with exon structure shown. **C)** Nucleotide diversity around classical Class II gene HLA-DRB1, with exon structure shown. **D)** Species tree showing the phylogenetic relationships among selected primates from this study (***Kuderna et al., 2023***). The colors of the icons are consistent with colors used throughout the paper to distinguish species. The pink vertical dashed lines indicate split times of the new-world monkeys (NWM) from the apes/old-world monkeys (OWM) (39 MYA), OWM from the apes (31 MYA), and the lesser apes (gibbons) from the great apes (23 MYA).

Figure 1—figure supplement 1. Nucleotide diversity around the rest of the HLA genes.

Figure 1—figure supplement 2. Color and abbreviation key/tree for all species used in this study.

for more detail.

The MHC locus is extraordinarily polymorphic. Haplotypes can vary widely in gene content, and thousands of distinct alleles are observed at the classical genes in humans and other primates (***Maccari et al., 2017***, ***2020***; ***Robinson et al., 2019***). Different alleles are functionally diverse, with distinct peptide-binding affinities and, consequently, allelic differences in pathogen detection (***Neefjes et al., 2011***; ***Adams and Luoma, 2013***). Given this huge diversity of functionally distinct alleles, the MHC is by far the most important locus in the genome for inter-individual variation in both infectious and autoimmune disease risk, with thousands of GWAS hits (***Buniello et al., 2019***; ***Smith et al., 2024***). In our companion paper (***Fortier and Pritchard, 2025***), we built large multi-gene trees to explore the relationships between the different classical and non-classical genes. Here, we look within 17 specific genes—representing classical, non-classical, Class I, and Class II —to characterize trans-species polymorphism, a phenomenon characteristic of long-term balancing selection.

Historically, the MHC provided some of the first clear examples of positive selection in early studies of molecular evolution. By the 1980s and 1990s, researchers had noted an excess of missense variants (i.e., $dN/dS > 1$) in the peptide-binding regions of classical MHC genes (***Hughes and Nei, 1988***, ***1989***), alleles shared across species (***Arden and Klein, 1982***; ***Mayer et al., 1988***), and high nucleotide diversity across the region (***Wakeland et al., 1987***; ***Nei and Hughes, 1991***) in rodents and primates. Indeed, modern data show that nucleotide diversity in the human MHC (HLA region) exceeds 70-times the genome-wide average near the classical genes, suggesting ancient balancing selection (***Figure 1***A-C). Meanwhile, the MHC also features prominently in genome-wide scans for short-term directional selection (***Mathieson et al., 2015***; ***Field et al., 2016***; ***Allentoft et al., 2022***; ***Cong et al., 2022***; ***Okada et al., 2018***; ***Yasumizu et al., 2020***).

In the present paper, we explore a particularly striking feature of the selection signals at MHC,

namely the evidence for extremely deep coalescence structure. Some alleles (haplotypes) are more closely related to corresponding alleles from another species than they are to distinct alleles from their own species. This phenomenon is referred to as *trans-species polymorphism* (TSP).

TSP is rare overall in humans. Across most of the genome, human alleles coalesce to a common ancestor well within the human lineage, typically around 2 million years (MY) ago (***Mallick et al., 2016***). Indeed, only ∼100 loci genome-wide show compelling evidence for sharing of ancestral alleles between humans and our closest relatives, chimpanzees (***Leffler et al., 2013***). TSP among humans and more distantly-related species is even rarer; besides the MHC, the only other clear example of deep TSP is at the ABO locus (which influences blood type) (***Azevedo et al., 2015***). At this locus, both the A and B alleles are shared by descent throughout the apes, implying that the A and B lineages date back to at least the divergence-point of humans and gibbons 23 million years ago (***Ségurel et al., 2012***; ***Kuderna et al., 2023***). Such deep coalescence is extraordinarily unlikely under a neutral model, and instead points to some form of balancing selection.

Meanwhile, TSP is evident at multiple MHC genes, and in many different phylogenetic clades. TSP at this locus was first proposed in the 1980s on the basis of unusual sequence similarity between mice and rats (***Klein, 1980***; ***Arden and Klein, 1982***; ***Klein, 1987***; ***Figueroa et al., 1988***; ***McConnell et al., 1988***; ***Wakeland et al., 1987***), and between humans and chimpanzees (***Lawlor et al., 1988***; ***Mayer et al., 1988***). Later work has reported likely TSP between humans and apes (***Slierendregt et al., 1995***; ***Boyson et al., 1996***; ***McKenzie et al., 1999***; ***Wroblewski et al., 2017***) and humans and old world monkeys (***Mayer et al., 1992***; ***Brändle et al., 1992***; ***Kupfermann et al., 1992***; ***Slierendregt et al., 1992***; ***Geluk et al., 1993***; ***Satta et al., 1996***; ***Otting et al., 2000***; ***Kriener et al., 2000***; ***Gyllensten et al., 1990***; ***Kriener et al., 2001***; ***Otting et al., 1992***; ***Otting and Bontrop, 1995***; ***Otting et al., 1992***, ***2002***); deep TSP is also consistent with the high levels of genetic diversity within the MHC. Such ancient TSP would make the MHC unique compared to any other locus in the genome. However, most previous work has not fully accounted for the inherent uncertainty in phylogenetic inference, especially given the potential for convergent evolution at functional sites. Although there is clear evidence for TSP, its exact age at each gene is still uncertain.

To address these questions, we used data from the IPD-MHC/HLA database—a large repository for MHC allele sequences from humans, non-human primates, and other vertebrates—along with supplementary sequences from NCBI RefSeq (***Maccari et al., 2017***, ***2020***; ***Robinson et al., 2019***). This represents the most complete sampling of primate MHC genes to date, spanning the entire primate tree (***Figure 1***D; ***Table 2-Table 4***). We account for the uncertainty in phylogenetic inference using a Bayesian MCMC approach (*BEAST2*) which is well-suited to handle highly variable and rapidly-evolving sequences. In our companion paper (***Fortier and Pritchard, 2025***), we built trees to compare genes across dozens of species. When paired with previous literature, these trees helped us infer orthology and assign sequences to genes in some cases. That process helped inform this work, where we assess support for TSP within individual genes.

We find support for TSP among the African apes for genes MHC-C, -DPA1, and -DRB3, among the great apes for MHC-DPB1, and among all apes for MHC-B. We also find conclusive evidence for TSP at least back to the ancestor of humans and OWM in MHC-DQB1, implying—remarkably—that allelic lineages have been maintained by balancing selection for at least 31 million years. Rapidly-evolving sites are mainly located in the critical peptide-binding regions of the classical genes, but are spread throughout the coding region of the non-classical genes. Moreover, the most rapidly-evolving sites are also frequently associated with immune phenotypes and diseases in the literature, connecting our evolutionary findings with their functional consequences. These results highlight the contrasting roles of ancient balancing selection and short-term directional selection within the peptide-binding regions of the classical genes, and motivate further evolutionary and functional studies to better understand this unique system.

Results

Data

We collected MHC nucleotide sequences for all genes from the IPD-MHC/HLA database, a large repository for MHC alleles from humans, non-human primates, and other vertebrates (***Maccari et al., 2017***, ***2020***; ***Robinson et al., 2024***). Although extensive, this database includes few or no sequences from important primates such as the gibbon, tarsier, and lemur. Thus, we supplemented our set of alleles using sequences from NCBI RefSeq (***O'Leary et al., 2016***). Because the MHC genes make up an evolutionarily-related family, they can all be aligned (***Kaufman, 2022***; ***Adams and Luoma, 2013***). In our companion paper (***Fortier and Pritchard, 2025***), we utilized these large multigene alignments for Class I, Class IIA, and Class IIB to compare genes. Here, we analyze subsets of those alignments, each focusing on a single gene or group of closely-related genes.

We considered 16 gene groups spanning MHC classes and functions. These include the classical Class I genes (MHC-A-related, MHC-B-related, MHC-C-related), non-classical Class I genes (MHC-E-related, MHC-F-related, MHC-G-related), classical Class IIA genes (MHC-DRA-related, MHC-DQA-related, MHC-DPA-related), classical Class IIB genes (MHC-DRB-related, MHC-DQB-related, MHC-DPB-related), non-classical Class IIA genes (MHC-DMA-related, MHC-DOA-related), and non-classical Class IIB genes (MHC-DMB-related, MHC-DOB-related). See ***Table 2-Table 4*** for a breakdown of the sequences from each species included in each group. We studied two or three different genic regions for each group: exon 2 alone, exon 3 alone, and (for Class I) exon 4 alone. Exons 2 and 3 encode the peptide-binding region (PBR) for the Class I proteins, and exon 2 alone encodes the PBR for the Class II proteins. For the Class I genes, we also considered exon 4 alone because it is comparable in size to exons 2 and 3 and provides a good contrast to the PBR-encoding exons. Because few intron sequences were available for non-human species, we did not include them in our analyses.

Trans-Species Polymorphism is Widespread.

For each gene group and genic region, we used the Bayesian phylogenetics software *BEAST2* (***Bouckaert et al., 2014***, ***2019***) with package *SubstBMA* (***Wu et al., 2013***) to infer phylogenies. One major advantage of *BEAST2* over less tuneable methods is that it can allow evolutionary rates to vary across sites, which is important for genes such as these which experience rapid evolution in functional regions (***Wu et al., 2013***). We also considered each exon separately to minimize the impact of recombination as well as to compare and contrast the binding-site-encoding exons with non-binding-site-encoding exons.

We can visualize each set of phylogenies as a single summary tree, which maximizes the sum of posterior clade probabilities (***BEA, 2024***). Three of these summary trees are shown in ***Figure 2***, constructed from the second exons of classical Class I gene MHC-C, classical Class II gene MHC-DQB, and non-classical Class II gene MHC-DOA, respectively (see ***Figure 2—figure Supplement 1-Figure 2—figure Supplement 10*** for the other exons and genes).

MHC-C is a classical Class I gene which duplicated from MHC-B in the ancestor of the great apes (***Piontkivska and Nei, 2003***; ***Fukami-Kobayashi et al., 2005***; ***Abi-Rached et al., 2010***; ***Adams and Parham, 2001***; ***Lugo and Cadavid, 2015***). Its protein product participates in classical antigen presentation and also serves as the dominant Class I molecule for interacting with killer cell immunoglobulin-like receptors (KIRs) in innate immunity (***Adams and Parham, 2001***; ***Guethlein et al., 2015***; ***Vollmers et al., 2021***). MHC-DQB is a classical Class II gene which pairs with MHC-DQA. Apes have two MHC-DQ copies, MHC-DQA1/MHC-DQB1 and MHC-DQA2/MHC-DQB2, while the second copy was deleted in OWM. NWM can have two or three sets of MHC-DQ genes, depending on species, but it has been unclear whether any of them are 1:1 orthologous with the ape or OWM genes. Lastly, MHC-DOA is a non-classical Class II gene whose protein product modulates MHC-DM activity, indirectly affecting Class II peptide presentation (***Heijmans et al., 2020***; ***Neefjes et al., 2011***). The genes' differing roles result in different patterns in the phylogenetic trees.

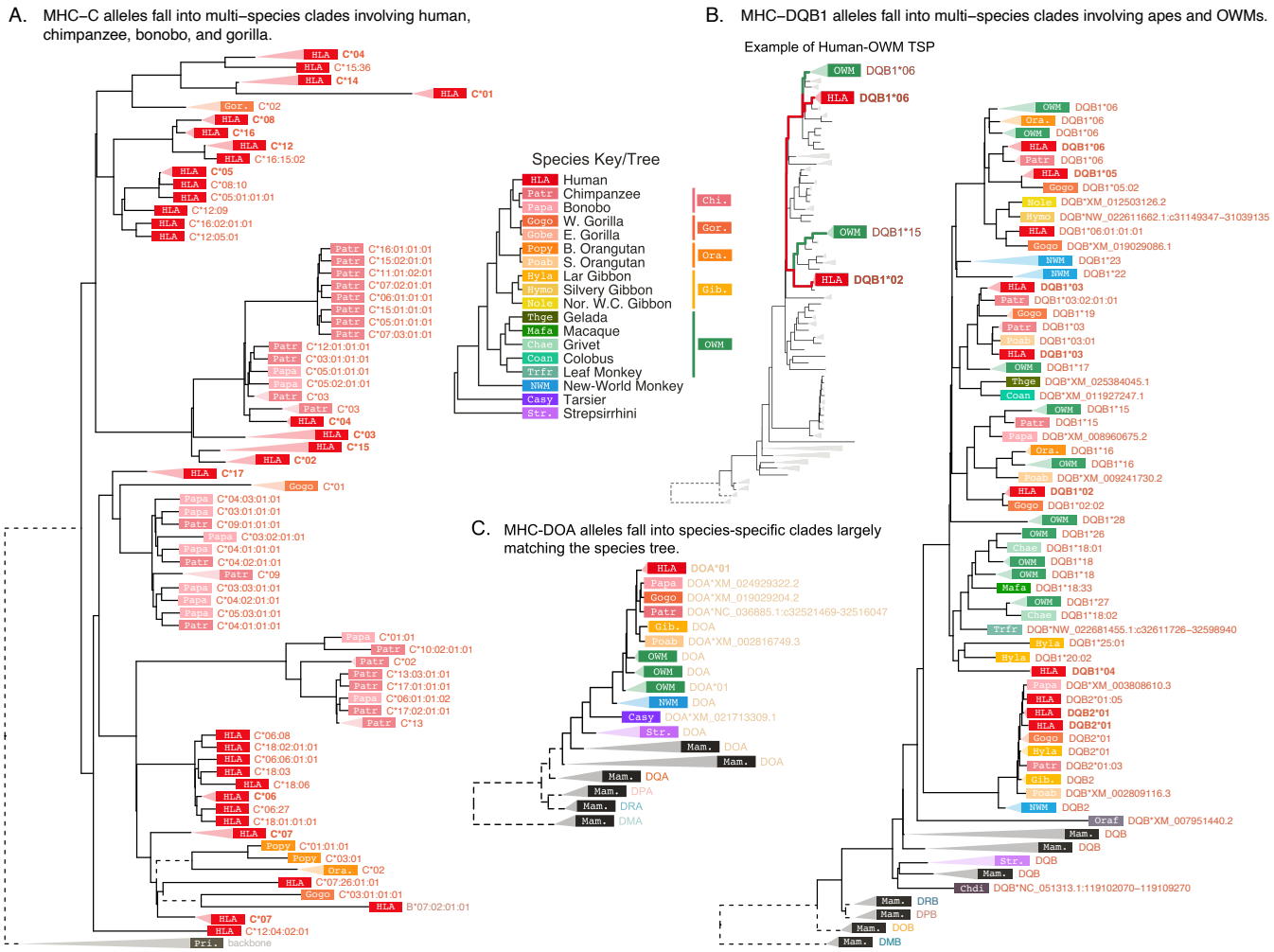

Figure 2. *BEAST2* allele summary trees using sequences from exon 2. A) MHC-C, **B)** MHC-DQB1, and **C)** MHC-DOA. Each tip represents an allele, with color and four-letter abbreviation representing the species (see ***Figure 1—figure Supplement 2*** for full species key). The species label is followed by the allele name (see ***Appendix 1*** for more details on nomenclature) or RefSeq accession number. For simplicity, monophyletic groups of similar alleles are collapsed with a triangle and labeled with their one-field allele name. The color/abbreviation key (center) also depicts the species tree (***Kuderna et al., 2023***). Human alleles (HLA; red) are bolded for emphasis. Dashed outgroup branches are scaled by a factor of $\frac{1}{10}$ to clarify tree structure within the clade of interest. The smaller inset tree in panel B highlights the relationships between two human allele groups (red) and two OWM allele groups (green). The indicated human and OWM lineages coalesce more recently between groups than within each group. Pri., primate backbone sequences; Mam., mammal outgroup sequences.

Figure 2—figure supplement 1. MHC-A-Related *BEAST2* tree using sequences from exon 2, with top Bayes factors.

Figure 2—figure supplement 2. MHC-B-Related *BEAST2* tree using sequences from exon 2, with top Bayes factors.

Figure 2—figure supplement 3. MHC-C-Related *BEAST2* tree using sequences from exon 2, with top Bayes factors.

Figure 2—figure supplement 4. MHC-E-Related *BEAST2* tree using sequences from exon 2, with top Bayes factors.

Figure 2—figure supplement 5. MHC-F-Related *BEAST2* tree using sequences from exon 2, with top Bayes factors.

Figure 2—figure supplement 6. MHC-G-Related *BEAST2* tree using sequences from exon 2, with top Bayes factors.

Figure 2—figure supplement 7. MHC-DRA-Related *BEAST2* tree using sequences from exon 2, with top Bayes factors.

Figure 2—figure supplement 8. MHC-DQA-Related *BEAST2* tree using sequences from exon 2, with top Bayes factors.

Figure 2—figure supplement 9. MHC-DPA-Related *BEAST2* tree using sequences from exon 2, with top Bayes factors.

Figure 2—figure supplement 10. MHC-DMA-Related *BEAST2* tree using sequences from exon 2, with top Bayes factors.

Figure 2—figure supplement 11. MHC-DOA-Related *BEAST2* tree using sequences from exon 2, with top Bayes factors.

Figure 2—figure supplement 12. MHC-DRB-Related *BEAST2* tree using sequences from exon 2, with top Bayes factors.

Figure 2—figure supplement 13. MHC-DQB-Related *BEAST2* tree using sequences from exon 2, with top Bayes factors.

Figure 2—figure supplement 14. MHC-DPB-Related *BEAST2* tree using sequences from exon 2, with top Bayes factors.

Figure 2—figure supplement 15. MHC-DMB-Related *BEAST2* tree using sequences from exon 2, with top Bayes factors.

Figure 2—figure supplement 16. MHC-DOB-Related *BEAST2* tree using sequences from exon 2, with top Bayes factors.

Critically, we observe that, at classical genes MHC-C (***Figure 2***A) and MHC-DQB (***Figure 2***B), the alleles fail to cluster together according to species, as indicated by the mixed-color clades throughout the trees. In MHC-C, human (HLA; red rectangles), chimpanzee (Patr; dark pink), bonobo (Papa; light pink), and even gorilla (Gogo; orange) alleles can be found throughout the tree, indicating that variation in this gene is almost as old as the gene itself.

Figure 2B displays the *BEAST2* tree consisting of MHC-DQB1, -DQB2, and outgroup -DQB alleles all together. It shows many mixed-color clades throughout, consisting of ape (red/orange/yellow rectangles) and OWM (green) alleles grouping together. Alleles often group by first-field name instead of by species, indicating that some allelic lineages have been maintained since before the split of humans and OWM—at least 31 million years. An example of this is shown in the inset to the left of this tree, "Example of Human-OWM TSP." Here, human alleles coalesce with OWM alleles before they coalesce with each other. Near the bottom of the tree is a clade consisting of ape and NWM MHC-DQB2 sequences, suggesting that they are orthologous. However, NWM species have expanded their MHC-DQ regions so these genes may not be 1:1 orthologous (see our companion paper, ***Fortier and Pritchard*** (***2025***)). Additionally, *Strepsirrhini* sequences do not group with either the MHC-DQB1 or -DQB2 clade, showing that the duplications of the MHC-DQB genes must have happened in or after the *Simiiformes* ancestor.

Figure 2C shows the *BEAST2* summary tree for non-classical MHC-DOA. In this tree, alleles group exclusively by species (clades are collapsed for clarity) and the branching order of the species deviates only slightly from the species tree. This shows that not all MHC genes are affected by long-term balancing selection, despite the complicated linkage disequilibrium across classical and non-classical genes in the region (***Smith et al., 2024***). This also suggests that antigen presentation specifically, as opposed to a general role in immune function, is the driving force behind this long-term balancing selection.

While the *BEAST2* summary trees in ***Figure 2*** are suggestive of deep TSP, they do not directly quantify the statistical confidence in the TSP model. Moreover, standard approaches to quantifying uncertainty in trees, such as bootstrap support or posterior probabilities for specific clades, do not relate directly to hypothesis testing for TSP. We therefore implemented an alternative approach using *BEAST2* output, as follows (see the Methods for details).

We performed formal model testing for TSP within quartets of alleles, where two alleles are taken from a species (or taxon) A, and two alleles are taken from a different species (or taxon) B. If the alleles from A group together (and the alleles from B group together) in the unrooted tree, this quartet supports monophyly of A (and of B). In a neutral genealogy, monophyly of each species' sequences is expected. But if alleles from A group more closely with alleles from B in the unrooted tree, then this comparison supports TSP. Since *BEAST2* samples from the posterior distribution of trees, we counted the number of trees that support TSP versus the number that support monophyly as an estimate of the posterior support for each model. We then summarized the relative support for each model by converting these to Bayes factors (see Methods for more detail). The precise interpretation of Bayes factors depends on one's prior expectation; however, following standard guidelines (***Jeffreys, 1998***) we suggest that Bayes factors >100 should be considered as strong support in favor of TSP. Bayes factors <1 are evidence against TSP. For each comparison of two taxa, we report the maximum Bayes factor across the possible quartets, as we are interested in whether *any* quartet shows compelling evidence for TSP.

Gene conversion, the unidirectional transfer of short tracts of DNA from a donor to an acceptor sequence, can affect the inferred trees. In particular, acceptor sequences may group more strongly with donor sequences than with sequences that share DNA by descent. This can make it difficult to distinguish trees influenced by trans-species polymorphism from those influenced by gene conversion. Thus, we inferred gene conversion tracts using *GENECONV* (***Sawyer, 1999***) and excluded significant gene-converted acceptor alleles from the Bayes factor calculations. While *GENECONV* cannot possibly infer all past events, this procedure should ameliorate any biasing effects. Additionally, we consider each exon separately; analyzing short tracts reduces the effect of

recombination on the tree (see our companion paper for more specifics (***Fortier and Pritchard, 2025***)). Note that the number of sequences available for comparison also affects the detectability of TSP. For example, if the only sequences available are from the same allelic lineage, they will coalesce more recently in the past than they would with alleles from a different lineage and would not show evidence for TSP. This means our method is well-suited to detect TSP when a diverse set of allele sequences are available, but it is conservative when there are few alleles to test. There were few available alleles for some non-classical genes, such as MHC-F, and some species, such as gibbon. This uneven sampling of taxa means that some TSPs cannot be detected at this time.

Bayes factors are shown in ***Figure 3*** and ***Figure 4***. See ***Figure 2—figure Supplement 1-Figure 2—figure Supplement 16***, ***Figure 3—figure Supplement 1-Figure 3—figure Supplement 12***, and ***Figure 4—figure Supplement 1-Figure 4—figure Supplement 10*** for examples of high-Bayes-factor quartets for each comparison.

At the Class I genes (***Figure 3***), MHC-C shows strong support for TSP within the African apes: human, chimpanzee, and gorilla. Having arisen fairly recently in the ancestor of human and orangutan, MHC-C has thus maintained some allelic lineages for most of its history. TSP has not previously been reported for this gene.

For MHC-A, Bayes factors vary considerably depending on exon and species pair. Past work suggests that this gene has had a long history of gene conversion affecting different exons, resulting in different evolutionary histories for different parts of the gene (***Hans et al., 2017***; ***Gleimer et al., 2011***; ***Adams and Parham, 2001***). Indeed, we excluded many MHC-A sequences from our Bayes factor calculations because they were identified as gene-converted in our *GENECONV* analysis or were previously suggested to be recombinants. As shown in ***Figure 3***, the lack of concordance in Bayes factors across the different exons for MHC-A is evidence for gene conversion, rather than balancing selection, being the most important factor in this gene's evolution. In contrast, the other gene groups generally show concordance in Bayes factors across exons. We interpret this as evidence in favor of TSP being the primary driver of the observed deep coalescence structure for MHC-B and -C (rather than recombination or gene conversion).

The non-classical Class I genes MHC-E, -F, and -G (bottom row of ***Figure 3***) are interspersed with the classical Class I genes in the MHC region (see ***Figure 1***), but their products have niche functions in innate immunity. Their indirect involvement in adaptive immunity means they experience different selective pressures. They exhibit lower polymorphism and $dN/dS < 1$, reflecting the fact that they have not been subject to the same pathogen-mediated balancing selection. The Bayes factors for all three of these genes show strong evidence against TSP, as expected. However, since there are fewer alleles available for the non-classical genes, we note that our method may be conservative here. Interestingly, despite its non-classical role, MHC-E has a known balanced polymorphism in humans; the two main alleles are at similar frequencies worldwide but may have different expression levels and peptide preferences (***Paganini et al., 2019***; ***Grant et al., 2020***). Our approach—meant to detect ancient TSP—does not reveal balancing selection in MHC-E, showing that this balanced polymorphism is young. For MHC-G, there were not enough sequences available to perform many of the tests (at least two from each species group are required). While we do not expect to see evidence of TSP in this gene, sequencing more alleles is necessary to address this.

Each Class II MHC molecule has an α and β component which are encoded by an A and B gene, respectively. Bayes factors for the Class IIA genes are shown in the top row of ***Figure 4***, while those for their Class IIB partners are shown in the bottom row. The non-classical MHC-DM and -DO molecules assist the classical Class II genes with peptide loading and are not believed to be shaped by balancing selection (***Heijmans et al., 2020***; ***Neefjes et al., 2011***). As expected, we see strong evidence against TSP between humans and all other primate species for these genes (first two columns of ***Figure 4***).

In contrast, we find evidence for deep TSP within the classical Class II genes. MHC-DPA1 shows TSP between human, chimpanzee, and gorilla in exon 2, but not in exon 3. We find that this TSP in MHC-DPA1 is less deep than has been previously suggested with non-Bayesian methods (***Ot-***

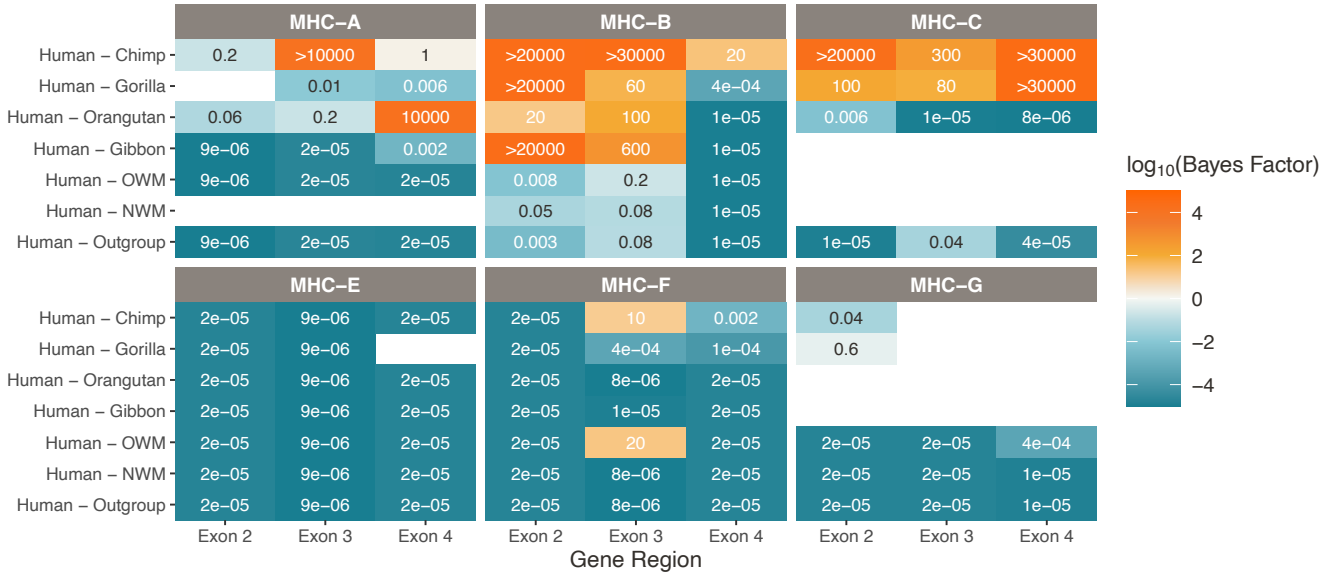

Figure 3. Strong support for TSP at Class I genes MHC-B and -C. Bayes factors computed over the set of BEAST trees indicate deep TSP. Different species comparisons are listed on the y-axis, and different gene regions are listed on the x-axis. Each table entry is colored and labeled with the maximum Bayes factor among all tested quartets of alleles belonging to that category. High Bayes factors (orange) indicate support for TSP among the given species for that gene region, while low Bayes factors (teal) indicate that alleles assort according to the species tree, as expected. Bayes factors above 100 are considered decisive. Tan values show poor support for either hypothesis, while white boxes indicate that there are not enough alleles in that category with which to calculate Bayes factors. MHC-A is not present in the NWMs, and MHC-C was not present before the human-orangutan ancestor, so it is not possible to calculate Bayes factors for these species comparisons.

Figure 3—figure supplement 1. MHC-A-Related *BEAST2* tree using sequences from exon 3, with top Bayes factors.

Figure 3—figure supplement 2. MHC-A-Related *BEAST2* tree using sequences from exon 4, with top Bayes factors.

Figure 3—figure supplement 3. MHC-B-Related *BEAST2* tree using sequences from exon 3, with top Bayes factors.

Figure 3—figure supplement 4. MHC-B-Related *BEAST2* tree using sequences from exon 4, with top Bayes factors.

Figure 3—figure supplement 5. MHC-C-Related *BEAST2* tree using sequences from exon 3, with top Bayes factors.

Figure 3—figure supplement 6. MHC-C-Related *BEAST2* tree using sequences from exon 4, with top Bayes factors.

Figure 3—figure supplement 7. MHC-E-Related *BEAST2* tree using sequences from exon 3, with top Bayes factors.

Figure 3—figure supplement 8. MHC-E-Related *BEAST2* tree using sequences from exon 4, with top Bayes factors.

Figure 3—figure supplement 9. MHC-F-Related *BEAST2* tree using sequences from exon 3, with top Bayes factors.

Figure 3—figure supplement 10. MHC-F-Related *BEAST2* tree using sequences from exon 4, with top Bayes factors.

Figure 3—figure supplement 11. MHC-G-Related *BEAST2* tree using sequences from exon 3, with top Bayes factors.

Figure 3—figure supplement 12. MHC-G-Related *BEAST2* tree using sequences from exon 4, with top Bayes factors.

Figure 3—figure supplement 13. Support for TSP between OWM clades for the Class I genes.

Figure 3—figure supplement 14. Support for TSP between NWM clades for the Class I genes.

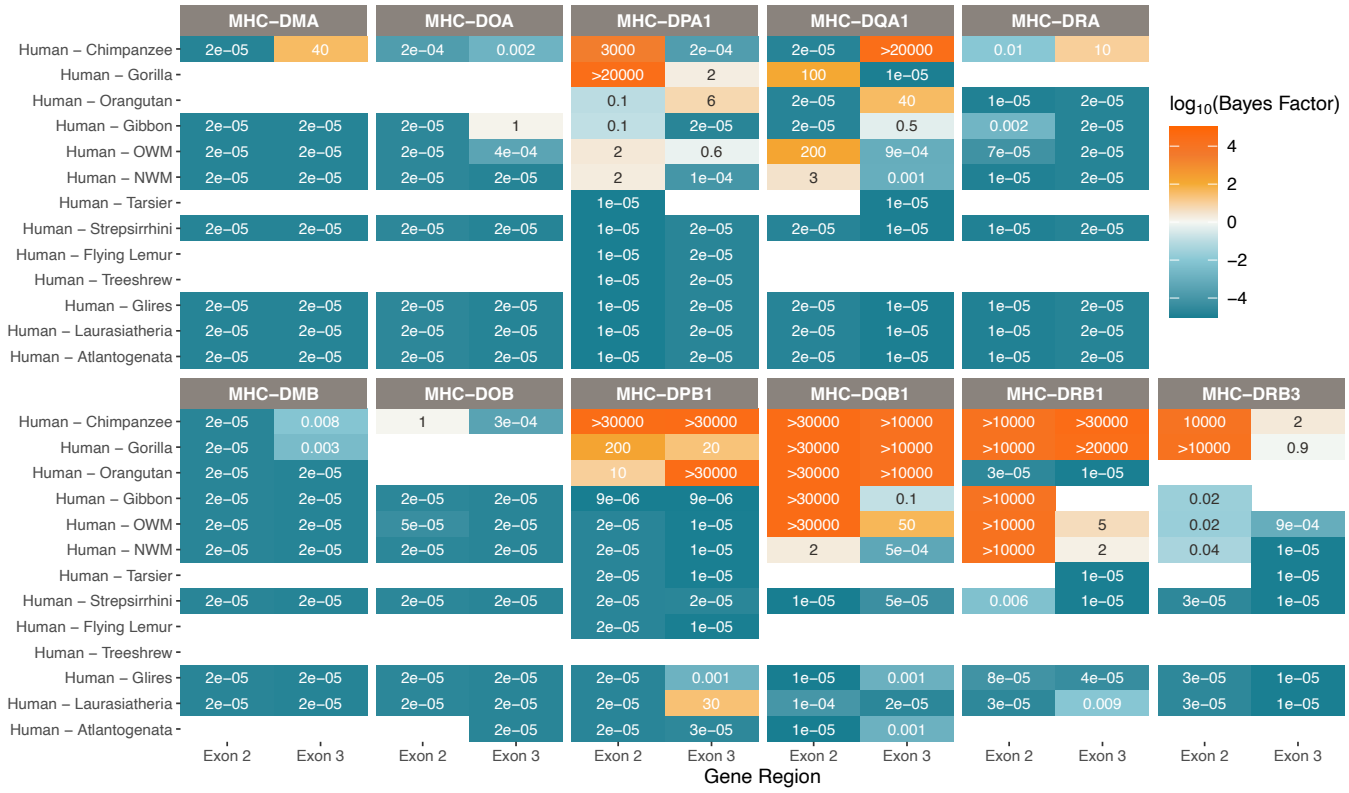

Figure 4. Strong support for TSP at the classical Class II genes. Bayes factors computed over the set of BEAST trees indicate deep TSP. Different species comparisons are listed on the y-axis, and different gene regions are listed on the x-axis. Each table entry is colored and labeled with the maximum Bayes factor among all tested quartets of alleles belonging to that category. High Bayes factors (orange) indicate support for TSP among the given species for that gene region, while low Bayes factors (teal) indicate that alleles assort according to the species tree, as expected. Bayes factors above 100 are considered decisive. Tan values show poor support for either hypothesis, while white boxes indicate that there are not enough alleles in that category with which to calculate Bayes factors.

Figure 4—figure supplement 1. MHC-DRA-Related *BEAST2* tree using sequences from exon 3, with top Bayes factors.

Figure 4—figure supplement 2. MHC-DQA-Related *BEAST2* tree using sequences from exon 3, with top Bayes factors.

Figure 4—figure supplement 3. MHC-DPA-Related *BEAST2* tree using sequences from exon 3, with top Bayes factors.

Figure 4—figure supplement 4. MHC-DMA-Related *BEAST2* tree using sequences from exon 3, with top Bayes factors.

Figure 4—figure supplement 5. MHC-DOA-Related *BEAST2* tree using sequences from exon 3, with top Bayes factors.

Figure 4—figure supplement 6. MHC-DRB-Related *BEAST2* tree using sequences from exon 3, with top Bayes factors.

Figure 4—figure supplement 7. MHC-DQB-Related *BEAST2* tree using sequences from exon 3, with top Bayes factors.

Figure 4—figure supplement 8. MHC-DPB-Related *BEAST2* tree using sequences from exon 3, with top Bayes factors.

Figure 4—figure supplement 9. MHC-DMB-Related *BEAST2* tree using sequences from exon 3, with top Bayes factors.

Figure 4—figure supplement 10. MHC-DOB-Related *BEAST2* tree using sequences from exon 3, with top Bayes factors.

Figure 4—figure supplement 11. Support for TSP between OWM clades for the Class II genes.

Figure 4—figure supplement 12. Support for TSP between NWM clades for the Class II genes.

ting and Bontrop, 1995), underscoring the importance of this methodology for handling the MHC. Meanwhile, its partner MHC-DPB1 shows strong evidence for TSP between human and orangutan in exon 3 and suggestive evidence in exon 2; our work provides the first evidence of TSP between humans and other apes for this gene (***Slierendregt et al., 1995***).

The MHC-DR genes behave somewhat differently than the other classical Class II molecules. While the α and β components of all the other molecules engage in exclusive binding, there are many different MHC-DRβ molecules which all bind to the same MHC-DRα. The MHC-DRA gene is conserved across species with little polymorphism, while the MHC-DRB region is highly variable both in gene content and allelic diversity. Consistent with this, Bayes factors for the MHC-DRA gene reveal strong evidence against TSP for all species pairs, while MHC-DRB1 shows strong evidence in favor of TSP between human, chimpanzee, gorilla, OWM, and even NWM in exon 2. However, because the Bayes factors only support TSP between humans and OWM/NWM in MHC-DRB1 in exon 2, but not in exon 3, this could mean alleles are not actually that ancient. We show in our companion paper that individual MHC-DRB genes are short-lived, and only three are truly orthologous between apes and OWM (***Fortier and Pritchard, 2025***). These pieces of evidence suggest previous work may have overstated the extent of TSP at this locus.

Remarkably, the MHC-DQB1 gene shows definitive evidence for TSP back to at least the ancestor of humans and OWM. While this result has been presented previously, we confirm it with decisive evidence (Bayes factor >100) for allelic lineages being maintained for over 31 million years (***Otting et al., 1992***, ***2002***; ***Loisel et al., 2006***; ***Simons et al., 2017***).

Many of our *BEAST* trees also showed intermingling of sequences from different species within the OWM or NWM (e.g. ***Figure 2—figure Supplement 4***), even if they did not form trans-species clades with ape sequences. This could indicate trans-species polymorphism *within* the OWM or NWM that is still ancient, but not old enough to be shared with the apes. Therefore, we also calculated Bayes factors across different clades of OWM and NWM (***Figure 3—figure Supplement 13***, ***Figure 3—figure Supplement 14***, ***Figure 4—figure Supplement 11***, and ***Figure 4—figure Supplement 12***). We see very strong evidence for TSP between all groups of OWM for MHC-DPA1, -DPB1, -DQA1, and -DQB1, indicating that allelic lineages at these genes have been maintained within the OWM for at least 19 million years. Unexpectedly, we also see evidence for TSP in some non-classical genes. MHC-E, a gene which is non-classical in humans and is presumed non-classical in OWM (yet is duplicated in some species), shows evidence for 15-MY-old TSP within the OWM. In non-classical MHC-DMB, we also observe TSP within the OWM as old as 11 MY. This could indicate differing roles for these genes in the OWM lineage, and functional experiments are needed to explore this. Due to the uncertainty of locus assignments for alleles of the OWM MHC-A, -B, and -DRB genes and of the NWM genes, we cannot make definitive conclusions about TSP within these clades for these other genes.

In summary, the phylogenetic analyses point to ancient TSP in classical genes MHC-B, -C, -DPA1, -DPB1, -DQB1, -DRB1, and -DRB3. Bayes factors for the non-classical genes MHC-E, -F, -G, -DMA, -DMB, -DOA, and -DOB do not indicate TSP involving apes at these loci—as expected for non-classical genes. However, we detected possible TSP at some of these genes within other clades, such as the OWM, hinting at possible functional differences. Overall, TSP is more ancient among the Class II genes than the Class I genes, consistent with the genes' older age.

From Evolution to Function.

Alongside the evidence for ancient TSP, the MHC region is also notable for its high rate of missense substitutions ($dN/dS > 1$) (***Hughes and Nei, 1988***, ***1989***) and its large number of GWAS hits for autoimmune and infectious diseases (***Buniello et al., 2019***; ***Kennedy et al., 2017***). We next aimed to understand how these observations relate to signals of TSP and known features of the MHC proteins.

To explore these questions, we first estimated the per-site evolutionary rates within each gene. As in our TSP analysis, we used the *BEAST2* package *SubstBMA*, which estimates evolutionary rates

at every site concurrently with a tree. We averaged these rates over all states in the chain to get per-site evolutionary rates for each site, then calculated their fold-change relative to the average rate among mostly-gap sites in the alignment ("baseline"; see Methods).

Figure 5A shows the substitution rate fold-change for each nucleotide along the concatenated coding sequence of Class I genes MHC-B, -C, and -E. In classical genes MHC-B and -C, nearly all the rapidly-evolving sites lie within exons 2 and 3, which encode the protein's peptide-binding domain. While exons 2 and 3 make up only ∼50% of the gene's length, they contain 94% and 90% of the sites evolving at more than 4 times the baseline evolutionary rate for the classical genes MHC-B and MHC-C, respectively. In MHC-B, exons 2 and 3 each show significantly higher proportions of rapidly-evolving sites compared to the "other" exons (exons in the gene excluding 2, 3, or 4), while the difference is not significant for MHC-C (***Figure 5—figure Supplement 2***). This result could reflect the relatively young age of MHC-C or its additional role as the dominant Class I molecule for interacting with KIRs (***Adams and Parham, 2001***; ***Guethlein et al., 2015***; ***Vollmers et al., 2021***; ***Piontkivska and Nei, 2003***).

In contrast to these classical genes, non-classical MHC-E primarily presents self-peptides for recognition by NK cell receptors, and its peptide-binding groove is tailored to accommodate a very specific set of self-peptides—leader peptides cleaved from other Class I MHC proteins during processing (***Miller et al., 2003***). As shown in ***Figure 5***A, this gene shows fewer rapidly-evolving sites than the classical genes. These sites are also relatively evenly distributed across the gene, with exons 2 and 3 (which cover ∼50% of the gene's length) containing 45% of the sites evolving at over 4 times the baseline evolutionary rate. Interestingly, exon 4—a non-peptide-binding exon of equal size—displays a significantly lower proportion of rapidly-evolving sites compared with the "other" exons (***Figure 5—figure Supplement 2***). These results support that MHC-E has been remarkably conserved across the primates and that its evolution may not be driven by differential peptide binding (***Heijmans et al., 2020***).

We then examined where the rapidly-evolving sites lie within the physical protein structures. To do this, we averaged the per-site rates within each codon to get per-amino-acid rates, then mapped these onto the known human protein structures. Unfortunately, there are few non-human primate protein structures in the Protein Data Bank (***Berman et al., 2000***), but the macaque structures we found were nearly identical to those of human. ***Figure 5***B shows structures for human HLA-B, -C, and -E; this view features the peptide (black) sitting in the peptide-binding groove (flanked on top and bottom by helices). In MHC-B and -C, rapidly-evolving amino acids (orange) tend to be located within the peptide-binding groove. To quantify this, we measured the minimum distance between each amino acid and the bound peptide. We averaged these distances over several structures, which are listed in the Methods (***Table 5***). For all three proteins, amino acids closer to the peptide have significantly higher evolutionary rates than amino acids further from the peptide, as shown in ***Figure 5***C (see also ***Figure 5—figure Supplement 4*** and ***Figure 5—figure Supplement 5***). The effect is much less pronounced in non-classical MHC-E, where even the amino acids closest to the peptide do not exhibit high evolutionary rates. These results are consistent with the expectation that rapid evolution and diversity at the classical MHC genes would be mediated by selective pressures for changes in peptide binding.

The rapidly-evolving sites for the Class II genes are shown in ***Figure 6***. Panel A shows the substitution rate fold-change for each nucleotide along the concatenated coding sequence of the Class II MHC-DRA, -DQA, -DRB, and -DQB gene groups. Both MHC-DQA and -DQB are extraordinarily polymorphic, but MHC-DRA is conserved compared to its multiple, highly-variable MHC-DRB partners. Indeed, ***Figure 6***A shows that rapidly-evolving sites are concentrated in binding-site-encoding exon 2 for MHC-DRB, -DQB, and to a lesser extent MHC-DQA. Exon 2, which makes up ∼30% of the coding region, contains 32% of sites evolving at more than twice the baseline rate in MHC-DRA, but 57% of such sites in MHC-DQA, 61% in MHC-DQB, and 73% in MHC-DRB. Comparing across exons, exon 2 contains a significantly higher proportion of rapidly-evolving sites compared to the "other" exons in classical MHC-DQA, -DQB, -DRB, and -DPB, but also—curiously—in non-classical MHC-DMA and

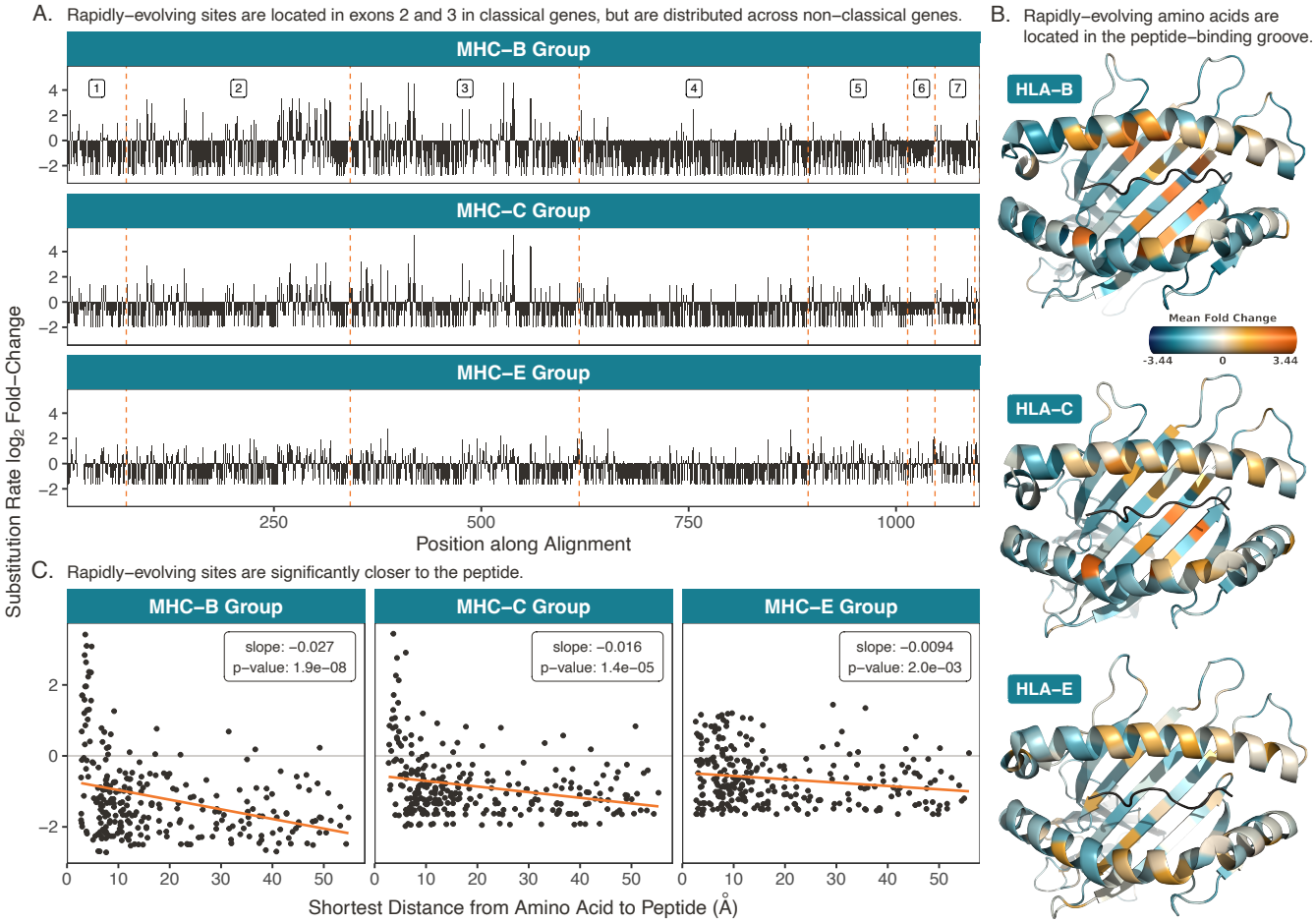

Figure 5. Rapidly-evolving sites in the Class I genes. A) Rapidly-evolving sites are primarily located in exons 2 and 3. Here, the exons are concatenated such that the cumulative position along the coding region is on the x-axis. The dashed orange lines denote exon boundaries. The three genes are aligned such that the same vertical position indicates an evolutionarily equivalent site. The y-axis shows the substitution rate at each site, expressed as a fold-change (the base-2 logarithm of each site's evolutionary rate divided by the mean rate among mostly-gap sites in each alignment; see Methods). **B)** Rapidly-evolving sites are located in each protein's peptide-binding pocket. Structures are Protein Data Bank (***Berman et al., 2000***) 4BCE (***Teze et al., 2014***) for HLA-B, 4NT6 (***Choo et al., 2014***) for HLA-C, and 7P4B (***Walters et al., 2022***) for HLA-E, with images created in *PyMOL* (***Sch, 2021***). Substitution rates for each amino acid are computed as the mean substitution rate of the three sites composing the codon. Orange indicates rapidly-evolving amino acids, while teal indicates conserved amino acids. **C)** Rapidly-evolving amino acids are significantly closer to the peptide than conserved amino acids. The y-axis shows the *BEAST2* substitution rate and the x axis shows the minimum distance to the bound peptide, measured in *PyMOL* (***Sch, 2021***). Each point is an amino acid, and distances are averaged over several structures (see ***Table 5***). The orange line is a linear regression of substitution rate on minimum distance, with slope and p-value annotated on each panel.

Figure 5—figure supplement 1. Rapidly-evolving sites along the coding region for all Class I genes.

Figure 5—figure supplement 2. Proportions of rapidly-evolving sites within each exon for Class I.

Figure 5—figure supplement 3. Rapidly-evolving sites mapped to Class I protein structures.

Figure 5—figure supplement 4. Evolutionary rate as a function of minimum distance to peptide for all Class I and Class II proteins.

Figure 5—figure supplement 5. Class I rapidly-evolving sites by binned distance to peptide.

-DMB (***Figure 6—figure Supplement 2*** and ***Figure 6—figure Supplement 4***). It is interesting that MHC-DM appears to be evolving rapidly in its binding-site-encoding exons, despite the fact that it is not thought to bind peptides. Instead, it is responsible for assisting with peptide loading onto the classical genes. Co-evolution with MHC-DR in particular seems possible; the interaction between the MHC-DM and -DR molecules depends on the affinity of the peptide trying to bind with MHC-DR. MHC-DM thus shapes the repertoire of peptides presented by MHC-DR, favoring high-affinity peptides (***Dijkstra and Yamaguchi, 2019***; ***Schulze and Wucherpfennig, 2012***). It is plausible that the host-pathogen evolution shaping the MHC-DRB genes has resulted in co-evolution of MHC-DMA and -DMB to maintain this regulatory interaction.

We again mapped the evolutionary rates onto human protein structures, shown in ***Figure 6***B. In each molecule, the α chain is positioned at the top and encompasses the upper helix forming the binding site, while the β chain is oriented toward the bottom and encompasses the lower helix. The peptide is shown in black. Rapidly-evolving sites are concentrated in each protein's binding site, although in MHC-DR this is more prominent in the bottom helix (MHC-DRB).

We then measured the distance between each amino acid and the bound peptide, shown in ***Figure 6***C. MHC-DRA did not show a significant relationship between evolutionary rate and distance, as expected by its relatively uniform distribution of evolutionary rates across the sequence (***Figure 6***A). For the other three proteins, amino acids closer to the peptide had significantly higher evolutionary rates. This held true for the classical MHC-DPA and -DPB genes as well (***Figure 5—figure Supplement 4***). Again, this is consistent with differential peptide binding and TCR responsiveness driving the diversity and long-term balancing selection at the classical genes. We could not measure peptide distances for non-classical MHC-DOA, -DOB, -DMA, and -DMB genes because they do not engage in peptide presentation.

Lastly, since the rapidly-evolving sites are likely involved in peptide binding, they also influence the response to pathogens and self-antigens, presumably affecting risk for infectious and autoimmune diseases. To bridge the gap between evolution and complex traits, we collected HLA fine-mapping studies for infectious, autoimmune, and other diseases, as well as for biomarkers and TCR phenotypes. These studies report associations between a disease or trait and classical HLA alleles, SNPs, and amino acid variants, often with multiple independent hits per gene. They demonstrate that HLA variation affects disease in complex ways—sometimes, a single variant is strongly associated with a condition, while other times, a combination of amino acids or even entire alleles (haplotypes) are the strongest indicators of disease susceptibility or protection.

We were interested in whether our rapidly-evolving amino acids from the *BEAST2* analysis corresponded with disease-associated amino acids from the literature. ***Table 1*** lists disease, trait, and TCR-phenotype associations for the most rapidly-evolving amino acids (fold-change ≥ 1) of the MHC-B group (see ***Table 1—source data 1*** for the other genes). The majority of rapidly-evolving positions in MHC-B have at least one association. Furthermore, all three classical Class I genes (MHC-A, -B, and -C) show a significant positive relationship between per-amino-acid evolutionary rate and the number of amino acid associations (***Figure 6—figure Supplement 7***). Interestingly, this relationship is not significant for the Class II genes, possibly because they evolve more slowly overall.

Thus, in summary, we find that rapid evolution has primarily targeted amino acids within the peptide-binding region of each gene, and that these specific positions are likely the primary drivers of phenotypic associations at the MHC locus.

Discussion

The MHC region contains the clearest signals of balancing and directional selection in mammalian genomes, including extreme diversity, ancient trans-species polymorphism, and high rates of non-synonymous evolution between allelic lineages. In humans, MHC/HLA variation is associated with risk for infectious and autoimmune diseases and many other traits, and HLA matching is critical for successful tissue transplantation (***Kennedy et al., 2017***; ***Smith et al., 2024***; ***Lee et al., 2007***).

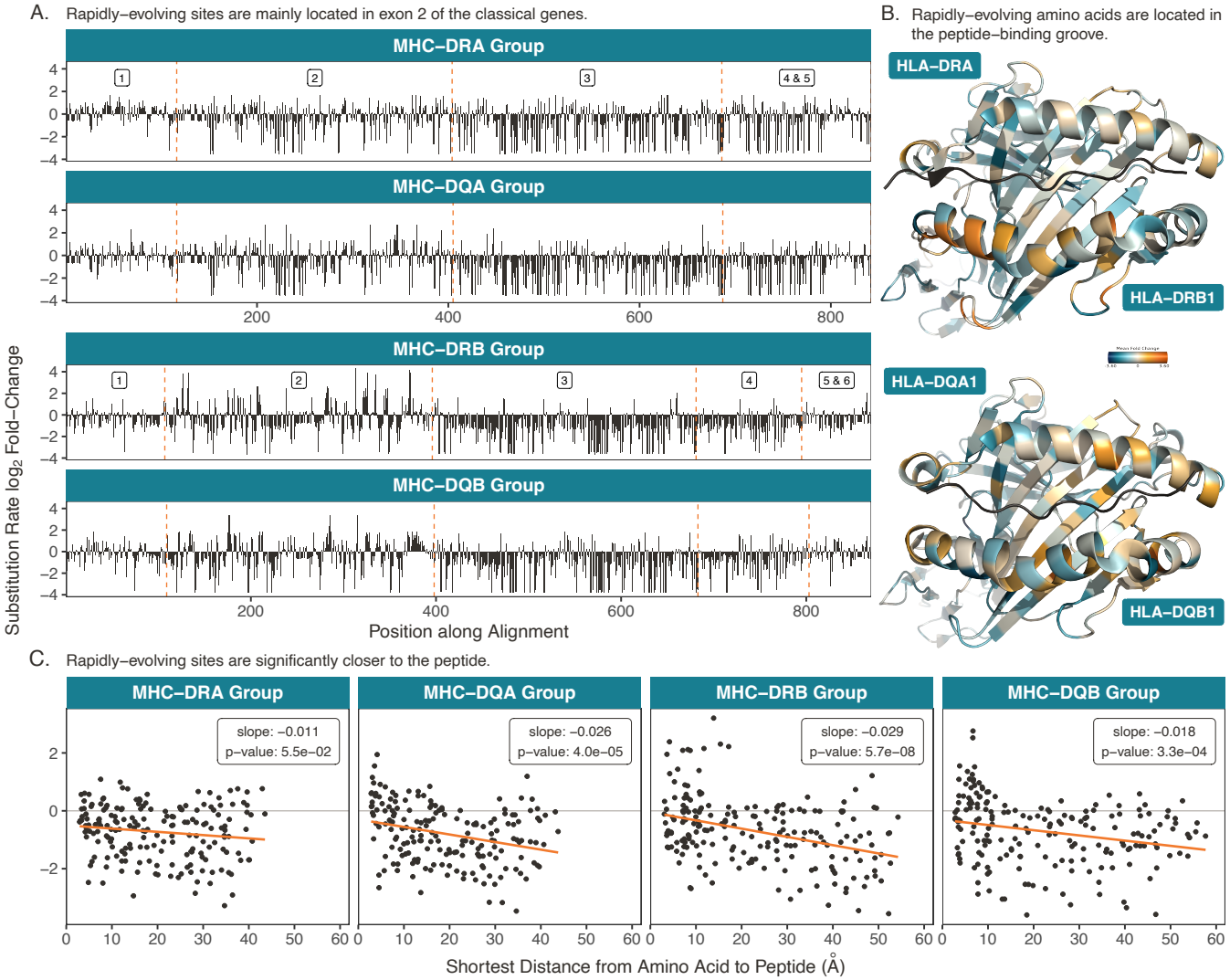

Figure 6. Rapidly-evolving sites in the Class II genes. A) Rapidly-evolving sites are primarily located in exon 2. Here, the exons are concatenated such that the cumulative position along the coding region is on the x-axis. The dashed orange lines denote exon boundaries. The α genes (top two plots) are aligned such that the same vertical position indicates an evolutionarily equivalent site; the same is true for the β genes (bottom two plots). The y-axis shows the substitution rate at each site, expressed as a fold-change (the base-2 logarithm of each site's evolutionary rate divided by the mean rate among mostly-gap sites in each alignment; see Methods). **B)** Rapidly-evolving sites are located in each protein's peptide-binding pocket. Structures are Protein Data Bank (***Berman et al., 2000***) 5JLZ (***Gerstner et al., 2016***) for HLA-DR and 2NNA (***Henderson et al., 2007***) for HLA-DQ, with images created in *PyMOL* (***Sch, 2021***). Substitution rates for each amino acid are computed as the mean substitution rate of the three sites composing the codon. Orange indicates rapidly-evolving amino acids, while teal indicates conserved amino acids. **C)** Rapidly-evolving amino acids are significantly closer to the peptide than conserved amino acids. The y-axis shows the *BEAST2* substitution rate and the x axis shows the minimum distance to the bound peptide, measured in *PyMOL* (***Sch, 2021***). Each point is an amino acid, and distances are averaged over several structures (see ***Table 5***). The orange line is a linear regression of substitution rate on minimum distance, with slope and p-value annotated on each panel.

Figure 6—figure supplement 1. Rapidly-evolving sites along the coding region for all Class IIA genes.

Figure 6—figure supplement 2. Proportions of rapidly-evolving sites within each exon for Class IIA.

Figure 6—figure supplement 3. Rapidly-evolving sites along the coding region for all Class IIB genes.

Figure 6—figure supplement 4. Proportions of rapidly-evolving sites within each exon for Class IIB.

Figure 6—figure supplement 5. Rapidly-evolving sites mapped to Class II protein structures.

Figure 6—figure supplement 6. Class II rapidly-evolving sites by binned distance to peptide.

Table 1. Rapidly-evolving amino acids in MHC-B and their trait and disease associations. Shown here are all amino acid positions in the MHC-B group evolving at more than twice the baseline rate (fold-change ≥ 1). Many corresponding positions in human HLA-B have associations with autoimmune or infectious diseases, biomarkers, or TCR phenotypes. Disease associations were collected from a literature search of HLA fine-mapping studies with over 1,000 cases (see Methods).

Amino Acid Position	Evol. Rate Fold-Change	Distance to Peptide (Å)	Associations
156	3.42	3.55	Chronic Hepatitis C (***Hirata et al., 2019***), HIV Set Point Viral Load (***Luo et al., 2021***), Asthma (***Sakaue et al., 2021***), Eosinophil Count (***Sakaue et al., 2021***), Hypothyroidism (***Sakaue et al., 2021***), Pediatric Asthma (***Sakaue et al., 2021***), Systolic Blood Pressure (***Sakaue et al., 2021***), Total Protein (***Sakaue et al., 2021***), TCR β Interaction Probability >50% (***Sharon et al., 2016***), Plasma Protein Levels of ADAM8, AGER, ASPSCR1, B2M, CCL16, CCL28, CCL4, CD200R1, CD5L, CDSN, CX3CL1, FCRL5, IGF2R, IL12A, IL12B, IL5RA, MICB, NUCB2, PDCD1, RARRES2, SFTPD, SIGLEC6, SNX2, TIMD4, TNFRSF4, TNR, TYRP1 (***Krishna et al., 2024***)
95	3.10	3.82	KLRF1 Plasma Protein Level (***Krishna et al., 2024***)
114	3.08	4.80	Rheumatoid Arthritis (***Sakaue et al., 2021***), Plasma Protein Levels of AIF1, CD1C, DDR1, IL15, LILRB2, MICB (***Krishna et al., 2024***)
116	2.84	3.44	Eosinophil Count (***Hirata et al., 2019***), HIV Control (***McLaren et al., 2012***), Angina (***Sakaue et al., 2021***), Allergic Rhinitis (***Waage et al., 2018***), Psoriasis (***Zhou et al., 2016***), Plasma Protein Levels of ADAM15, APOM, BTN2A1, CD1C, CFB, CXCL11, CXCL9, FLT4, GNLY, KLRF1, LILRB1, MICB, PLXDC2, TNF, TNFRSF13C, TNXB (***Krishna et al., 2024***)
70	2.64	3.71	Platelet (***Sakaue et al., 2021***), Plasma Protein Levels of CD8A, GZMA, MICB, NRP2 (***Krishna et al., 2024***)
97	2.37	4.29	Ankylosing Spondylitis (***Butler-Laporte et al., 2023***), HIV Set Point Viral Load (***Luo et al., 2021***), HIV Control (***McLaren et al., 2012***), Adult Height (***Sakaue et al., 2021***), Alkaline Phosphatase (***Sakaue et al., 2021***), Body Weight (***Sakaue et al., 2021***), C-reactive Protein (***Sakaue et al., 2021***), IgA Nephritis (***Sakaue et al., 2021***), Mean Arterial Pressure (***Sakaue et al., 2021***), Mean Corpuscular Hemoglobin (***Sakaue et al., 2021***), Pneumonia (***Tian et al., 2017***), Tonsillectomy (***Tian et al., 2017***), Plasma Protein Levels of ADGRE2, BTN3A2, CCL21, CCL3, CD1C, CD8A, CDSN, CPVL, DXO, EBI3, EFCAB14, HBEGF, HCG22, IL12A, IL12B, LILRB2, LRP1, LRPAP1, LTB, LY75, MANF, MANSC1, MICB, OSCAR, PLA2G10, PRTN3, SIGLEC10, STAB2, TEK, TNFSF13, ZNRD2 (***Krishna et al., 2024***)
24	2.35	4.68	Hepatic Cancer (***Sakaue et al., 2021***), Plasma Protein Levels of ADAM15, CXCL10, FCRL6, GZMB, MICB, TNFSF8 (***Krishna et al., 2024***)
163	2.23	4.13	Lung Cancer (Squamous Cell Carcinoma) (***Ferreiro-Iglesias et al., 2018***), Alanine Aminotransferase (***Sakaue et al., 2021***), TCR Expression (TRAV38-1) (***Sharon et al., 2016***), TCR α Interaction Probability >50% (***Sharon et al., 2016***), Plasma Protein Levels of DDR1, GZMA, LILRB1, MICB, NPTX1, SEPTIN3, TEK, WFDC2 (***Krishna et al., 2024***)
67	1.96	3.72	Graves' Disease (***Hirata et al., 2019***), HIV Set Point Viral Load (***Luo et al., 2021***), Asthma (***Sakaue et al., 2021***), Psoriasis (***Stuart et al., 2022***), Plasma Protein Levels of AMBP, C2, CD160, CD28, CD48, CFB , FCRL1, FCRL6, FRZB, GP1BB, LILRB1, LTA, LY96, NID1, SIGLEC9, SORT1, THBD, TNFRSF4, TNFSF13B, TNXB, TP53BP1, VCAM1 (***Krishna et al., 2024***)
152	1.96	3.53	JIA (Oligoarthritis/RF-negative Polyarthritis) (***Hinks et al., 2017***), Plasma Protein Levels of LTBR, MICB, PLXNA4, RARRES2 (***Krishna et al., 2024***)
63	1.71	2.94	HIV Control (***McLaren et al., 2012***), Skin Cancer (***Sakaue et al., 2021***), B2M Plasma Protein Level (***Krishna et al., 2024***)
99	1.70	3.00	Plasma Protein Levels of APOM, CRTAM, DXO, IL15, MICB, OSCAR (***Krishna et al., 2024***)
66	1.58	3.41	TNFSF11 Plasma Protein Level (***Krishna et al., 2024***)
69	1.56	4.69	Parkinson's Disease (***Naito et al., 2021***)
74	1.31	4.30	Chronic Sinusitis (***Sakaue et al., 2021***)
62	1.29	3.89	PGLYRP1 Plasma Protein Level (***Krishna et al., 2024***)
138	1.26	9.18	
9	1.20	3.36	Primary Biliary Cholangitis (***Darlay et al., 2018***), Systemic Lupus Erythematosus (***Molineros et al., 2019***), Rheumatoid Arthritis (***Raychaudhuri et al., 2012***), Hyperthyroidism (***Sakaue et al., 2021***), Monocyte Count (***Sakaue et al., 2021***), Serum Creatinine (***Sakaue et al., 2021***), Psoriasis (***Zhou et al., 2016***), Plasma Protein Levels of CD1C, CX3CL1, IL12B, LIPF, LTA, MICB, PDCD1, RGMA, SGSH, SLAMF7, TNFRSF8 (***Krishna et al., 2024***)
81	1.03	4.04	

Table 1—source data 1. Rapidly-evolving amino acids and their trait and disease associations for all studied genes.
Figure 6—figure supplement 7. Number of associations per amino acid as a function of evolutionary rate.

Despite its evolutionary and clinical importance, the extreme diversity of the MHC makes it challenging to study, and basic questions about its evolutionary history remain unresolved. While past work has suggested ultra-deep TSP at this locus, in this study we re-examined the region with modern, comprehensive data and a unified analysis framework. Using Bayesian evolutionary analysis, we report conclusive evidence for long-term TSP in seven classical genes, including between humans and OWM at MHC-DQB1. Thus, remarkably, allelic lineages at this gene have been maintained for at least 31 million years.

Our evidence for TSP at MHC-DQB1 spanning at least 31 million years places it among the most ancient examples of balancing selection known in any species, and almost certainly the oldest in primates. Aside from MHC, the deepest example within primates is at the ABO locus controlling blood type; it exhibits trans-species polymorphism between humans and gibbons, an age of 23 million years (***Ségurel et al., 2012***). In various chimpanzee species, *OAS1*, which helps inhibit viral replication, contains alleles up to 13MY old (***Ferguson et al., 2012***). TSP between chimpanzee and human includes *LAD1*, a protein that maintains cell cohesion (6MY) (***Teixeira et al., 2015***), retroviral transcription factor *TRIM5α* (4-7MY in apes and >8MY in OWM) (***Cagliani et al., 2010***; ***Newman et al., 2006***), and *ZC3HAV1*, an antiviral protein leading to viral RNA degradation (6MY) (***Cagliani et al., 2012***), among others (***Leffler et al., 2013***).

Looking more broadly across the tree of life, ancient trans-species polymorphism occurs widely, albeit rarely. Several of the oldest examples are found in the MHC locus: MHC polymorphisms have been maintained for 35MY in cetaceans (***Xu et al., 2009***), 40MY in herons (***Li et al., 2011***), 48MY in mole rats (***Kundu and Faulkes, 2007***), 70MY in tree frogs (***Zhao et al., 2013***), and over 105MY in salmonid fishes (***Kiryu et al., 2005***; ***Grimholt et al., 2015***). There are examples in non-MHC loci as well; in cyanobacteria, polymorphism at the HEP island controlling heterocyst function has been maintained for 74 million years (***Sano et al., 2018***), in plants, S-genes determining self-incompatibility exhibit TSP spanning 36 million years (***Ioerger et al., 1990***; ***Igic et al., 2006***; ***Fujii et al., 2016***), and in *Formica* ants, alleles at a supergene underlying colony queen number have been maintained for over 30 million years (***Purcell et al., 2021***).

Paradoxically, given the extremely long-lived balancing selection acting in these lineages, many authors have also reported strong directional selection at the MHC (***Brandt et al., 2018***; ***Nunes et al., 2021***; ***Bhatia et al., 2011***). Indeed, within the phylogeny we find that the most rapidly-evolving codons are substituted at around 2–4-fold the baseline rate, generating ample mutations upon which selection may act. For the classical genes (except MHC-DRA), these rapidly-evolving sites lie within the peptide binding regions of the corresponding proteins, usually very close to the peptide-contact surfaces. This does not hold true for the non-classical genes, supporting the fact that selection at the MHC is mainly driven by the peptide presentation pathway. Non-classical MHC-DMA and -DMB are a surprising exception, showing significantly elevated proportions of rapidly-evolving sites in exon 2 similarly to the classical genes (even though the MHC-DM molecule does not bind peptides). This pattern may be caused by its co-evolution with the classical Class II genes, and more research is needed to address this.

The primary role of classical MHC proteins is to present peptides for T cell recognition; we found that the same rapidly-evolving amino acids are associated with shaping T cell receptor (TCR) repertoires. Moreover, these amino acids are frequently associated with autoimmune and infectious diseases in HLA fine-mapping studies, particularly for Class I.

Taken together, we begin to see a comprehensive picture of the nature of primate MHC evolution. In response to rapidly-changing pathogen pressures, the PBRs of classical MHC proteins evolve to bind changing pathogen antigens and present them to TCRs. Broad lineages of MHC alleles are maintained over tens of millions of years by strong balancing selection, providing defense against a wide variety of different pathogens. Yet within these lineages, alleles turn over quickly in response to new specific threats. This reconciles evidence for TSP, the presence of thousands of alleles, and the existence of rapidly-evolving sites.

MHC molecules must evolve to detect pathogens with both specificity and sensitivity, and dis-

tinguishing self from non-self peptides is a challenging task. As MHC proteins evolve, there is an unavoidable flux between infection defense and autoimmune susceptibility. Additionally, many MHC proteins have roles in both innate and adaptive immunity. As a result, rapidly-evolving amino acids are associated with both infections and autoimmune conditions. In the future, disease studies within other primate species could provide insight into the trajectory of MHC evolution and might reveal evolutionary trade-offs. Perhaps balancing selection has kept the same amino acids disease-relevant across the entire primate evolutionary tree, or maybe the rapid turnover of MHC variation means different primate clades will have different disease associations.

One limitation of the data we used is that the vast majority of nonhuman MHC sequences were obtained via Sanger sequencing or next-generation sequencing methods. While highly accurate sequence-wise, these methods are limited by PCR-related technical artifacts such as heteroduplexes and chimeras. Allelic dropout is also a problem, because similar genes may not be amplified uniformly, resulting in alleles or entire genes being missed when the entire region is amplified simultaneously (***Cheng et al., 2022***). Additionally, MHC allele assignments require sequences from multiple exons, so the phasing of distant variants can make it difficult to assign alleles confidently (***Liu, 2021***). Many nonhuman MHC regions are also more complex than their human counterparts, containing unknown numbers of recently duplicated paralogs, copy number variants, and structural variants (***Cheng et al., 2022***; ***Heijmans et al., 2020***). This makes it difficult to assemble MHC sequences spanning the entire region and assign sequences to genes, which can make the inference of TSP challenging. For example, if sequences from two entirely different genes are thought to be from the same gene, one may falsely conclude that they are highly-diverged alleles and suspect TSP. We relied mostly on common alleles from the IPD-MHC/HLA database, which have been confirmed in multiple individuals often from different research groups. This helps reduce the issue of chimeric or heteroduplex alleles being wrongly considered to be highly-diverged alleles. We also did not assess TSP when orthology was too ambiguous, instead only calculating Bayes factors when our trees and other work strongly supported sequences coming from the same gene. Nevertheless, convergent evolution and shared history can still result in ambiguous gene assignments (***Dilthey, 2021***). Luckily, long-read sequencing of the MHC region has the potential to solve many of these issues. Oxford Nanopore and PacBio HiFi sequencing have already been used to obtain high-quality MHC sequences in humans (***Wenger et al., 2019***; ***Jain et al., 2018***; ***Liu, 2021***; ***Bruijnesteijn, 2023***), and researchers are beginning to explore its potential in non-model organisms (***Cheng et al., 2022***). These methods will be instrumental in increasing the number of alleles detected at MHC loci, resolving entire MHC haplotypes (thus facilitating detection of copy number and structural variation), and even detecting epigenetic modifications (***Bruijnesteijn, 2023***; ***Cheng et al., 2022***; ***Karl et al., 2023***; ***Viluma et al., 2017***; ***Fuselli et al., 2018***; ***Maibach et al., 2017***).

Although the primate MHC has been of interest to evolutionary biologists for more than 30 years, there is still much to be done to more fully document the evolution of the MHC genes within and between species. Moreover, we still have a limited understanding of how sequence changes map to functional differences among alleles, and how these relate to allele-specific profiles of pathogen protection (and autoimmunity risk). However, functional and computational advances will provide key opportunities for progress on these problems (***Radwan et al., 2020***; ***Vizcaíno et al., 2020***).

Methods and Materials

Data

We downloaded MHC allele nucleotide sequences for all human and nonhuman genes from the IPD Database (updated January 2023) (***Barker et al., 2023***; ***Maccari et al., 2017***, ***2020***). To supplement the alleles available in the database, we also collected nucleotide sequences from NCBI using the Entrez E-utilities with query "histocompatibility AND txidX AND alive[prop]", where X is a taxon of interest.

We wanted to provide "zoomed-in" versions of various subtrees within the multi-gene trees presented in our companion paper (***Fortier and Pritchard, 2025***). Thus, we included more species and more alleles per species than in the original trees. In each tree, we also included a "backbone" of sequences from the overall multi-gene tree to provide context for each expanded clade (lists of alleles provided as Supplementary Files).

For Class I, we expanded the following clades: 1) MHC-A-related genes (MHC-A group), 2) MHC-B-related genes (MHC-B group), 3) MHC-C-related genes (MHC-C group), 4) MHC-E-related genes (MHC-E group), 5) MHC-F-related genes (MHC-F group), and 6) MHC-G-related genes (MHC-G group). For Class IIA, we expanded: 1) MHC-DMA-related genes (MHC-DMA group), 2) MHC-DOA-related genes (MHC-DOA group), 3) MHC-DRA-related genes (MHC-DRA group), 4) MHC-DPA-related genes (MHC-DPA group), and 5) MHC-DQA-related genes (MHC-DQA group). For Class IIB, we expanded: 1) MHC-DMB-related genes (MHC-DMB group), 2) MHC-DOB-related genes (MHC-DOB group), 3) MHC-DRB-related genes (MHC-DRB group), 4) MHC-DPB-related genes (MHC-DPB group), and 5) MHC-DQB-related genes (MHC-DQB group). These sets were inclusive of all orthologs and paralogs of a given human gene across all species we included (see our companion paper for more information (***Fortier and Pritchard, 2025***)). For example, the MHC-A group includes human HLA-A and its 1:1 orthologs in the apes, the expanded MHC-A and -AG paralogs of the OWM, chimpanzee specific Patr-AL, gorilla-specific Gogo/Gobe-OKO, orangutan-specific Poab/Popy-Ap, and pseudogenes MHC-H and -Y. ***Table 2-Table 4*** provide an overview of which genes from which species were included in each of these named groups. See Supplementary Files for lists of all alleles included within each group.

We aligned each group separately using *MUSCLE* (***Edgar, 2004***) with default settings and manually adjusted, following the alignments we already produced for the multi-gene trees in our companion paper (***Fortier and Pritchard, 2025***).

Table 2. **Data summary for Class I.** Each row represents a species, and each column represents a gene group. Each cell lists the number of alleles included for each gene represented by that gene group. Bolded entries are “backbone" sequences that are included in every group.

Clade	Species Group	Species	Latin Name	Pref.	MHC-A Group	MHC-B Group	MHC-C Group	MHC-E Group	MHC-F Group	MHC-G Group
Ape	Human	Human	*Homo sapiens*	Hosa	63 -A, **1 -A**, 4 -H, **1 -H**, 2 -Y, **1 -B**, **1 -L**, **1 -C**, **1 -E**, **1 -F**, **1 -G**, **1 -J**, **1 -K**, **1 -V**, **1 -W**	**1 -A**, **1 -H**, 91 -B, **1 -B**, **1 -L**, **1 -C**, **1 -E**, **1 -F**, **1 -G**, **1 -J**, **1 -K**, **1 -V**, **1 -W**	**1 -A**, **1 -H**, **1 -B**, **1 -L**, 90 -C, **1 -C**, **1 -E**, **1 -F**, **1 -G**, **1 -J**, **1 -K**, **1 -V**, **1 -W**	**1 -A**, **1 -H**, **1 -B**, **1 -L**, **1 -C**, 15 -E, **1 -E**, **1 -F**, **1 -G**, **1 -J**, **1 -K**, **1 -V**, **1 -W**	**1 -A**, **1 -H**, **1 -B**, **1 -L**, **1 -C**, **1 -E**, 10 -F, **1 -F**, **1 -G**, **1 -J**, **1 -K**, **1 -V**, **1 -W**	**1 -A**, **1 -H**, **1 -B**, **1 -L**, **1 -C**, **1 -E**, **1 -F**, 17 -G, **1 -G**, **1 -J**, **1 -K**, **1 -V**, **1 -W**
	Chimpanzee	Bonobo	*Pan paniscus*	Papa	10 -A, 1 -H	26 -B	11 -C	1 -E	1 -F	2 -G
		Chimpanzee	*Pan troglodytes*	Patr	30 -A, 3 -A/AL/OKO, 1 -H	48 -B	28 -C	2 -E	3 -F	1 -G
	Gorilla	Eastern gorilla	*Gorilla beringei*	Gobe	1 -A/AL/OKO	1 -B	1 -C			
		Western gorilla	*Gorilla gorilla*	Gogo	4 -A, 4 -A/AL/OKO, 1 -H, 3 -Y	10 -B, 3 -B	8 -C	2 -E	3 -F	2 -G

Continuation of Table 2										
Clade	**Species Group**	**Species**	**Latin Name**	**Pref.**	**MHC-A Group**	**MHC-B Group**	**MHC-C Group**	**MHC-E Group**	**MHC-F Group**	**MHC-G Group**
	Orangutan	Sumatran orangutan	*Pongo abelii*	Poab	5 -A/AL/OKO, 1 -H	12 -B	2 -C	1 -E	1 -F	1 -G
		Bornean orangutan	*Pongo pygmaeus*	Popy	12 -A/AL/OKO, 1 -H, 7 NA	20 -B	5 -C	1 -E	1 -F	
	Gibbon	Lar gibbon	*Hylobates lar*	Hyla	2 -A	1 -B				
		Silvery gibbon	*Hylobates moloch*	Hymo	1 -A	1 unknown		1 -E	1 -F	
		Northern w.c. gibbon	*Nomascus leucogenys*	Nole	1 -A	2 unknown		1 -E	1 -F	
OWM	Baboon	Olive baboon	*Papio anubis*	Paan	1 -A, 1 -AG	1 -B		1 -E	3 -F	1 -AG
		Hamadryas baboon	*Papio hamadryas*	Paha		2 -B				
		Yellow baboon	*Papio cynocephalus*	Pacy				1 -E		
	Gelada	Gelada	*Theropithecus gelada*	Thge	1 -A, 1 -AG			1 -E	1 -F	1 -G
	Mangabey	Sooty mangabey	*Cercocebus atys*	Ceat	3 -A, 1 -AG	1 -B, 1 -I		5 -E	5 -F	
	Drill	Drill	*Mandrillus leucophaeus*	Male				1 -E	1 -F	2 -G
	Macaque	Crab-eating macaque	*Macaca fascicularis*	Mafa	**1 -L**, **1 -V**, **1 -W**, 1 -A8	1 -B, **1 -L**, **1 -V**, **1 -W**	**1 -L**, **1 -V**, **1 -W**	**1 -L**, 17 -E, **1 -V**, **1 -W**	**1 -L**, 24 -F, **1 -V**, **1 -W**	**1 -L**, 9 -G, **1 -V**, **1 -W**
		Rhesus macaque	*Macaca mulatta*	Mamu	8 -A, **1 -A**, 5 -AG, **1 -AG**, **1 -B**, **1 -I**, **1 -E**, **1 -F**, **1 -G**, **1 -J**, **1 -K**	**1 -A**, **1 -AG**, 9 -B, **1 -B**, **1 -I**, **1 -E**, **1 -F**, **1 -G**, **1 -J**, **1 -K**	**1 -A**, **1 -AG**, **1 -B**, **1 -I**, **1 -E**, **1 -F**, **1 -G**, **1 -J**, **1 -K**	**1 -A**, **1 -AG**, **1 -B**, **1 -I**, 30 -E, **1 -E**, **1 -F**, **1 -G**, **1 -J**, **1 -K**	**1 -A**, **1 -AG**, **1 -B**, **1 -I**, **1 -E**, 18 -F, **1 -F**, **1 -G**, **1 -J**, **1 -K**	**1 -A**, 5 -AG, **1 -AG**, **1 -B**, **1 -I**, **1 -E**, **1 -F**, 4 -G, **1 -G**, **1 -J**, **1 -K**
		Stump-tailed macaque	*Macaca arctoides*	Maar		1 -B				
		Assam macaque	*Macaca assamensis*	Maas		1 -B				
		N. pig-tailed macaque	*Macaca leonina*	Malo		1 -B				
		S. pig-tailed macaque	*Macaca nemestrina*	Mane		2 -B		10 -E	7 -F	

Continuation of Table 2										
Clade	**Species Group**	**Species**	**Latin Name**	**Pref.**	**MHC-A Group**	**MHC-B Group**	**MHC-C Group**	**MHC-E Group**	**MHC-F Group**	**MHC-G Group**
		Tibetan macaque	*Macaca thibetana*	Math		1 -B		1 -E	1 -F	1 -G
	Grivet	Grivet	*Chlorocebus aethiops*	Chae						2 -G
	Vervet Monkey	Vervet monkey	*Chlorocebus pygerythrus*	Chpy		2 -B				
	Green Monkey	Green monkey	*Chlorocebus sabaeus*	Chsa	1 -A, 1 -AG, 1 -A8	1 -B		5 -E	1 -F	1 -AG
	Guenon	Blue monkey	*Cercopithecus mitis*	Cemi		2 -B				
	Colobus	Angola colobus	*Colobus angolensis*	Coan	1 -AG			2 -E	1 -F	
		Ugandan red colobus	*Piliocolobus tephroscelles*	Pite				1 -E	1 -F	1 -G
	Langur	Francois' langur	*Trachypithecus francoisi*	Trfr	1 -A, 1 -AG			1 -E	1 -F	1 -G
	Snub-Nosed Monkey	Golden snub-nosed monkey	*Rhinopithecus roxellana*	Rhro	1 -A, 1 -AG			1 -E		1 -G
		B&W snub-nosed mon.	*Rhinopithecus bieti*	Rhbi				1 -E		
NWM	Tamarin	Cotton-top tamarin	*Saguinus oedipus*	Saoe				1 -E	4 -F	9 -G, 1 -PS, 3 -N1/3/4
		Brown-mantled tamarin	*Leontocebus fuscicollis*	Lefu						5 -G
		Golden lion tamarin	*Leontopithecus rosalia*	Lero						2 -G
		White-lipped tamarin	*Saguinus labiatus*	Sala						9 -G
	Marmoset	Common marmoset	*Callithrix jacchus*	Caja	**1 -B**, **1 -E**, **1 -F**, **1 -G**	8 -B, **1 -B**, **1 -E**, **1 -F**, **1 -G**	**1 -B**, **1 -E**, **1 -F**, **1 -G**	**1 -B**, 2 -E, **1 -E**, **1 -F**, **1 -G**	**1 -B**, **1 -E**, 17 -F, **1 -F**, **1 -G**	**1 -B**, **1 -E**, **1 -F**, 76 -G, **1 -G**, 1 -PS
	Night Monkey	Three-striped night monkey	*Aotus trivirgatus*	Aotr				1 -E		3 -G, 1 -PS
		Gray-bellied night monkey	*Aotus lemurinus*	Aole					5 -F	

Continuation of Table 2										
Clade	**Species Group**	**Species**	**Latin Name**	**Pref.**	**MHC-A Group**	**MHC-B Group**	**MHC-C Group**	**MHC-E Group**	**MHC-F Group**	**MHC-G Group**
		Nancy Ma's night monkey	*Aotus nancymaae*	Aona					3 -F	1 -B, 7 -G
	Capuchin	Panamanian white-faced capuchin	*Cebus imitator*	Ceim				1 -E	1 -F	6 -G, 1 unknown
		Tufted capuchin	*Sapajus apella*	Saap				1 -E	1 -F	4 -G, 2 unknown
	Squirrel Monkey	Black-capped squirrel monkey	*Saimiri boliviensis*	Sabo				3 -E	2 -F	1 -B, 3 -G, 1 unknown
		Common squirrel monkey	*Saimiri sciureus*	Sasc						1 -G
	Spider Monkey	White-bellied spider monkey	*Ateles belzebuth*	Atbe		1 -B		1 -E		3 -G
		Black-headed spider monkey	*Ateles fusciceps*	Atfu		1 -B		2 -E		9 -G
	Saki	White-faced saki	*Pithecia pithecia*	Pipi		1 -B		1 -E		4 -G
Tarsier	Tarsier	Philippine tarsier	*Carlito syrichta*	Casy	**1 unknown**	**1 unknown**	**1 unknown**	**1 unknown**	**1 unknown**	**1 unknown**
Strepsirrhini	Lemur	Ring-tailed lemur	*Lemur catta*	Leca	**1 unknown**	**1 unknown**	**1 unknown**	**1 unknown**	**1 unknown**	**1 unknown**

Table 3. **Data summary for Class IIA.** Each row represents a species, and each column represents a gene group. Each cell lists the number of alleles included for each gene represented by that gene group. Bolded entries are "backbone" sequences that are included in every group.

Clade	**Species Group**	**Species**	**Latin Name**	**Pref.**	**MHC-DPA Group**	**MHC-DQA Group**	**MHC-DRA Group**	**MHC-DMA Group**	**MHC-DOA Group**
Ape	Human	Human	*Homo sapiens*	Hosa	22 -DPA, **2 -DPA**, **2 -DQA**, **1 -DRA**, **1 -DMA**, **1 -DOA**	**2 -DPA**, 22 -DQA, **2 -DQA**, **1 -DRA**, **1 -DMA**, **1 -DOA**	**2 -DPA**, **2 -DQA**, 4 -DRA, **1 -DRA**, **1 -DMA**, **1 -DOA**	**2 -DPA**, **2 -DQA**, **1 -DRA**, 8 -DMA, **1 -DMA**, **1 -DOA**	**2 -DPA**, **2 -DQA**, **1 -DRA**, **1 -DMA**, 14 -DOA, **1 -DOA**
	Chimpanzee	Bonobo	*Pan paniscus*	Papa	1 -DPA	2 -DQA	1 -DRA	1 -DMA	1 -DOA
		Chimpanzee	*Pan troglodytes*	Patr	5 -DPA	6 -DQA	3 -DRA	1 -DMA	1 -DOA
	Gorilla	Western gorilla	*Gorilla gorilla*	Gogo	3 -DPA	10 -DQA	1 -DRA	1 -DMA	1 -DOA

Continuation of Table 3									
Clade	**Species Group**	**Species**	**Latin Name**	**Pref.**	**MHC-DPA Group**	**MHC-DQA Group**	**MHC-DRA Group**	**MHC-DMA Group**	**MHC-DOA Group**
	Orang-utan	Sumatran orangutan	*Pongo abelii*	Poab	4 -DPA	6 -DQA	4 -DRA	1 -DMA	1 -DOA
		Bornean orangutan	*Pongo pygmaeus*	Popy	4 -DPA	4 -DQA	2 -DRA		
	Gibbon	Silvery gibbon	*Hylobates moloch*	Hymo	1 -DPA	3 -DQA	1 -DRA	1 -DMA	1 -DOA
		Northern white-cheeked gibbon	*Nomascus leucogenys*	Nole	1 -DPA	2 -DQA	1 -DRA	1 -DMA	1 -DOA
		Lar gibbon	*Hylobates lar*	Hyla		6 -DQA			
OWM	Baboon	Olive baboon	*Papio anubis*	Paan	13 -DPA	8 -DQA	3 -DRA	1 -DMA	1 -DOA
		Hamadryas baboon	*Papio hamadryas*	Paha	1 -DPA	3 -DQA			
		Yellow baboon	*Papio cynocephalus*	Pacy		7 -DQA			
		Guinea baboon	*Papio papio*	Papp		4 -DQA			
	Gelada	Gelada	*Theropithecus gelada*	Thge	2 -DPA	3 -DQA	1 -DRA	1 -DMA	1 -DOA
	Mangabey	Sooty mangabey	*Cercocebus atys*	Ceat	2 -DPA	2 -DQA	1 -DRA	1 -DMA	1 -DOA
		Black crested mangabey	*Lophocebus aterrimus*	Loat		1 -DQA			
	Drill	Drill	*Mandrillus leucophaeus*	Male	1 -DPA	2 -DQA	1 -DRA	1 -DMA	1 -DOA
	Macaque	Crab-eating macaque	*Macaca fascicularis*	Mafa	30 -DPA, **1 -DMA**, **1 -DOA**	11 -DQA, **1 -DMA**, **1 -DOA**	16 -DRA, **1 -DMA**, **1 -DOA**	7 -DMA, **1 -DMA**, **1 -DOA**	**1 -DMA**, 6 -DOA, **1 -DOA**
		Northern pig-tailed macaque	*Macaca leonina*	Malo	6 -DPA	8 -DQA	5 -DRA	2 -DMA	7 -DOA
		Rhesus macaque	*Macaca mulatta*	Mamu	22 -DPA, **1 -DPA**, **2 -DQA**, **1 -DRA**	**1 -DPA**, 9 -DQA, **2 -DQA**, **1 -DRA**	**1 -DPA**, **2 -DQA**, 12 -DRA, **1 -DRA**	**1 -DPA**, **2 -DQA**, **1 -DRA**, 4 -DMA	**1 -DPA**, **2 -DQA**, **1 -DRA**, 1 -DOA
		Southern pig-tailed macaque	*Macaca nemestrina*	Mane	14 -DPA	10 -DQA	11 -DRA	1 -DMA	1 -DOA
		Tibetan macaque	*Macaca thibetana*	Math	7 -DPA	1 -DQA	1 -DRA	10 -DMA	
		Stump-tailed macaque	*Macaca arctoides*	Maar	1 -DPA	2 -DQA			
	Grivet	Grivet	*Chlorocebus aethiops*	Chae		6 -DQA			
	Green Monkey	Green monkey	*Chlorocebus sabaeus*	Chsa	5 -DPA	2 -DQA	1 -DRA		1 -DOA

Continuation of Table 3									
Clade	**Species Group**	**Species**	**Latin Name**	**Pref.**	**MHC-DPA Group**	**MHC-DQA Group**	**MHC-DRA Group**	**MHC-DMA Group**	**MHC-DOA Group**
	Guenon	Blue monkey	*Cercopithecus mitis*	Cemi		5 -DQA			
		De Brazza's monkey	*Cercopithecus neglectus*	Cene		2 -DQA			
	Colobus	Angola colobus	*Colobus angolensis*	Coan		2 -DQA	1 -DRA	1 -DMA	1 -DOA
		Ugandan red colobus	*Piliocolobus tephrosceles*	Pite	1 -DPA	1 -DQA	1 -DRA	1 -DMA	1 -DOA
		Mantled guereza	*Colobus guereza*	Cogu		1 -DQA			
	Langur	Francois' langur	*Trachypithecus francoisi*	Trfr	1 -DPA	1 -DQA	1 -DRA	1 -DMA	1 -DOA
	Snub-Nosed Monkey	Black-and-white snub-nosed monkey	*Rhinopithecus bieti*	Rhbi			1 -DRA	1 -DMA	1 -DOA
		Golden snub-nosed monkey	*Rhinopithecus roxellana*	Rhro	1 -DPA	1 -DQA	1 -DRA	1 -DMA	1 -DOA
NWM	Tamarin	Cotton-top tamarin	*Saguinus oedipus*	Saoe		4 -DQA			
	Marmoset	Common marmoset	*Callithrix jacchus*	Caja	**1 -DPA**, **2 -DQA**, **1 -DMA**, **1 -DOA**	**1 -DPA**, 6 -DQA, **2 -DQA**, **1 -DMA**, **1 -DOA**	**1 -DPA**, **2 -DQA**, 1 -DRA, **1 -DMA**, **1 -DOA**	**1 -DPA**, **2 -DQA**, **1 -DMA**, **1 -DOA**	**1 -DPA**, **2 -DQA**, **1 -DMA**, **1 -DOA**
	Night Monkey	Nancy Ma's night monkey	*Aotus nancymaae*	Aona	1 -DPA, **1 -DRA**	6 -DQA, **1 -DRA**	2 -DRA, **1 -DRA**	**1 -DRA**, 1 -DMA	**1 -DRA**, 1 -DOA
		Gray-bellied night monkey	*Aotus lemurinus*	Aole		3 -DQA			
		Spix's night monkey	*Aotus vociferans*	Aovo			3 -DRA		
	Capuchin	Panamanian white-faced capuchin	*Cebus imitator*	Ceim	1 -DPA	3 -DQA	1 -DRA	1 -DMA	1 -DOA
		Tufted capuchin	*Sapajus apella*	Saap	1 -DPA	3 -DQA	1 -DRA	1 -DMA	1 -DOA
	Squirrel Monkey	Black-capped squirrel monkey	*Saimiri boliviensis*	Sabo		2 -DQA	1 -DRA	1 -DMA	1 -DOA
		Common squirrel monkey	*Saimiri sciureus*	Sasc	3 -DPA				
Tarsier	Tarsier	Philippine tarsier	*Carlito syrichta*	Casy	3 -DPA	2 -DQA	1 -DRA	1 -DMA	1 -DOA

Continuation of Table 3									
Clade	**Species Group**	**Species**	**Latin Name**	**Pref.**	**MHC-DPA Group**	**MHC-DQA Group**	**MHC-DRA Group**	**MHC-DMA Group**	**MHC-DOA Group**
Strepsirrhini	Lemur	Ring-tailed lemur	*Lemur catta*	Leca	**1 -DPA**, **1 -DQA**, **1 -DRA**, **1 -DMA**, **1 -DOA**	**1 -DPA**, **1 -DQA**, **1 -DRA**, **1 -DMA**, **1 -DOA**	**1 -DPA**, **1 -DQA**, **1 -DRA**, **1 -DMA**, **1 -DOA**	**1 -DPA**, **1 -DQA**, **1 -DRA**, **1 -DMA**, **1 -DOA**	**1 -DPA**, **1 -DQA**, **1 -DRA**, **1 -DMA**, **1 -DOA**
		Gray mouse lemur	*Microcebus murinus*	Mimu	1 -DPA	1 -DQA	1 -DRA	1 -DMA	1 -DOA
	Loris	Sunda slow loris	*Nycticebus coucang*	Nyco	1 -DPA		2 -DRA	1 -DMA	1 -DOA
	Galago	Northern greater galago	*Otolemur garnettii*	Otga	1 -DPA	1 -DQA	1 -DRA	1 -DMA	1 -DOA
	Sifaka	Coquerel's sifaka	*Propithecus coquereli*	Prco	2 -DPA	1 -DQA	1 -DRA	1 -DMA	1 -DOA
Flying Lemur	Flying Lemur	Sunda flying lemur	*Galeopterus variegatus*	Gava	2 -DPA		1 -DRA	1 -DMA	1 -DOA
Tree Shrew	Tree Shrew	Chinese tree shrew	*Tupaia chinensis*	Tuch	4 -DPA	1 -DQA	1 -DRA	1 -DMA	1 -DOA
Glires	Rodent	Groundhog	*Marmota monax*	Mamo	1 -DPA, **1 -DPA**	**1 -DPA**	**1 -DPA**, 1 -DRA	**1 -DPA**, 1 -DMA	**1 -DPA**, 1 -DOA
		Brown rat	*Rattus norvegicus*	Rano	**1 -DQA**, **1 -DRA**, **1 -DMA**, **1 -DOA**	2 -DQA, **1 -DQA**, **1 -DRA**, **1 -DMA**, **1 -DOA**	**1 -DQA**, 2 -DRA, **1 -DRA**, **1 -DMA**, **1 -DOA**	**1 -DQA**, **1 -DRA**, **1 -DMA**, **1 -DOA**	**1 -DQA**, **1 -DRA**, **1 -DMA**, 1 -DOA, **1 -DOA**
	Pika	Plateau pika	*Ochotona curzoniae*	Occu	2 -DPA	2 -DQA	1 -DRA	1 -DMA	1 -DOA
		American pika	*Ochotona princeps*	Ocpr	2 -DPA	1 -DQA	1 -DRA	1 -DMA	1 -DOA
Laurasiatheria	Artiodactyla	Bactrian camel	*Camelus bactrianus*	Caba	1 -DPA	1 -DQA		1 -DMA	1 -DOA
		Wild boar	*Sus scrofa*	SLA	**1 -DQA**, **1 -DRA**, **1 -DMA**, **1 -DOA**	1 -DQA, **1 -DQA**, **1 -DRA**, **1 -DMA**, **1 -DOA**	**1 -DQA**, 3 -DRA, **1 -DRA**, **1 -DMA**, **1 -DOA**	**1 -DQA**, **1 -DRA**, 4 -DMA, **1 -DMA**, **1 -DOA**	**1 -DQA**, **1 -DRA**, **1 -DMA**, 1 -DOA, **1 -DOA**
		Even-toed ungulates	*Bos sp.*	BoLA		2 -DQA			
		Domestic yak	*Bos grunniens*	Bogr		2 -DQA			
		Water buffalo	*Bubalus bubalis*	Bubu		2 -DQA			
		Sheep	*Ovis aries*	Ovar		4 -DQA	3 -DRA		

Continuation of Table 3									
Clade	**Species Group**	**Species**	**Latin Name**	**Pref.**	**MHC-DPA Group**	**MHC-DQA Group**	**MHC-DRA Group**	**MHC-DMA Group**	**MHC-DOA Group**
		Dromedary camel	*Camelus dromedarius*	Cadr			1 -DRA		
		Bighorn sheep	*Ovis canadensis*	Ovca			3 -DRA		
	Ferungulata	Sea otter	*Enhydra lutris*	Enlu		1 -DQA	1 -DRA	1 -DMA	1 -DOA
		Cat	*Felis catus*	Feca			1 -DRA	1 -DMA	1 -DOA
		Sunda pangolin	*Manis javanica*	Maja		1 -DQA	1 -DRA	1 -DMA	1 -DOA
		Cougar	*Puma concolor*	Puco	1 -DPA			1 -DMA	1 -DOA
		Jaguarundi	*Puma yagouaroundi*	Puya	1 -DPA		1 -DRA	1 -DMA	1 -DOA
		Steller sea lion	*Eumetopias jubatus*	Euju	1 -DPA	1 -DQA			
		Horse	*Equus caballus*	Eqca		5 -DQA	3 -DRA		
	Bat	Big brown bat	*Eptesicus fuscus*	Epfu	1 -DPA	2 -DQA	1 -DRA	1 -DMA	
		Kuhl's pipistrelle	*Pipistrellus kuhlii*	Piku	1 -DPA	1 -DQA	1 -DRA	1 -DMA	
		Large flying fox	*Pteropus vampyrus*	Ptva		2 -DQA	1 -DRA		1 -DOA
	Mole	Star-nosed mole	*Condylura cristata*	Cocr		3 -DQA			1 -DOA
Atlantogenata	Xenarthra	Linnaeus's two-toed sloth	*Choloepus didactylus*	Chdi	1 -DPA	1 -DQA	1 -DRA	1 -DMA	1 -DOA
		Nine-banded armadillo	*Dasypus novemcinctus*	Dano	1 -DPA	2 -DQA	1 -DRA	1 -DMA	1 -DOA
	Afrotheria	Cape golden mole	*Chrysochloris asiatica*	Chas	1 -DPA		1 -DRA	1 -DMA	1 -DOA
		Cape elephant shrew	*Elephantulus edwardii*	Eled	**1 -DPA**	**1 -DPA**, 1 -DQA	**1 -DPA**, 1 -DRA	**1 -DPA**, 1 -DMA	**1 -DPA**, 1 -DOA
		Aardvark	*Orycteropus afer*	Oraf	1 -DPA	1 -DQA		1 -DMA	1 -DOA
		West Indian manatee	*Trichechus manatus*	Trma	2 -DPA	1 -DQA	1 -DRA	1 -DMA	
		Lesser hedgehog tenrec	*Echinops telfairi*	Ecte			1 -DRA		1 -DOA

Table 4. **Data summary for Class IIB.** Each row represents a species, and each column represents a gene group. Each cell lists the number of alleles included for each gene represented by that gene group. Bolded entries are "backbone" sequences that are included in every group.

Clade	Species Group	Species	Latin Name	Pref.	MHC-DPB Group	MHC-DQB Group	MHC-DRB Group	MHC-DMB Group	MHC-DOB Group
Ape	Human	Human	*Homo sapiens*	Hosa	74 -DPB, **2 -DPB**, **2 -DQB**, **9 -DRB**, **1 -DMB**, **1 -DOB**	**2 -DPB**, 24 -DQB, **2 -DQB**, **9 -DRB**, **1 -DMB**, **1 -DOB**	**2 -DPB**, **2 -DQB**, 46 -DRB, **9 -DRB**, **1 -DMB**, **1 -DOB**	**2 -DPB**, **2 -DQB**, **9 -DRB**, 6 -DMB, **1 -DMB**, **1 -DOB**	**2 -DPB**, **2 -DQB**, **9 -DRB**, **1 -DMB**, 14 -DOB, **1 -DOB**
	Chimp-anzee	Bonobo	*Pan paniscus*	Papa	8 -DPB	2 -DQB	5 -DRB	2 -DMB	1 -DOB
		Chimpanzee	*Pan troglodytes*	Patr	6 -DPB	9 -DQB	17 -DRB	2 -DMB	2 -DOB
	Gorilla	Western gorilla	*Gorilla gorilla*	Gogo	5 -DPB	10 -DQB	7 -DRB	2 -DMB	1 -DOB
	Orangutan	Sumatran orangutan	*Pongo abelii*	Poab	5 -DPB	6 -DQB	7 -DRB	1 -DMB	1 -DOB
		Bornean orangutan	*Pongo pyg-maeus*	Popy	5 -DPB	3 -DQB	7 -DRB	3 -DMB	
	Gibbon	Silvery gib-bon	*Hylobates moloch*	Hymo	1 -DPB	2 -DQB	5 -DRB	1 -DMB	1 -DOB
		Northern white-cheeked gibbon	*Nomascus leucogenys*	Nole	1 -DPB	2 -DQB		1 -DMB	1 -DOB
		Lar gibbon	*Hylobates lar*	Hyla		4 -DQB			
OWM	Baboon	Olive baboon	*Papio anubis*	Paan	5 -DPB	5 -DQB	11 -DRB	1 -DMB	
		Hamadryas baboon	*Papio hamadryas*	Paha		3 -DQB	1 -DRB		
		Chacma baboon	*Papio ursinus*	Paur			8 -DRB		
	Gelada	Gelada	*Theropithecus gelada*	Thge	2 -DPB	1 -DQB	3 -DRB	1 -DMB	1 -DOB
	Mangabey	Sooty mangabey	*Cercocebus atys*	Ceat	3 -DPB	2 -DQB	1 -DRB	1 -DMB	1 -DOB
	Drill	Drill	*Mandrillus leucophaeus*	Male	1 -DPB		1 -DRB	1 -DMB	1 -DOB
	Mandrill	Mandrill	*Mandrillus sphinx*	Masp			10 -DRB		
	Macaque	Crab-eating macaque	*Macaca fascic-ularis*	Mafa	7 -DPB, **2 -DRB**, **1 -DMB**, **1 -DOB**	5 -DQB, **2 -DRB**, **1 -DMB**, **1 -DOB**	6 -DRB, **2 -DRB**, **1 -DMB**, **1 -DOB**	**2 -DRB**, 4 -DMB, **1 -DMB**, **1 -DOB**	**2 -DRB**, **1 -DMB**, 6 -DOB, **1 -DOB**
		Northern pig-tailed macaque	*Macaca leon-ina*	Malo	5 -DPB	5 -DQB	3 -DRB	2 -DMB	3 -DOB

Continuation of Table 4									
Clade	**Species Group**	**Species**	**Latin Name**	**Pref.**	**MHC-DPB Group**	**MHC-DQB Group**	**MHC-DRB Group**	**MHC-DMB Group**	**MHC-DOB Group**
		Rhesus macaque	*Macaca mulatta*	Mamu	5 -DPB, **2 -DPB**, **1 -DQB**, **4 -DRB**	**2 -DPB**, 4 -DQB, **1 -DQB**, **4 -DRB**	**2 -DPB**, **1 -DQB**, 10 -DRB, **4 -DRB**	**2 -DPB**, **1 -DQB**, **4 -DRB**, 5 -DMB	**2 -DPB**, **1 -DQB**, **4 -DRB**, 1 -DOB
		Southern pig-tailed macaque	*Macaca nemestrina*	Mane	5 -DPB	5 -DQB	6 -DRB	1 -DMB	1 -DOB
		Tibetan macaque	*Macaca thibetana*	Math	13 -DPB	6 -DQB	1 -DRB	1 -DMB	1 -DOB
		Stump-tailed macaque	*Macaca arctoides*	Maar		5 -DQB	2 -DRB		
		Japanese macaque	*Macaca fuscata*	Mafu			3 -DRB		
		Lion-tailed macaque	*Macaca silenus*	Masi			3 -DRB		
	Grivet	Grivet	*Chlorocebus aethiops*	Chae		3 -DQB	6 -DRB		
	Green Monkey	Green monkey	*Chlorocebus sabaeus*	Chsa	3 -DPB	4 -DQB	7 -DRB	1 -DMB	1 -DOB
	Colobus	Angola colobus	*Colobus angolensis*	Coan	2 -DPB	2 -DQB		1 -DMB	1 -DOB
		Ugandan red colobus	*Piliocolobus tephrosceles*	Pite	1 -DPB	1 -DQB	3 -DRB	1 -DMB	1 -DOB
	Langur	Francois' langur	*Trachypithecus francoisi*	Trfr	2 -DPB	1 -DQB	3 -DRB	1 -DMB	1 -DOB
		Gray langur	*Semnopithecus entellus*	Seen	1 -DPB				
	Snub-Nosed Monkey	Black-and-white snub-nosed monkey	*Rhinopithecus bieti*	Rhbi				1 -DMB	1 -DOB
		Golden snub-nosed monkey	*Rhinopithecus roxellana*	Rhro	1 -DPB	1 -DQB	2 -DRB	1 -DMB	1 -DOB
NWM	Tamarin	Cotton-top tamarin	*Saguinus oedipus*	Saoe	3 -DPB	4 -DQB	8 -DRB		
		White-lipped tamarin	*Saguinus labiatus*	Sala			3 -DRB		
	Marmoset	Common marmoset	*Callithrix jacchus*	Caja	1 -DPB, **1 -DPB**, **2 -DQB**, **1 -DRB**, **1 -DMB**, **1 -DOB**	**1 -DPB**, 3 -DQB, **2 -DQB**, **1 -DRB**, **1 -DMB**, **1 -DOB**	**1 -DPB**, **2 -DQB**, 3 -DRB, **1 -DRB**, **1 -DMB**, **1 -DOB**	**1 -DPB**, **2 -DQB**, **1 -DRB**, **1 -DMB**, **1 -DOB**	**1 -DPB**, **2 -DQB**, **1 -DRB**, **1 -DMB**, **1 -DOB**
	Night Monkey	Nancy Ma's night monkey	*Aotus nancymaae*	Aona	4 -DPB	3 -DQB	6 -DRB	1 -DMB	1 -DOB

Continuation of Table 4									
Clade	**Species Group**	**Species**	**Latin Name**	**Pref.**	**MHC-DPB Group**	**MHC-DQB Group**	**MHC-DRB Group**	**MHC-DMB Group**	**MHC-DOB Group**
		Gray-bellied night monkey	*Aotus lemurinus*	Aole	3 -DPB	1 -DQB			
		Azara's night Monkey	*Aotus azarae*	Aoaz			2 -DRB		
		Black-headed night monkey	*Aotus nigriceps*	Aoni			3 -DRB		
		Three-striped night monkey	*Aotus trivirgatus*	Aotr			3 -DRB		
		Spix's night monkey	*Aotus vociferans*	Aovo			3 -DRB		
	Capuchin	Panamanian white-faced capuchin	*Cebus imitator*	Ceim	1 -DPB	3 -DQB	1 -DRB	1 -DMB	1 -DOB
		Tufted capuchin	*Sapajus apella*	Saap	1 -DPB	4 -DQB	3 -DRB	1 -DMB	
	Squirrel Monkey	Black-capped squirrel monkey	*Saimiri boliviensis*	Sabo	1 -DPB	3 -DQB		1 -DMB	1 -DOB
		Common squirrel monkey	*Saimiri sciureus*	Sasc			2 -DRB		
	Spider Monkey	White-bellied spider monkey	*Ateles belzebuth*	Atbe			2 -DRB		
	Howler Monkey	Guatemalan black howler	*Alouatta pitta*	Alpi			2 -DRB		
	Saki	White-faced saki	*Pithecia pithecia*	Pipi			3 -DRB		
Tarsier	Tarsier	Philippine tarsier	*Carlito syrichta*	Casy	2 -DPB	1 -DQB	2 -DRB	1 -DMB	1 -DOB
Strepsirrhini	Lemur	Ring-tailed lemur	*Lemur catta*	Leca	1 -DPB, **1 -DPB**, **1 -DQB**, **1 -DRB**, **1 -DMB**, **1 -DOB**	**1 -DPB**, **1 -DQB**, **1 -DRB**, **1 -DMB**, **1 -DOB**	**1 -DPB**, **1 -DQB**, **1 -DRB**, **1 -DMB**, **1 -DOB**	**1 -DPB**, **1 -DQB**, **1 -DRB**, **1 -DMB**, **1 -DOB**	**1 -DPB**, **1 -DQB**, **1 -DRB**, **1 -DMB**, **1 -DOB**
		Gray mouse lemur	*Microcebus murinus*	Mimu	1 -DPB	3 -DQB	2 -DRB	1 -DMB	1 -DOB
	Loris	Sunda slow loris	*Nycticebus coucang*	Nyco	1 -DPB				
	Galago	Northern greater galago	*Otolemur garnettii*	Otga	1 -DPB	1 -DQB	1 -DRB	1 -DMB	1 -DOB
	Sifaka	Coquerel's sifaka	*Propithecus coquereli*	Prco	1 -DPB	1 -DQB		1 -DMB	1 -DOB
Flying Lemur	Flying Lemur	Sunda flying lemur	*Galeopterus variegatus*	Gava	2 -DPB		2 -DRB	1 -DMB	1 -DOB

Continuation of Table 4									
Clade	**Species Group**	**Species**	**Latin Name**	**Pref.**	**MHC-DPB Group**	**MHC-DQB Group**	**MHC-DRB Group**	**MHC-DMB Group**	**MHC-DOB Group**
Tree Shrew	Tree Shrew	Chinese tree shrew	*Tupaia chinensis*	Tuch	1 -DPB			1 -DMB	1 -DOB
Glires	Rodent	Groundhog	*Marmota monax*	Mamo	1 -DPB, **1 -DPB**	**1 -DPB**	**1 -DPB**	**1 -DPB**, 1 -DMB	**1 -DPB**
		Brown rat	*Rattus norvegicus*	Rano	**1 -DQB**, **1 -DRB**, **1 -DMB**, **1 -DOB**	2 -DQB, **1 -DQB**, **1 -DRB**, **1 -DMB**, **1 -DOB**	**1 -DQB**, 3 -DRB, **1 -DRB**, **1 -DMB**, **1 -DOB**	**1 -DQB**, **1 -DRB**, 1 -DMB, **1 -DMB**, **1 -DOB**	**1 -DQB**, **1 -DRB**, **1 -DMB**, **1 -DOB**
	Pika	American pika	*Ochotona princeps*	Ocpr		1 -DQB	1 -DRB	1 -DMB	
		Plateau pika	*Ochotona curzoniae*	Occu	1 -DPB	2 -DQB			1 -DOB
Laurasiatheria	Artiodactyla	Bactrian camel	*Camelus bactrianus*	Caba				1 -DMB	1 -DOB
		Dromedary camel	*Camelus dromedarius*	Cadr	**1 -DPB**	**1 -DPB**	**1 -DPB**	**1 -DPB**	**1 -DPB**
		Wild boar	*Sus scrofa*	SLA	**1 -DQB**, **1 -DRB**, **1 -DMB**, **1 -DOB**	2 -DQB, **1 -DQB**, **1 -DRB**, **1 -DMB**, **1 -DOB**	**1 -DQB**, 4 -DRB, **1 -DRB**, **1 -DMB**, **1 -DOB**	**1 -DQB**, **1 -DRB**, **1 -DMB**, **1 -DOB**	**1 -DQB**, **1 -DRB**, **1 -DMB**, 2 -DOB, **1 -DOB**
		Even-toed ungulates	*Bos sp.*	BoLA		1 -DQB	2 -DRB		
		Water buffalo	*Bubalus bubalis*	Bubu		1 -DQB			
		Wild Bactrian camel	*Camelus ferus*	Cafe		1 -DQB			
		Sheep	*Ovis aries*	Ovar		6 -DQB	1 -DRB		
		Goat	*Capra hircus*	Cahi			2 -DRB		
		Bighorn sheep	*Ovis canadensis*	Ovca			1 -DRB		
	Ferungulata	Horse	*Equus caballus*	Eqca		6 -DQB	3 -DRB	5 -DMB	3 -DOB
		Sunda pangolin	*Manis javanica*	Maja				1 -DMB	1 -DOB
		Cougar	*Puma concolor*	Puco	1 -DPB			1 -DMB	
		Jaguarundi	*Puma yagouaroundi*	Puya				1 -DMB	
		Northern elephant seal	*Mirounga angustirostris*	Mian			1 -DRB		1 -DOB
		Sea otter	*Enhydra lutris*	Enlu	1 -DPB	1 -DQB			
		Steller sea lion	*Eumetopias jubatus*	Euju		1 -DQB			

Continuation of Table 4									
Clade	**Species Group**	**Species**	**Latin Name**	**Pref.**	**MHC-DPB Group**	**MHC-DQB Group**	**MHC-DRB Group**	**MHC-DMB Group**	**MHC-DOB Group**
	Bat	Big brown bat	*Eptesicus fuscus*	Epfu		2 -DQB	1 -DRB	1 -DMB	
		Large flying fox	*Pteropus vampyrus*	Ptva		1 -DQB			1 -DOB
		Kuhl's pipistrelle	*Pipistrellus kuhlii*	Piku	1 -DPB	1 -DQB			
	Mole	Star-nosed mole	*Condylura cristata*	Cocr		2 -DQB	1 -DRB	1 -DMB	1 -DOB
Atlantogenata	Xenarthra	Linnaeus's two-toed sloth	*Choloepus didactylus*	Chdi	2 -DPB	1 -DQB		1 -DMB	1 -DOB
		Nine-banded armadillo	*Dasypus novemcinctus*	Dano	1 -DPB				
	Afrotheria	Aardvark	*Orycteropus afer*	Oraf		1 -DQB			1 -DOB
		Cape elephant shrew	*Elephantulus edwardii*	Eled	1 -DPB				
		West Indian manatee	*Trichechus manatus*	Trma	1 -DPB				
		Lesser hedgehog tenrec	*Echinops telfairi*	Ecte			1 -DRB		

Nucleotide Diversity

The classical MHC region is defined as chr6:28,510,120-33,480,577 (GRCh38) (***MHC, 2022***). Nucleotide diversity (π) was calculated on modern human data from the 1000 Genomes Project (***Auton et al., 2015***) using *VCFtools (0.1.15)* (***Danecek et al., 2011***). For the entire MHC region (***Figure 1***A), π was calculated in 5000bp sliding windows with a step size of 1000bp. For each gene separately (***Figure 1***B-C and ***Figure 1—figure Supplement 1***), π was calculated in 50bp sliding windows with a step size of 10bp.

Bayesian Phylogenetic Analysis

We constructed phylogenetic trees using *BEAST2* (***Bouckaert et al., 2014***, ***2019***) with package *SubstBMA* (***Wu et al., 2013***). *SubstBMA* implements a spike-and-slab mixture model that simultaneously estimates the phylogenetic tree, the number of site partitions, the assignment of sites to partitions, the nucleotide substitution model, and a rate multiplier for each partition. Since we were chiefly interested in the partitions and their rate multipliers, we used the RDPM model as described by ***Wu et al.*** (***2013***). In the RDPM model, the number of nucleotide substitution model categories is fixed to 1, so that all sites, regardless of rate partition, share the same estimated nucleotide substitution model. This reduces the number of parameters to be estimated and ensures that only evolutionary rates vary across site partitions, reducing overall model complexity. We used an uncorrelated lognormal relaxed molecular clock because in reality, evolutionary rates vary among branches (***Bergeron et al., 2023***).

Priors. For the Dirichlet process priors, we used the informative priors constructed by ***Wu et al.*** (***2013***) for their mammal dataset. This is appropriate because they include several of the same species and their mammals span approximately the same evolutionary time that we consider in

our study. We also use their same priors on tree height, base rate distribution, and a Yule process coalescent prior. We did not specify a calibration point—a time-based prior on a node—because we did not expect our sequences to group according to the species tree.

Running *BEAST2*. We aligned sequences across genes and species and ran *BEAST2* on various subsets of the alignment. For the Class I gene groups (MHC-A group, MHC-B group, MHC-C group, MHC-E group, MHC-F group, and MHC-G group), we repeated the analysis for 1) exon 2 only (PBR), 2) exon 3 only (PBR), 3) exon 4 only (non-PBR), and 4) exons 1, 5, 6, 7, and 8 together (non-PBR; "other" exons). For the Class IIA gene groups (MHC-DMA group, MHC-DOA group, MHC-DRA group, MHC-DPA group, and MHC-DQA group), we used 1) exon 2 only (PBR), 2) exon 3 only (non-PBR), and 3) exons 1, 3, 4, and 5 together (non-PBR; "other" exons). For Class IIB gene groups (MHC-DMB group, MHC-DOB group, MHC-DRB group, MHC-DPB group, and MHC-DQB group), we analyzed 1) exon 2 only (PBR), 2) exon 3 only (non-PBR), and 3) exons 1, 3, 4, and 5 together (non-PBR; "other" exons). In the following, each "analysis" is a collection of *BEAST2* runs using one of these sets of exons of a particular gene group.

The xml files we used to run *BEAST2* were based closely on those used for the mammal dataset with the RDPM model and uncorrelated relaxed clock in ***Wu et al.*** (***2013***)(https://github.com/jessiewu/substBMA/blob/master/examples/mammal/mammal_rdpm_uc.xml). Running a model with per-site evolutionary rate categories and a relaxed clock means there are many parameters to estimate. Along with the large number of parameters, the highly-polymorphic and often highly-diverged sequences in our alignments makes it difficult for *BEAST2* to explore the state space. Thus, we undertook considerable effort to ensure good mixing and convergence of the chains. First, we employed coupled MCMC for all analyses. Coupled MCMC is essentially the same as the regular MCMC used in *BEAST2*, except that it uses additional "heated" chains with increased acceptance probabilities that can traverse unfavorable intermediate states and allow the main chain to move away from an inferior local optimum (***Müller and Bouckaert, 2020***). Using coupled MCMC both speeds up *BEAST2* runs and improves mixing and convergence. We used four heated chains for each run with a delta temperature of 0.025. Second, we ran each *BEAST2* run for 40,000,000 states, discarding the first 4,000,000 states as burn-in and sampling every 10,000 states. Third, we ran at least 8 independent replicates of each analysis. The replicates use the exact same alignment, but explore state space independently and thus are useful for improving the effective sample size of tricky parameters. As recommended by *BEAST2*, we examined all replicates in *Tracer* version 1.7.2 (***Rambaut et al., 2018***) to ensure that they were sampling from the same parameter distributions and had reached convergence. We excluded replicates for which this was not true, as these chains were probably stuck in suboptimal state space. Additionally, Tracer provides estimates of the effective sample size (ESS) for the combined set of states from all chosen replicates, and we required that the ESS be larger than 100 for all parameters. If there were fewer than 4 acceptable replicates or if the ESS was below 100 for any parameter, we re-ran more independent replicates of the analysis until these requirements were satisfied. We obtained between 5 and 18 acceptable replicates per analysis (median 8).

For some analyses, computational limitations prevented *BEAST2* from being able to reach 40,000,000 states. In these situations, more replicates (of fewer states) were usually required to achieve good mixing and convergence. The first 4,000,000 states from each run were still discarded as burn-in even though this represented more than 10% of states in these cases.

This stringent procedure ensured that all of the replicates were exploring the same parameter space and were converging upon the same global optimum, allowing the $\geq$4 independent runs to be justifiably combined. We combined the acceptable replicates using *LogCombiner* version 2.6.7 (***Drummond and Rambaut, 2007***), which aggregates the results across all states. We then used the combined results to perform downstream analyses.

The xml files required to run *BEAST2* are provided as Supplementary Files.

Phylogenetic Trees

After combining acceptable replicates, we obtained 12,382 - 64,818 phylogenies per group/gene region (mean 34,499). These trees are provided as Supplementary Files. We used *TreeAnnotator* version 2.6.3 (***Drummond and Rambaut, 2007***) to summarize each set of possible trees as a maximum clade credibility tree, which is the tree that maximizes the sum of posterior clade probabilities. Since *BEAST2* samples trees from the posterior, one could in principle perform model testing directly from the posterior samples; the complete set of trees can typically be reduced to a smaller 95% credible set of trees representing the "true" tree (***BEA, 2024***). However, given the high complexity of the model space, all our posterior trees were unique, meaning this was not possible in practice. (Since the prior over tree topologies is unstructured, this effectively puts minuscule prior weight on trees with monophyly. Thus, sampling directly from the posterior provides an unacceptably high-variance estimator.)

Gene Conversion

We calculated gene conversion fragments using *GENECONV* version 1.81a (***Sawyer, 1999***) on each alignment. It is generally advisable to use only synonymous sites when running the program on a protein-coding alignment, since silent sites within the same codon position are likely to be correlated. However, the extreme polymorphism in these MHC genes meant there were too few silent sites to use in the analysis. Thus, we considered all sites but caution that this could slightly overestimate the lengths of our inferred conversion tracts. However, we were mainly concerned with the presence of a conversion tract rather than its precise length. For each alignment, we ran *GENECONV* with options *ListPairs*, *Allouter*, *Numsims* $= 10000$, and *Startseed* $= 310$. We collected all inferred "Global Inner" (GI) fragments with $sim\_pval < 0.05$ (this is pre-corrected for multiple comparisons by the program). GI fragments represent a possible gene conversion event between two sequences in the alignment.

For each GI fragment, we made an educated guess on which sequence was the donor sequence and which was the acceptor sequence by comparing how sequences clustered using sites within the fragment bounds to how sequences clustered using sites outside of the fragment bounds (but within the same exon). Sequences that were confidently determined to be acceptor sequences were excluded from the Bayes factor analyses for the relevant exon because their non-tree-like behavior has the potential to bias results. For sequence pairs where the direction could not be determined, both sequences were excluded from subsequent analyses.

Bayes Factors

Because we could not perform model testing directly on the full phylogenies, we used an alternative approach—computing Bayes factors for TSP within manageable subsets of the data, i.e., quartets of alleles. Let D be a sample of phylogenies from *BEAST2*, sampled from the posterior with uniform prior. For a chosen species, we have a null hypothesis H, that human alleles form a monophyletic group, and an alternative hypothesis, H^c, that is also the complement of H—that the human alleles do not form a monophyletic group. The Bayes factor, K, is a ratio quantifying support for the alternative hypothesis:

$$K = \frac{\Pr(D|H^c)}{\Pr(D|H)} = \frac{\Pr(H^c|D)}{\Pr(H|D)} \cdot \frac{\Pr(H)}{\Pr(H^c)}$$

where the first term on the right hand side is the posterior odds in favor of the alternative hypothesis and the second term is the prior odds in favor of the null hypothesis. Bayes factors above 100 are considered decisive support for the alternative hypothesis (***Jeffreys, 1998***).

Because it is difficult to evaluate monophyly using a large number of alleles, we evaluate Bayes factors considering 4 alleles at a time: 2 alleles of a single species and 2 alleles of different species. For example, to assess support for TSP between humans and chimpanzees, we could use 2 human alleles and 2 bonobo alleles. Or, to assess support for TSP between humans and OWM, we could

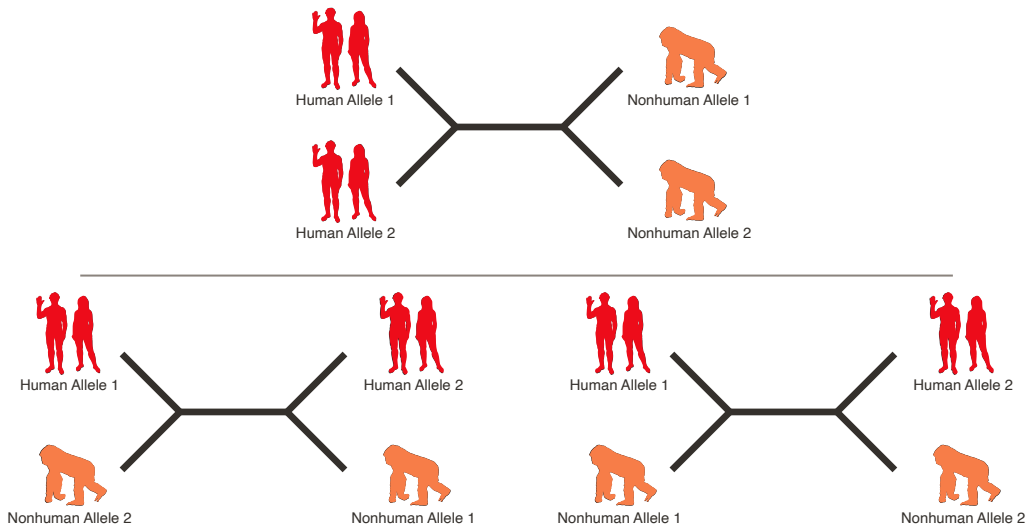

Figure 7. Possible unrooted trees of 4 alleles. There is one tree where the human alleles are monophyletic, and two trees where they are non-monophyletic.

use 2 human alleles, one baboon, and one macaque allele. Because there are many possible sets of 4 alleles for each comparison, we tested a large number of quartets. We reported the *maximum* Bayes factor among all tested allele sets to represent evidence for TSP for that species comparison, because our aim was to find *any* evidence of TSP among *any* set of 4 alleles.

Next, we calculated the prior odds of the null hypothesis (that the chosen species, i.e. humans, form a monophyletic group). The prior odds $\frac{\Pr(H)}{\Pr(H^c)} = \frac{1}{2}$, because if the trees were assembled at random, there is 1 possible unrooted tree where the 2 human alleles would form a monophyletic group and 2 possible unrooted trees where the 2 human alleles would not form a monophyletic group, as shown in ***Figure 7***.

The data, D, is the set of *BEAST2* trees, so the posterior odds $\frac{\Pr(H^c|D)}{\Pr(H|D)}$ is the fraction of *BEAST2* trees where the 2 human alleles **do not** form a monophyletic group divided by the fraction of *BEAST2* trees where the 2 human alleles **do** form a monophyletic group. If either fraction is 0, we set its probability to $p = \frac{1}{n+1}$, where n is the number of *BEAST2* trees for that gene/sequence subset, and set the complement's probability to $1 - p$. This is the reason that some labels in ***Figure 3-Figure 4*** contain a $>$ sign (e.g. if no trees in a set of $14,000$ were monophyletic, then the Bayes factor must be at minimum $7,000$).

Bayes factors K were then computed as follows and interpreted according to the scale given by ***Jeffreys*** (***1998***).

$$K = \frac{\Pr(H^c|D)}{\Pr(H|D)} \cdot \frac{1}{2}$$

For each gene and genic region, we tested for TSP between human and chimpanzee, gorilla, orangutan, gibbon, OWM, and NWM. For the Class II genes, which have orthologs beyond the primates, we also tested for TSP between human and tarsier, *Strepsirrhini*, Flying Lemur, Treeshrew, *Glires*, *Laurasiatheria*, and *Atlantogenata*. For the Class I genes, we considered outgroup species to be the tarsier and *Strepsirrhini*.

Rapidly-Evolving Sites

BEAST2 places sites into partitions and estimates evolutionary rates for each partition. We averaged these rates over all sampled states, resulting in an overall (relative) evolutionary rate for each nucleotide position. We then normalized these rates. In designing the gene groups, we included common "backbone sequences" in every set, although we expanded one particular clade for each

focused tree. The inclusion of backbone genes spanning the whole MHC family caused the alignments to contain many gaps. To normalize the rates, we took advantage of the fact that every alignment had many mostly-gap sites. We defined "gappy" sites as those in which the alignment had a gap in all of the following human backbone alleles: HLA-A*01:01:01:01, HLA-B*07:02:01:01, HLA-C*01:02:01:01, HLA-E*01:01:01:01, HLA-F*01:01:01:01, HLA-G*01:01:01:01, and HLA-J*01:01:01:01 for Class I, HLA-DRA*01:01:01:01, HLA-DQA1*01:01:01:01, HLA-DPA1*01:03:01:01, HLA-DMA*01:01:01:01, and HLA-DOA*01:01:01:01 for Class IIA, and HLA-DRB1*01:01:01:01, HLA-DQB1*02:01:01:01, HLA-DPB1*01:01:01:01, HLA-DMB*01:01:01:01, and HLA-DOB*01:01:01:01 for Class IIB. Because mostly-gap sites are not expected to affect the *BEAST2* run very much and were common to all focused gene group alignments, we considered these sites' *BEAST2* evolutionary rates as a baseline. Since the rates obtained from *SubstBMA* are relative anyway, we simply needed a set of sites that behaved similarly across each *BEAST2* run so that we could normalize the rates in a consistent manner. For each group and gene region, we calculated the mean rate among all of these baseline gappy sites. Then, we expressed normalized per-site rates as fold-changes by taking the base-2 logarithm of the ratio of each site's evolutionary rate to the baseline mean.

Protein Structures.

To map the rapidly-evolving sites onto protein structures, we first translated our nucleotide alignments into protein sequences using Expasy translate (***Gasteiger et al., 2003***). We then aligned our translated sequences with amino acid sequences from selected Protein Data Bank (PDB) (***Berman et al., 2000***)(https://www.rcsb.org/) structures (listed below) using *MUSCLE* (***Edgar, 2004***) with default settings.

The translated alignments and the PDB structures' sequences allowed us to determine which nucleotides in the alignment corresponded to which amino acids in each structure. We then calculated per-amino-acid evolutionary rates by averaging the per-site evolutionary rates among the sites composing each codon. We caution that the vast majority of PDB structures we considered were from human (and were functional), and thus they cannot capture all of the indels and structural changes that define different primate proteins. Additionally, some of our alignments included pseudogenes and diverse sets of related genes, for which it may seem reductionist to map to a single human protein structure. However, we note that despite significant sequence variation, the structures of different MHC proteins (from different genes within the same class) are extremely similar, and thus we do not expect such complications to alter the overall conclusions.

We used *PyMOL* version 2.4.2 (***Sch, 2021***) to visualize the per-amino acid evolutionary rates on each gene's protein structure. We used model 4BCE (***Teze et al., 2014***) for HLA-B, 4NT6 (***Choo et al., 2014***) for HLA-C, 7P4B (***Walters et al., 2022***) for HLA-E, 5JLZ (***Gerstner et al., 2016***) for HLA-DR and 2NNA (***Henderson et al., 2007***) for HLA-DQ from Protein Data Bank (***Berman et al., 2000***) to prepare the main figures (https://www.rcsb.org/).

We calculated the distances between all atoms of all amino acids of the HLA molecule and all atoms of all amino acids of the peptide in *PyMOL*, then took the minimum distance to represent each amino acid's distance to the peptide. Where possible, we averaged the minimum distances over multiple alternative structures for each protein, to avoid relying too heavily on a particular structure. The structures chosen (***Table 5***) represented different alleles, different contexts (e.g. bound to a receptor or not, bound to a self or non-self peptide), and in a few cases different species.

Disease and Trait Literature.

We conducted a literature search for papers that used HLA fine-mapping to discover disease and trait associations, limiting our selection to those including at least 1,000 cases and which identified putatively independent signals via conditional analysis. We included all independent amino acid signals identified as significant by the original authors. If there was more than one study for the same disease/trait, but in different populations, we included all unique independent hits. We also collected associations between amino acids and TCR phenotypes.

Table 5. Structures used to calculate distances to peptide. This table lists the Protein Data Bank (***Berman et al., 2000***) structure codes and references for all structures used to calculate peptide distances.

Gene	Struct.	Reference	Gene	Struct.	Reference
MHC-A	1ZVS	***Chu et al.*** (***2007***)	MHC-C	4NT6	***Choo et al.*** (***2014***)
	3JTT	***Dai et al.*** (***2010***)		5VGD	***Kaur et al.*** (***2017***)
	3OX8	***Liu et al.*** (***2011***)		5VGE	***Kaur et al.*** (***2017***)
	3OXR	***Liu et al.*** (***2011***)		5W67	***Mobbs et al.*** (***2017***)
	3OXS	***Liu et al.*** (***2011***)		6PAG	***Moradi et al.*** (***2021***)
	3RL2	***Zhang et al.*** (***2011***)		7WJ3	***Asa et al.*** (***2022***)
	4HX1	***Niu et al.*** (***2013***)	MHC-E	2ESV	***Hoare et al.*** (***2006***)
	6J1V	***Zhu et al.*** (***2019***)		3CDG	***Petrie et al.*** (***2008***)
	6J1W	***Zhu et al.*** (***2019***)		5W1V	***Sullivan et al.*** (***2017***)
	6MPP	***Flores-Solis et al.*** (***2019***)		7P49	***Walters et al.*** (***2022***)
	6PBH	***van de Sandt et al.*** (***2019***)		7P4B	***Walters et al.*** (***2022***)
	7SR0	***Finton et al.*** (***2023***)	MHC-F	5IUE	***Dulberger et al.*** (***2017***)
	7SRK	***Finton et al.*** (***2023***)	MHC-G	1YDP	***Clements et al.*** (***2005***)
	7WT5	***Asa et al.*** (***2022***)		2DYP	***Shiroishi et al.*** (***2006***)
	8I5C	***Lu et al.*** (***2023***)		3KYN	***Walpole et al.*** (***2010***)
MHC-B	1JGD	(***Hillig et al., 2004***)	MHC-DM	1HDM	***Mosyak et al.*** (***1998***)
	3BVN	***Kumar et al.*** (***2009***)		2BC4	***Nicholson et al.*** (***2006***)
	3KPL	***Macdonald et al.*** (***2009***)		4FQX	***Pos et al.*** (***2012***)
	3KPN	***Macdonald et al.*** (***2009***)		4GBX	***Pos et al.*** (***2012***)
	3LN4	***Bade-Döding et al.*** (***2011***)		4I0P	***Guce et al.*** (***2013***)
	3LN5	***Bade-Döding et al.*** (***2011***)	MHC-DO	4I0P	***Guce et al.*** (***2013***)
	3RWJ	***Wu et al.*** (***2011***)	MHC-DP	3LQZ	***Dai et al.*** (***2010***)
	3W39	***Yagita et al.*** (***2013***)		3WEX	***Kusano et al.*** (***2014***)
	3X13	***Saunders et al.*** (***2015***)		7T2A	***Ciacchi et al.*** (***2023***)
	4JQV	***Rist et al.*** (***2013***)		7T6I	***Klobuch et al.*** (***2022***)
	4JRY	***Liu et al.*** (***2013***)		7ZAK	***Racle et al.*** (***2023***)
	4MJI	***Motozono et al.*** (***2014***)	MHC-DQ	2NNA	***Henderson et al.*** (***2007***)
	4O2E	***Sun et al.*** (***2014***)		4D8P	***Tollefsen et al.*** (***2012***)
	4PRA	***Liu et al.*** (***2014***)		5KSA	***Petersen et al.*** (***2016***)
	4PRB	***Liu et al.*** (***2014***)		5KSU	***Nguyen et al.*** (***2017***)
	5EO0	***Du et al.*** (***2016***)		6DIG	***Jiang et al.*** (***2019***)
	5IEK	***Alpizar et al.*** (***2016***)		6PX6	***Ting et al.*** (***2020***)
	5VUD	***Illing et al.*** (***2018***)	MHC-DR	1BX2	***Smith et al.*** (***1998***)
	5VVP	***Illing et al.*** (***2018***)		1FV1	***Li et al.*** (***2000***)
	5VWF	***Illing et al.*** (***2018***)		1H15	***Lang et al.*** (***2002***)
	6IWG	***Yamamoto et al.*** (***2019***)		1T5X	***Zavala-Ruiz et al.*** (***2004***)
	6MTM	***Grant et al.*** (***2018***)		2Q6W	***Parry et al.*** (***2007***)
	6PYL	***Sian et al.*** (***2019***)		3C5J	***Dai et al.*** (***2008***)
	6PYV	***Sian et al.*** (***2019***)		4FQX	***Pos et al.*** (***2012***)
	6UZP	***Schutte et al.*** (***2020***)		4H1L	***Yin et al.*** (***2012***)
	6VIU	***Schutte et al.*** (***2020***)		5JLZ	***Gerstner et al.*** (***2016***)
	6Y27	***Loll et al.*** (***2020***)		5V4M	***Ooi et al.*** (***2017***)
	7R7V	***Li et al.*** (***2023***)		6ATF	***Scally et al.*** (***2017***)
	7T0L	***Vivian and Rossjohn*** (***2022***)		8EUQ	***Kassardjian et al.*** (***2023***)
	7TUC	***Jiang et al.*** (***2022b***)			
	7X1C	***Huan et al.*** (***2023***)			
	7YG3	***Jiang et al.*** (***2022a***)			

For ***Figure 6—figure Supplement 7***, we counted the number of significant, unique trait associations for each amino acid and plotted them against each amino acid's evolutionary rate. We drew simple linear regression lines to evaluate the association for each gene. We caution that this simple analysis does not take into account the significance level of each hit nor the ranking (e.g. top hit, second independent hit) of the associations, and that each study's authors may have performed conditional analyses differently. References are listed in ***Table 1*** and in ***Table 1—source data 1***.

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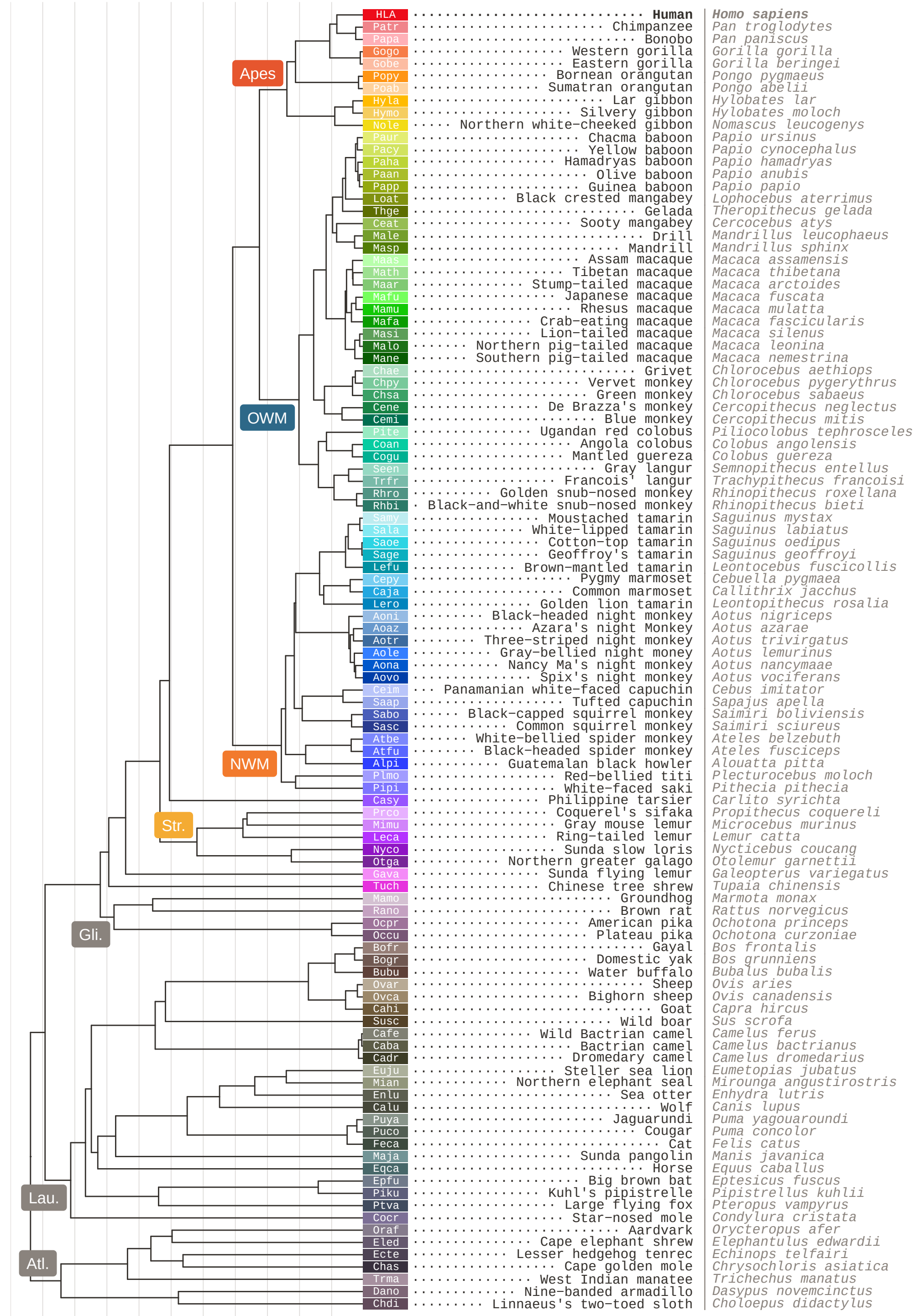
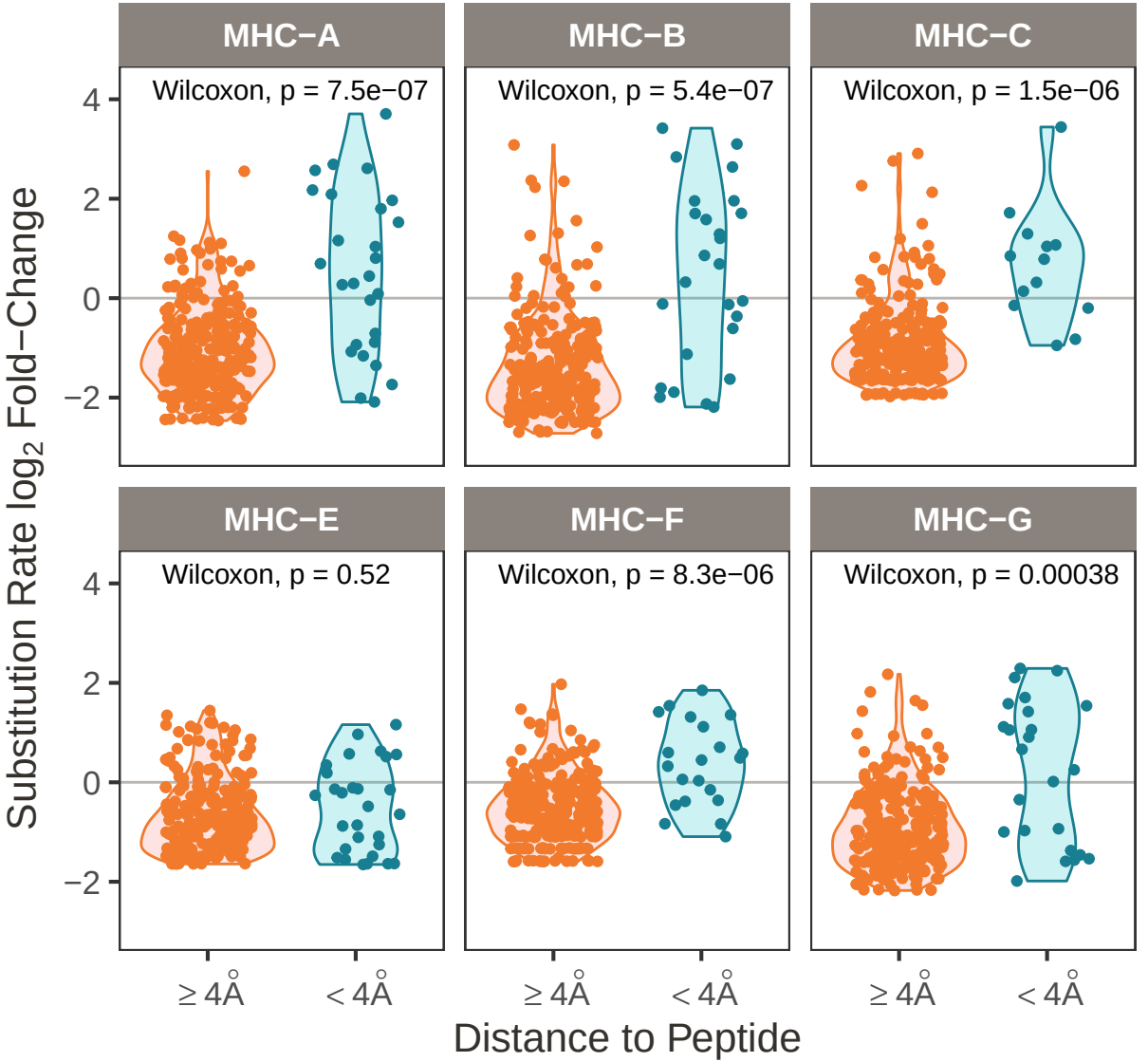
Species Abbreviation and Color Key

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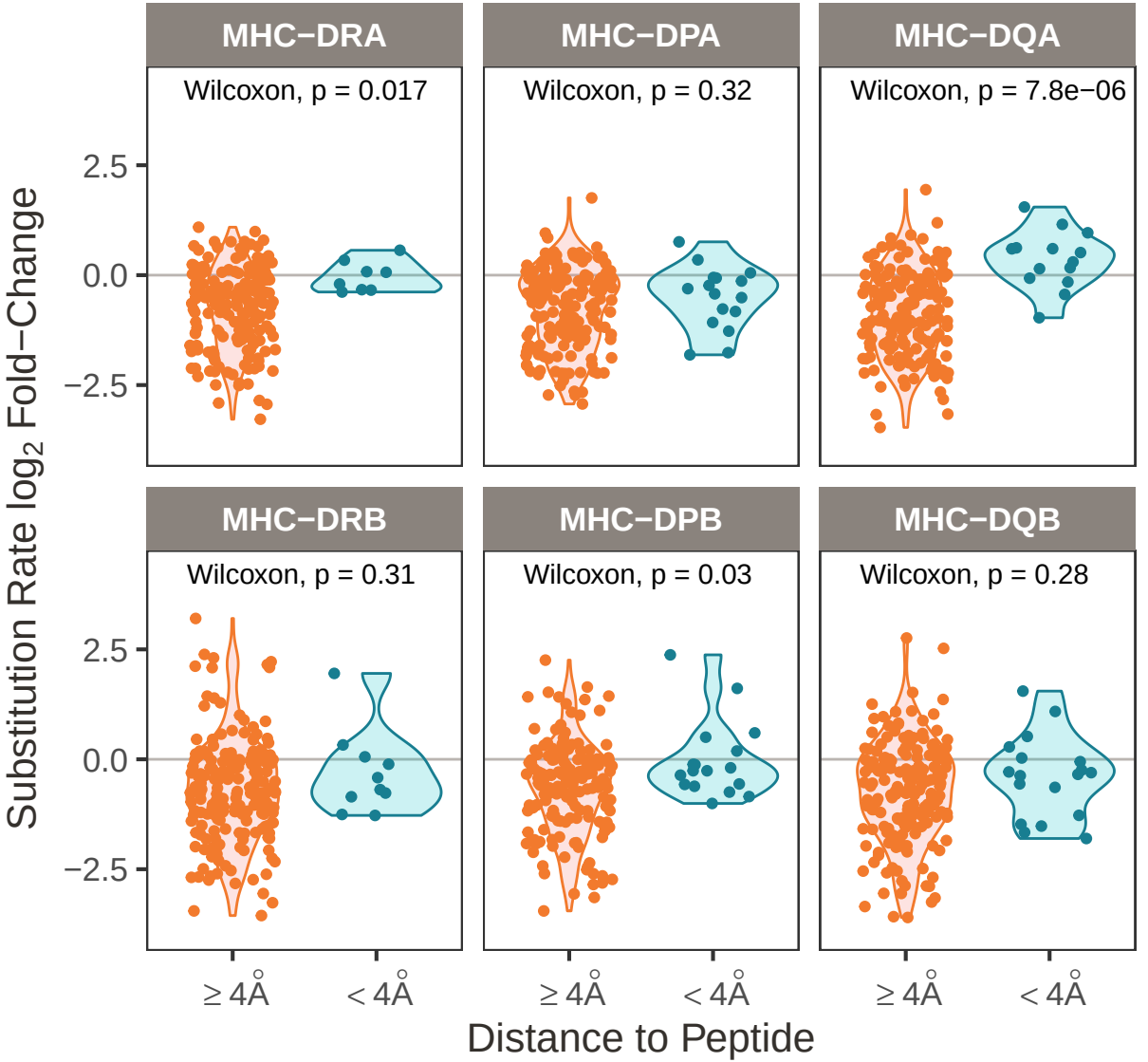
Wilcoxon, p = 7.5e−07
MHC−B
Wilcoxon, p = 5.4e−07
MHC−C
Wilcoxon, p = 1.5e−06
MHC−E
Wilcoxon, p = 0.52
MHC−F
Wilcoxon, p = 8.3e−06
MHC−G
Wilcoxon, p = 0.00038
Substitution Rate log2 Fold−Change
4
2
0
−2
≥ 4Å
< 4Å
Distance to Peptide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Wilcoxon, p = 0.017
MHC−DPA
Wilcoxon, p = 0.32
MHC−DQA
Wilcoxon, p = 7.8e−06
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Wilcoxon, p = 0.31
MHC−DPB
Wilcoxon, p = 0.03
MHC−DQB
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Substitution Rate log2 Fold−Change
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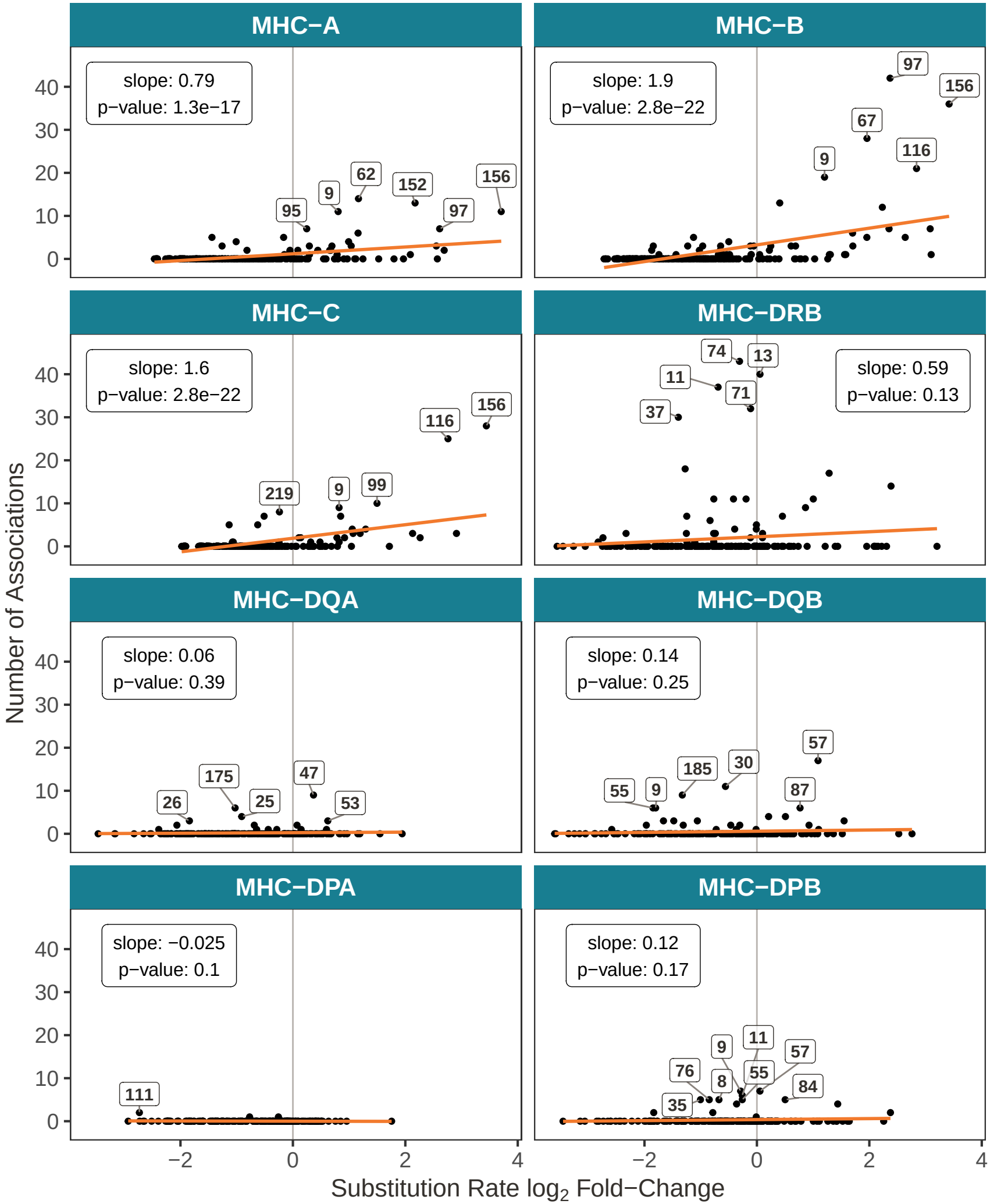
0.0
−2.5
≥ 4Å
< 4Å
Distance to Peptide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p−value: 1.3e−17
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9
62
152
97
156
MHC−B
slope: 1.9
p−value: 2.8e−22
9
67
97
116
156
MHC−C
slope: 1.6
p−value: 2.8e−22
219
9
99
116
156
MHC−DRB
slope: 0.59
p−value: 0.13
37
11
74
71
13
MHC−DQA
slope: 0.06
p−value: 0.39
26
175
25
47
53
MHC−DQB
slope: 0.14
p−value: 0.25
55
9
185
30
57
87
MHC−DPA
slope: −0.025
p−value: 0.1
111
MHC−DPB
slope: 0.12
p−value: 0.17
35
76
8
9
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Number of Associations
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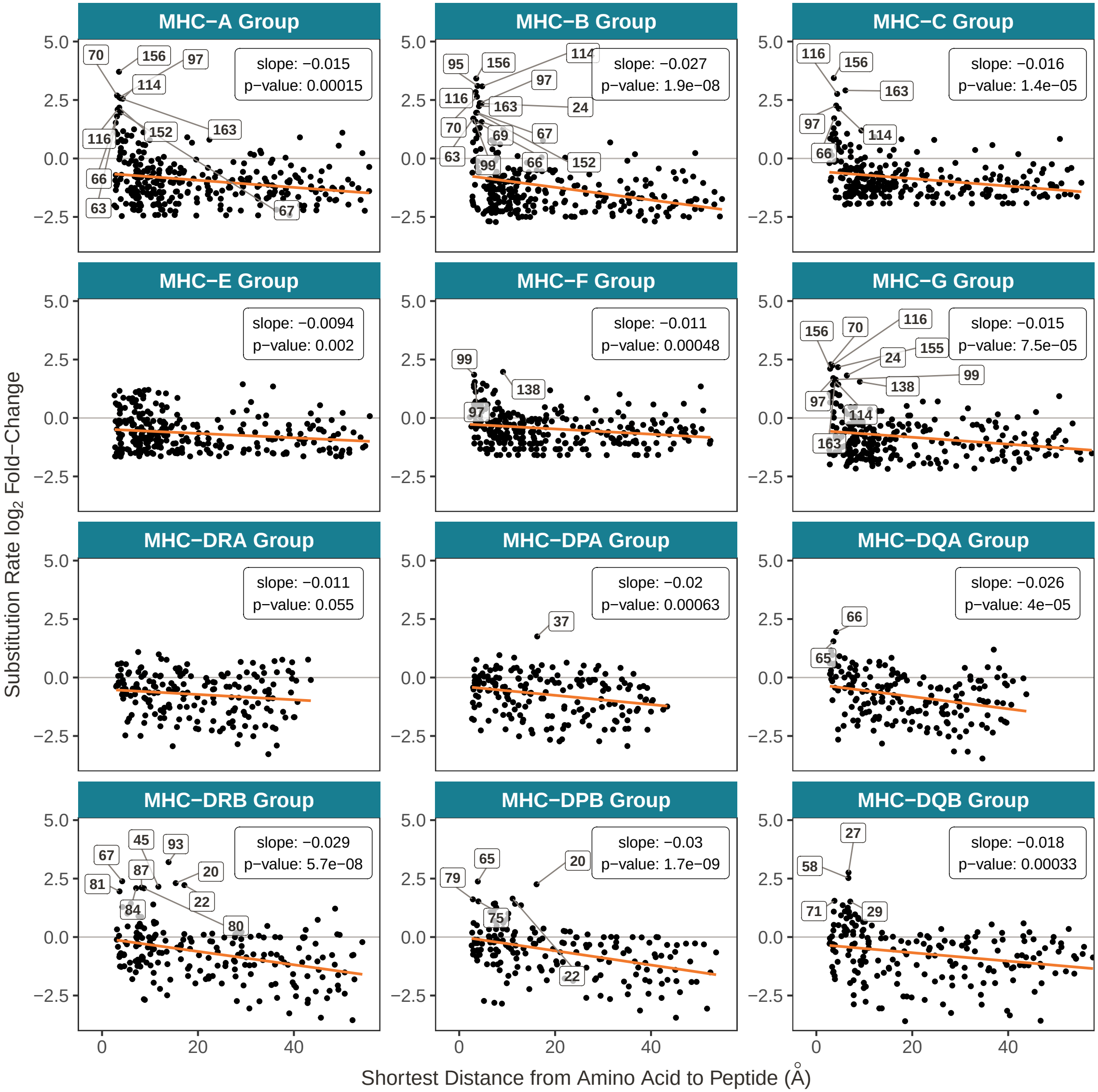
2
4
Substitution Rate log2 Fold−Change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MHC−C Group
slope: −0.016
p−value: 1.4e−05
MHC−E Group
slope: −0.0094
p−value: 0.002
MHC−F Group
slope: −0.011
p−value: 0.00048
MHC−G Group
slope: −0.015
p−value: 7.5e−05
MHC−DRA Group
slope: −0.011
p−value: 0.055
MHC−DPA Group
slope: −0.02
p−value: 0.00063
MHC−DQA Group
slope: −0.026
p−value: 4e−05
MHC−DRB Group
slope: −0.029
p−value: 5.7e−08
MHC−DPB Group
slope: −0.03
p−value: 1.7e−09
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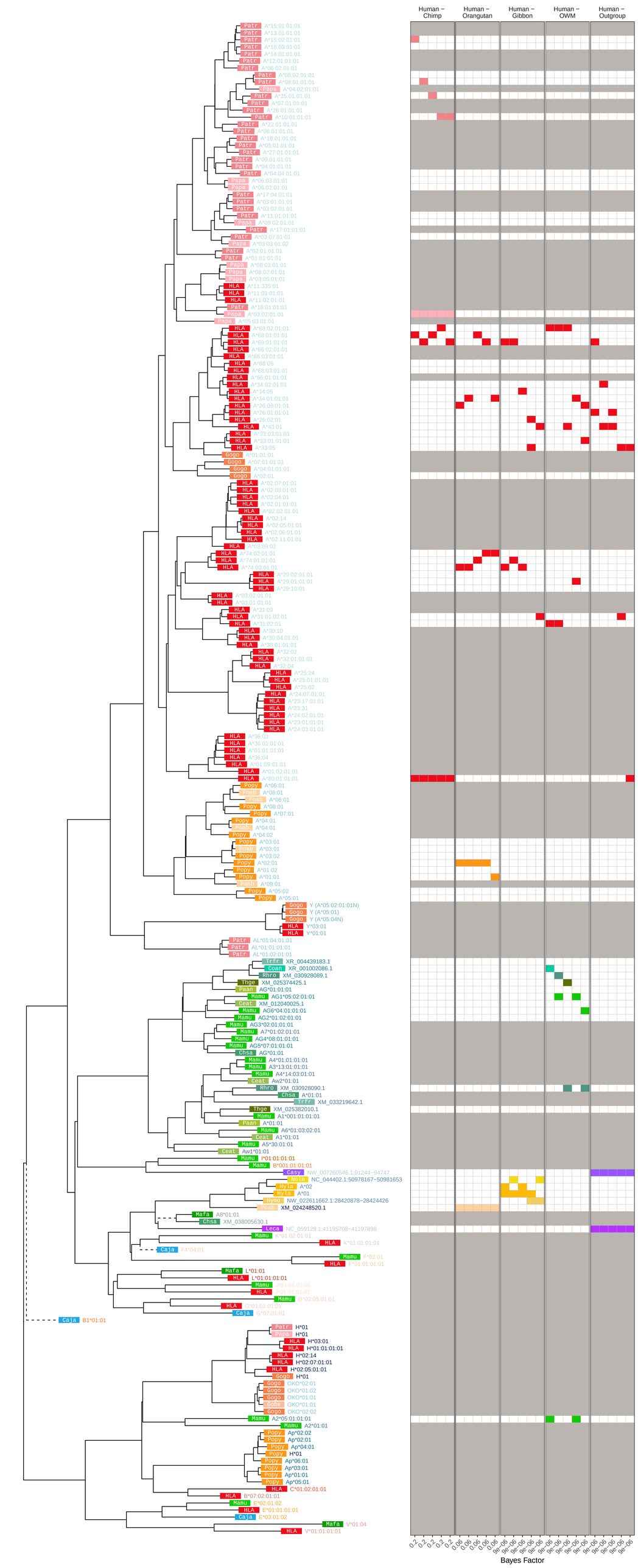
Substitution Rate log2 Fold−Change
Shortest Distance from Amino Acid to Peptide (Å)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Human − Orangutan
Human − Gibbon
Human − OWM
Human − Outgroup
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Papa A*04:02:01:01
Patr A*25:01:01:01
Patr A*07:01:01:01
Patr A*26:01:01:01
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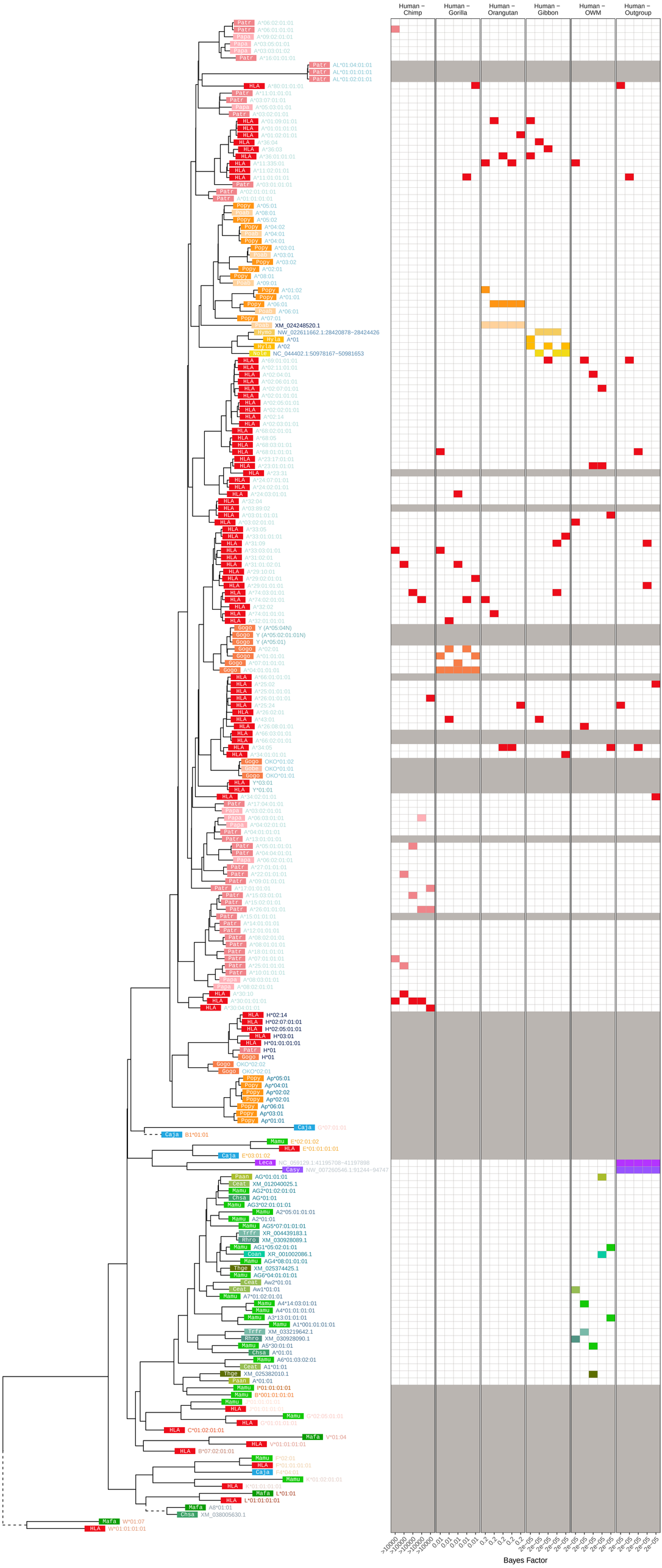
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Poab A*08:01
Popy A*05:02
Popy A*04:02
Poab A*04:01
Popy A*04:01
Popy A*03:01
Poab A*03:01
Popy A*03:02
Popy A*02:01
Popy A*08:01
Poab A*09:01
Popy A*01:02
Popy A*01:01
Popy A*06:01
Poab A*06:01
Popy A*07:01
Poab XM_024248520.1
Hymo NW_022611662.1:28420878–28424426
Hyla A*01
Hyla A*02
Nole NC_044402.1:50978167–50981653
HLA A*69:01:01:01
HLA A*02:11:01:01
HLA A*02:04:01
HLA A*02:06:01:01
HLA A*02:07:01:01
HLA A*02:01:01:01
HLA A*02:05:01:01
HLA A*02:02:01:01
HLA A*02:14
HLA A*02:03:01:01
HLA A*68:02:01:01
HLA A*68:05
HLA A*68:03:01:01
HLA A*68:01:01:01
HLA A*23:17:01:01
HLA A*23:01:01:01
HLA A*23:31
HLA A*24:07:01:01
HLA A*24:02:01:01
HLA A*24:03:01:01
HLA A*32:04
HLA A*03:89:02
HLA A*03:01:01:01
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HLA A*33:05
HLA A*33:01:01:01
HLA A*31:09
HLA A*33:03:01:01
HLA A*31:02:01
HLA A*31:01:02:01
HLA A*29:10:01
HLA A*29:02:01:01
HLA A*29:01:01:01
HLA A*74:03:01:01
HLA A*74:02:01:01
HLA A*32:02
HLA A*74:01:01:01
HLA A*32:01:01:01
Gogo Y (A*05:04N)
Gogo Y (A*05:02:01:01N)
Gogo Y (A*05:01)
Gogo A*02:01
Gogo A*01:01:01
Gogo A*07:01:01:01
Gogo A*04:01:01:01
HLA A*66:01:01:01
HLA A*25:02
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HLA A*26:01:01:01
HLA A*25:24
HLA A*26:02:01
HLA A*43:01
HLA A*26:08:01:01
HLA A*66:03:01:01
HLA A*66:02:01:01
HLA A*34:05
HLA A*34:01:01:01
Gogo OKO*01:02
Gobe OKO*01:01
Gogo OKO*01:01
HLA Y*03:01
HLA Y*01:01
HLA A*34:02:01:01
Patr A*17:04:01:01
Papa A*03:02:01:01
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Patr A*09:01:01:01
Patr A*17:01:01:01
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Patr A*15:01:01:01
Patr A*14:01:01:01
Patr A*12:01:01:01
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Patr A*08:01:01:01
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Patr A*07:01:01:01
Patr A*25:01:01:01
Patr A*10:01:01:01
Papa A*08:03:01:01
Papa A*08:02:01:01
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HLA A*30:04:01:01
HLA H*02:14
HLA H*02:07:01:01
HLA H*02:05:01:01
HLA H*03:01
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Patr H*01
Gogo H*01
Gogo OKO*02:02
Gogo OKO*02:01
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Popy Ap*04:01
Popy Ap*02:02
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Popy Ap*03:01
Popy Ap*01:01
Caja G*07:01:01
Caja B1*01:01
Mamu E*02:01:02
HLA E*01:01:01:01
Caja E*03:01:02
Leca NC_059129.1:41195708–41197898
Casy NW_007260546.1:91244–94747
Paan AG*01:01:01
Ceat XM_012040025.1
Mamu AG2*01:02:01:01
Chsa AG*01:01
Mamu AG3*02:01:01:01
Mamu A2*05:01:01:01
Mamu A2*01:01
Mamu AG5*07:01:01:01
Irrr XR_004439183.1
Rhro XM_030928089.1
Mamu AG1*05:02:01:01
Coan XR_001002086.1
Mamu AG4*08:01:01:01
Thge XM_025374425.1
Mamu AG6*04:01:01:01
Ceat Aw2*01:01
Ceat Aw1*01:01
Mamu A7*01:02:01:01
Mamu A4*14:03:01:01
Mamu A4*01:01:01:01
Mamu A3*13:01:01:01
Mamu A1*001:01:01:01
Irrr XM_033219642.1
Rhro XM_030928090.1
Mamu A5*30:01:01
Chsa A*01:01
Mamu A6*01:03:02:01
Ceat A1*01:01
Thge XM_025382010.1
Paan A*01:01
Mamu I*01:01:01:01
Mamu B*001:01:01:01
Mamu I*01:01:01:01
HLA I*01:01:01:01
Mamu G*02:05:01:01
HLA G*01:01:01:01
HLA C*01:02:01:01
Mafa V*01:04
HLA V*01:01:01:01
HLA B*07:02:01:01
Mamu F*02:01
HLA F*01:01:01:01
Chsa F4*04:01
Mamu K*01:02:01:01
HLA K*01:01:01:01
Mafa L*01:01
HLA L*01:01:01:01
Mafa A8*01:01
Chsa XM_038005630.1
Mafa W*01:07
HLA W*01:01:01:01
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0.01
0.2
2e-05
Bayes Factor

Human – Chimp
Human – Gorilla
Human – Orangutan
Human – Gibbon
Human – OWM
Human – Outgroup
HLA A*26:02:01
HLA A*25:02
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HLA A*25:01:01:01
HLA A*43:01
HLA A*26:01:01:01
HLA A*26:08:01:01
HLA A*66:02:01:01
HLA A*34:02:01:01
HLA A*66:03:01:01
HLA A*34:05
HLA A*34:01:01:01
HLA A*33:05
HLA A*33:01:01:01
HLA A*31:09
HLA A*33:03:01:01
HLA A*31:02:01
HLA A*31:01:02:01
HLA A*32:02
HLA A*32:01:01:01
HLA A*29:10:01
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HLA Y*01:01
Gogo A*04:01:01:01
Gogo A*02:01
Gogo A*07:01:01:01
Gogo A*01:01:01
HLA A*69:01:01:01
HLA A*02:14
HLA A*02:04:01
HLA A*02:03:01:01
HLA A*02:07:01:01
HLA A*02:05:01:01
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HLA A*68:05
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HLA A*68:01:01:01
HLA A*02:11:01:01
HLA A*02:02:01:01
HLA A*02:01:01:01
Gogo Y (A*05:04N)
Gogo Y (A*05:02:01:01N)
Gogo Y (A*05:01)
Popy A*07:01
Popy A*05:01
Popy A*05:02
Popy A*04:01
Poab A*04:01
Popy A*04:02
Popy A*06:01
Poab A*06:01
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Popy A*02:01
Popy A*03:01
Poab A*03:01
Poab A*08:01
Popy Ap*03:01
Popy Ap*01:01
Popy Ap*02:02
Popy Ap*02:01
Popy Ap*04:01
Popy Ap*05:01
Popy Ap*06:01
Patr AL*01:04:01:01
Patr AL*01:01:01:01
Patr AL*01:02:01:01
Popy A*01:02
Popy A*01:01
Gogo OKO*01:02
Gogo OKO*01:01
Gogo OKO*01:01
Gogo H*01
Gogo OKO*02:02
Gogo OKO*02:01
Nole NC_044402.1:50978167–50981653
Hyla A*02
Hyla NW_022611662.1:28420878–28424426
Hyla A*01
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Patr A*04:04:01:01
Patr A*12:01:01:01
Patr A*04:01:01:01
Patr A*13:01:01:01
Patr A*09:01:01:01
Patr A*16:01:01:01
Patr A*15:02:01:01
Patr A*15:03:01:01
Patr A*15:01:01:01
Patr A*05:01:01:01
Patr A*17:01:01:01
Papa A*06:03:01:01
Papa A*04:02:01:01
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Patr A*10:01:01:01
Papa A*06:02:01:01
Patr A*08:02:01:01
Patr A*08:01:01:01
Patr A*06:02:01:01
Patr A*06:01:01:01
Patr A*22:01:01:01
Patr A*18:01:01:01
Patr A*26:01:01:01
Patr A*07:01:01:01
HLA A*24:07:01:01
HLA A*23:17:01:01
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HLA A*23:01:01:01
HLA A*80:01:01:01
Papa A*03:05:01:01
Papa A*03:03:01:02
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Patr A*17:04:01:01
Papa A*09:02:01:01
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Patr A*03:02:01:01
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Patr A*01:01:01:01
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Patr A*02:01:01:01
Patr A*03:07:01:01
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HLA A*03:89:02
HLA Y*03:01
HLA H*02:14
HLA H*02:07:01:01
HLA A*11:335:01
Patr H*01
Patr XM_024248520.1
HLA H*03:01
HLA H*02:05:01:01
HLA H*01:01:01:01
Trtr XR_004439183.1
Coan XR_001002086.1
Rhro XM_030928089.1
Thge XM_025374425.1
Ceat XM_012040025.1
Mamu AG6*04:01:01:01
Paan AG*01:01:01
Mamu AG4*08:01:01:01
Mamu AG3*02:01:01:01
Mamu AG1*05:02:01:01
Chsa AG*01:01
Mamu AG2*01:02:01:01
Mamu AG5*07:01:01:01
Ceat Aw2*01:01
Mamu A3*13:01:01:01
Paan A*01:01
Mamu A6*01:03:02:01
Thge XM_025382010.1
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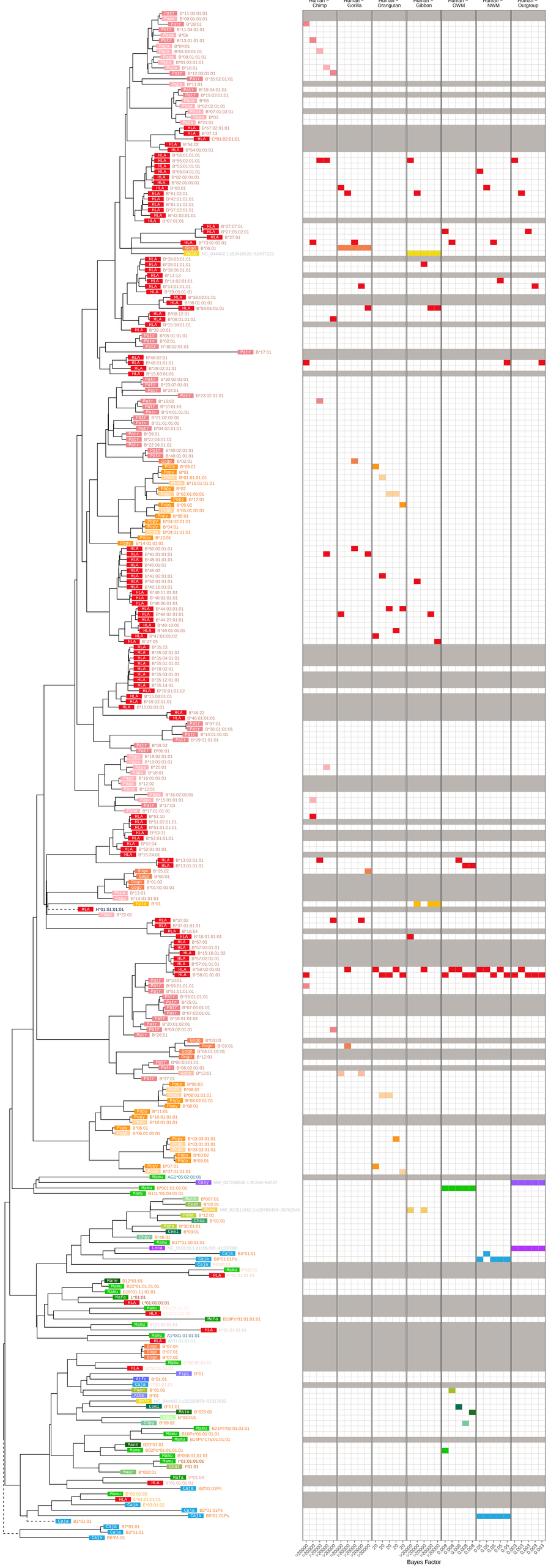
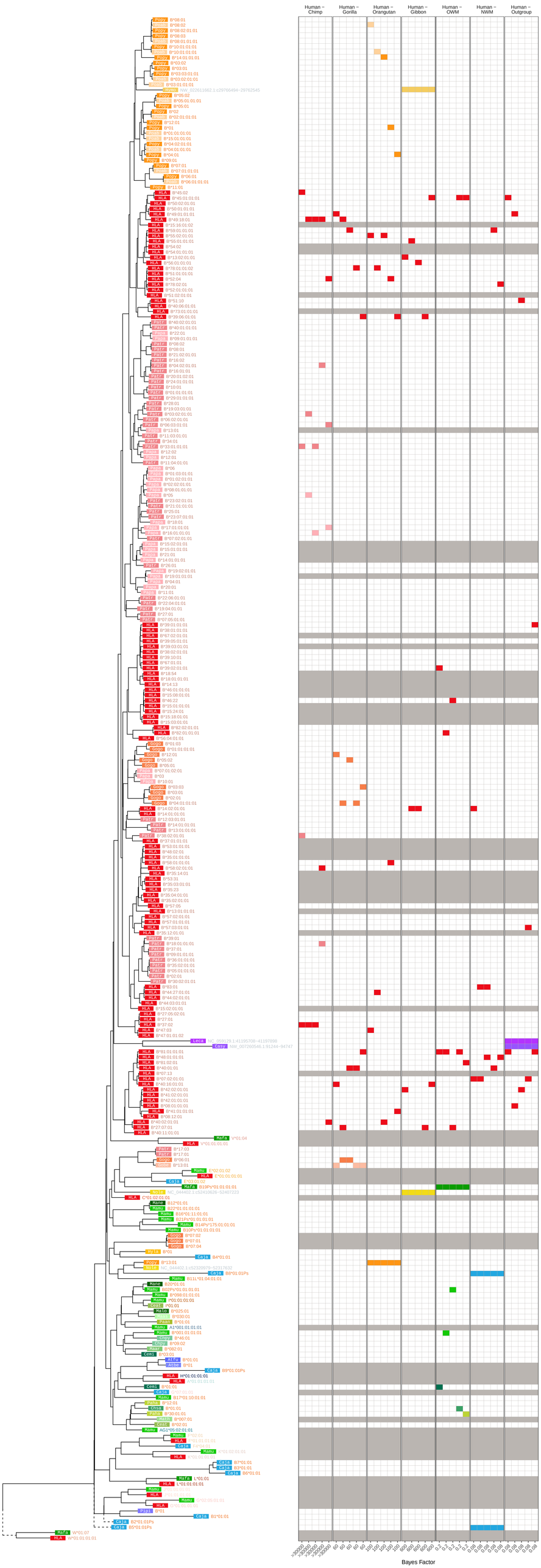
Mamu A5*30:01:01
Mamu A2*05:01:01:01
Mamu A2*01:01
Ceat Aw1*01:01
Ceat A1*01:01
Trtr XM_033219642.1
Rhro XM_030928090.1
Chsa A*01:01
Mamu A4*14:03:01:01
Mamu A4*01:01:01:01
Mamu A1*001:01:01:01
HLA F*01:01:01:01
Caja F4*04:01
Mamu F*02:01
Leca NC_059129.1:41195708–41197898
Cgsy NW_007260546.1:91244–94747
Mamu E*02:01:02
HLA E*01:01:01:01
Mafa W*01:07
HLA W*01:01:01:01
Mamu I*01:01:01:01
Mafa B*001:01:01:01
HLA C*01:02:01:01
HLA B*07:02:01:01
Mafa A8*01:01
Chsa XM_038005630.1
Caja E*03:01:02
Caja B1*01:01
Mafa L*01:01
HLA L*01:01:01:01
Mamu G*02:05:01:01
HLA G*01:01:01:01
Mamu J*01:01:01:01
Mamu K*01:02:01:01
HLA K*01:01:01:01
HLA J*01:01:01:01
Caja G*07:01:01
1 1 1 1 1
0.006 0.006 0.006 0.006 0.006
10000 10000 10000 10000 10000
0.002 0.002 0.002 0.002 0.002
2e−05 2e−05 2e−05 2e−05 2e−05
2e−05 2e−05 2e−05 2e−05 2e−05
Bayes Factor


Human – Chimp
Human – Gorilla
Human – Orangutan
Human – Gibbon
Human – OWM
Human – NWM
Human – Outgroup
Bayes Factor


Human – Chimp
Human – Gorilla
Human – Orangutan
Human – Gibbon
Human – OWM
Human – NWM
Human – Outgroup
Bayes Factor

Human – Chimp
Human – Gorilla
Human – Orangutan
Human – Gibbon
Human – OWM
Human – NWM
Human – Outgroup
HLA B*45:01:01:01
HLA B*15:16:01:02
HLA B*49:18:01
HLA B*37:01:01:01
HLA B*15:03:01:01
HLA B*82:02:01:01
HLA B*44:27:01:01
HLA B*50:01:01:01
HLA B*49:01:01:01
HLA B*15:24:01
HLA B*15:02:01:01
HLA B*82:01:01:01
HLA B*15:01:01:01
HLA B*83:01
HLA B*44:03:01:01
HLA B*44:02:01:01
HLA B*46:01:01:01
HLA B*15:01:01:01
HLA B*45:02
HLA B*15:18:01:01
HLA B*67:02:01:01
HLA B*39:01:01:01
HLA B*38:02:01:01
HLA B*39:03:01:01
HLA B*38:01:01:01
HLA B*14:02:01:01
HLA B*14:01:01:01
HLA B*67:01:01
HLA B*39:05:01:01
HLA B*39:06:01:01
HLA B*39:02:01:01
HLA B*39:10:01
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Patr B*14:01:01:01
Patr B*20:01:02:01
Patr B*08:02
Patr B*13:01:01:01
Patr B*02:01
Patr B*05:01:01:01
Patr B*16:02
Patr B*16:01:01
Patr B*08:01
Patr B*38:02:01:01
Patr B*04:02:01:01
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Patr B*09:01:01:01
Patr B*03:02:01:01
Patr B*01:01:01:01
Gogo B*05:02
Gogo B*05:01
Gogo B*01:03
Gogo B*01:01:01:01
Patr B*17:03
Patr B*17:01
Paan B*15:01:01:01
Paan B*08:01:01:01
Patr B*25:01
Patr B*19:04:01:01
Patr B*07:02:01:01
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Paan B*07:01:02:01
Patr B*33:01:01:01
Paan B*19:01:01:01
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Paan B*16:01:01:01
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Patr B*11:04:01:01
Paan B*03
Paan B*01:02:01:01
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Patr B*23:02:01:01
Paan B*04:01
Patr B*28:01
Hyla B*01
Pogy B*04:02:01:01
Pogo B*04:01:01:01
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Pogy B*02
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Pogy B*03:02
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Pogy B*08:01
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Pogy B*05:02
Pogy B*05:01
Pogy B*12:01
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Pogy B*13:01
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Pogy B*07:01
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Pogo B*13:01
Hyno NW_020311662.1:c29766494-29762545
Nole NC_044402.1:c52410626-52407223
Nole NC_044402.1:c52320979-52317632
Gogo B*12:01
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Gogo B*02:01
Gogo B*03:01
HLA B*73:01:01:01
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Gogo B*07:02
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Mamu B02Ps*01:01:01:01
Paar B*082:01
Mane B20*01:01
Mamu B14Ps*175:01:01:01
Chpy B*46:01
Mamu B*001:01:01:01
Ceat B*02:01
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Ceas B*03:01
Ceat B*01:01
Ceat I*01:01
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Paan B*01:01
Patr B*07:01
Rhlo B*025:01
Mnes B*030:01
Chpy B*09:02
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Mane B12*01:01
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Ptro B*01
Caja B7*01:01
Caja B3*01:01
Caja B6*01:01
Caja B9*01:01Ps
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Athe B*01
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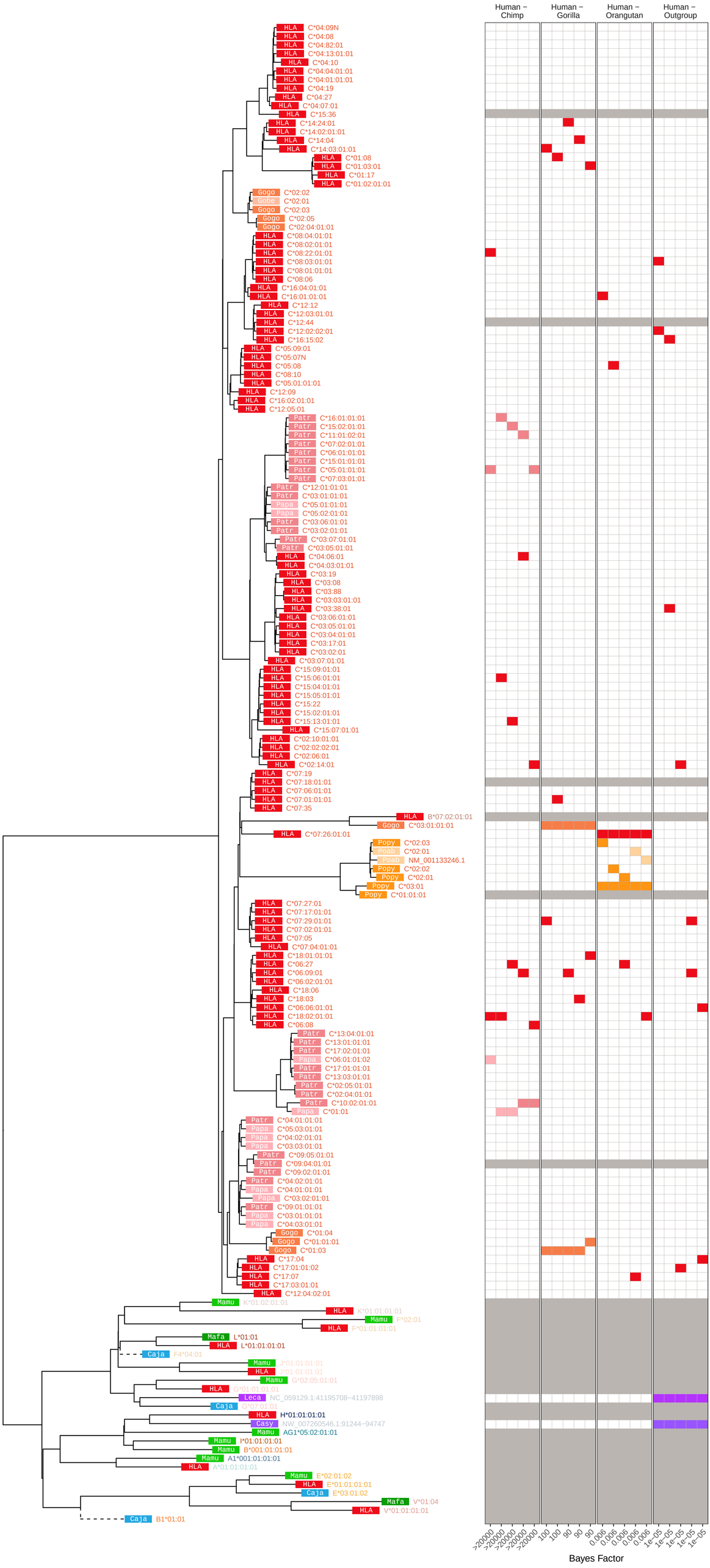
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Human − Gorilla
Human − Orangutan
Human − Outgroup
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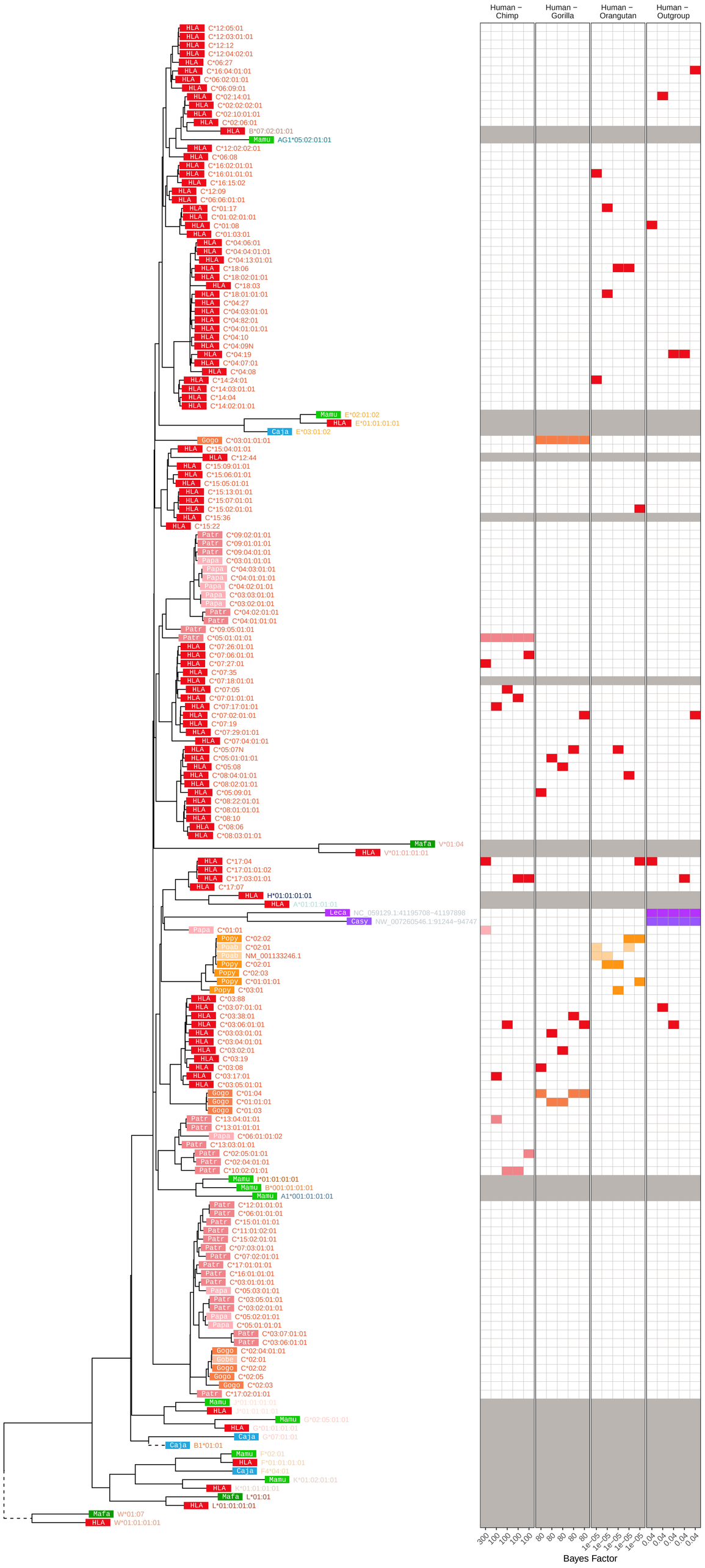
Bayes Factor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Human − Gorilla
Human − Orangutan
Human − Outgroup
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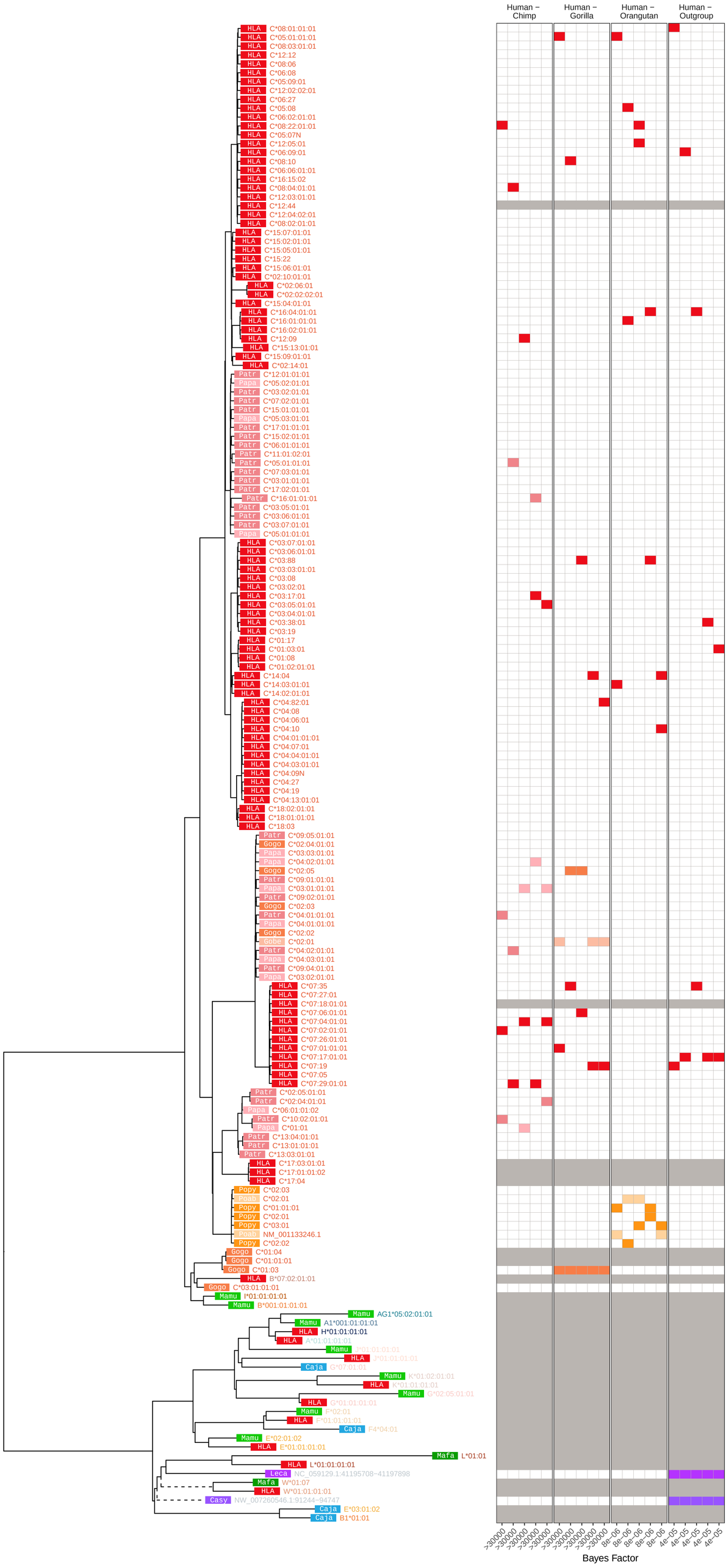
Bayes Factor


Human − Chimp
Human − Gorilla
Human − Orangutan
Human − Outgroup
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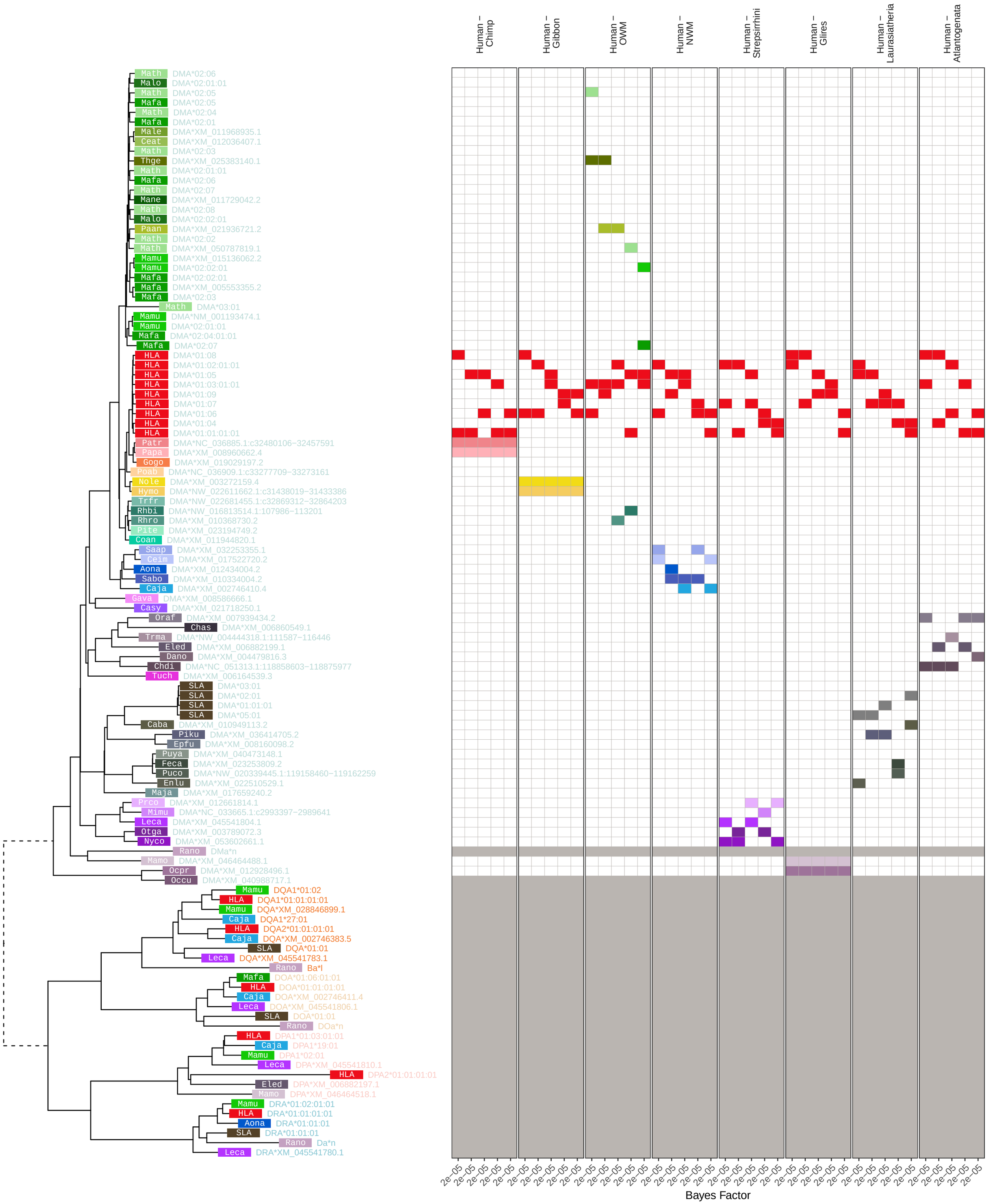
Bayes Factor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Human – OWM
Human – NWM
Human – Strepsirrhini
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Human – Atlantogenata
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Nyco DMA*XM_053602661.1
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Mamu DQA*XM_028846899.1
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Rano Ba*l
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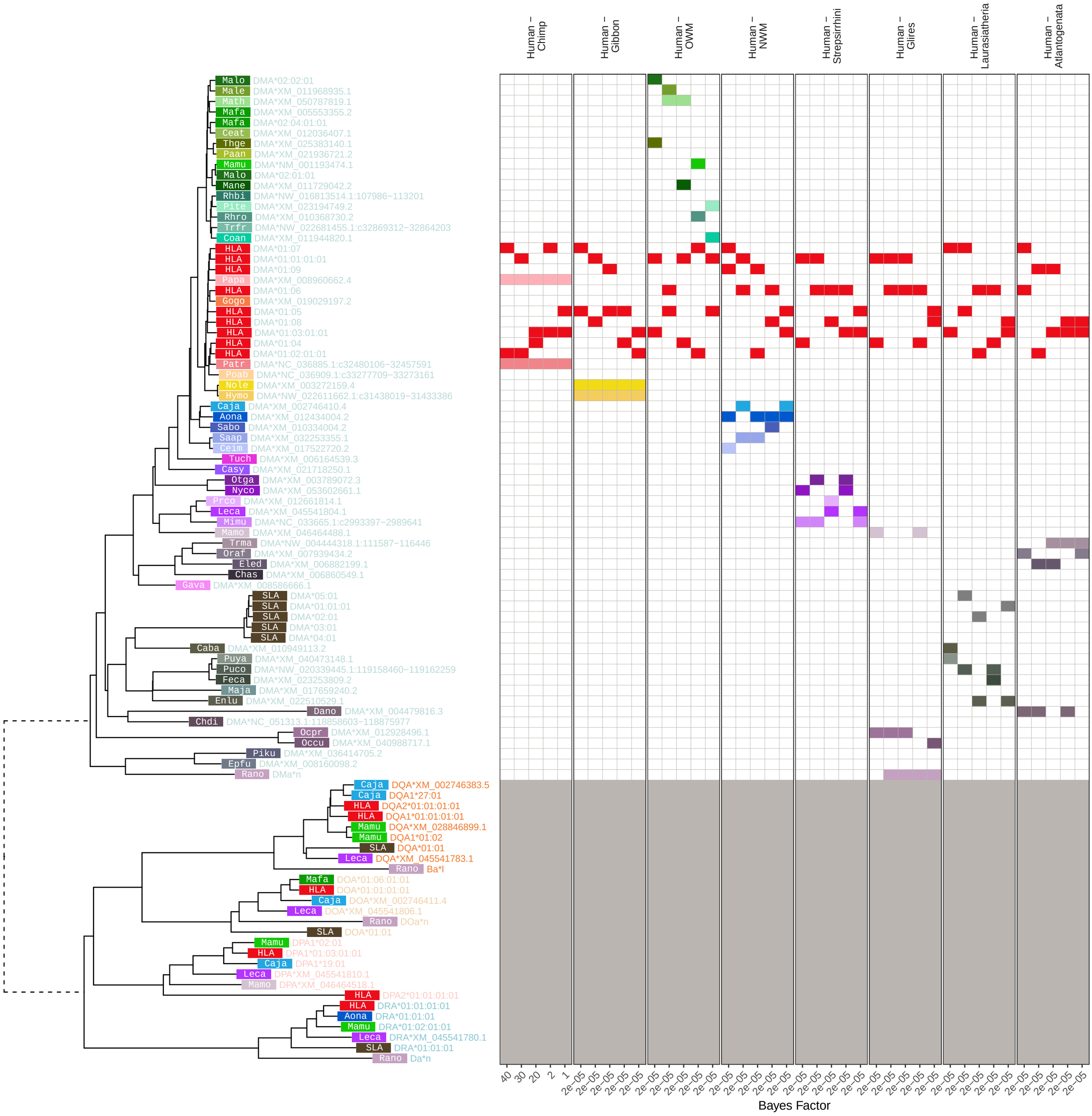
Bayes Factor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Human – Gibbon
Human – OWM
Human – NWM
Human – Strepsirrhini
Human – Glires
Human – Laurasiatheria
Human – Atlantogenata
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Mane DMA*XM_011729042.2
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Papa DMA*XM_008960662.4
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Eled DMA*XM_006882199.1
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Feca DMA*XM_023253809.2
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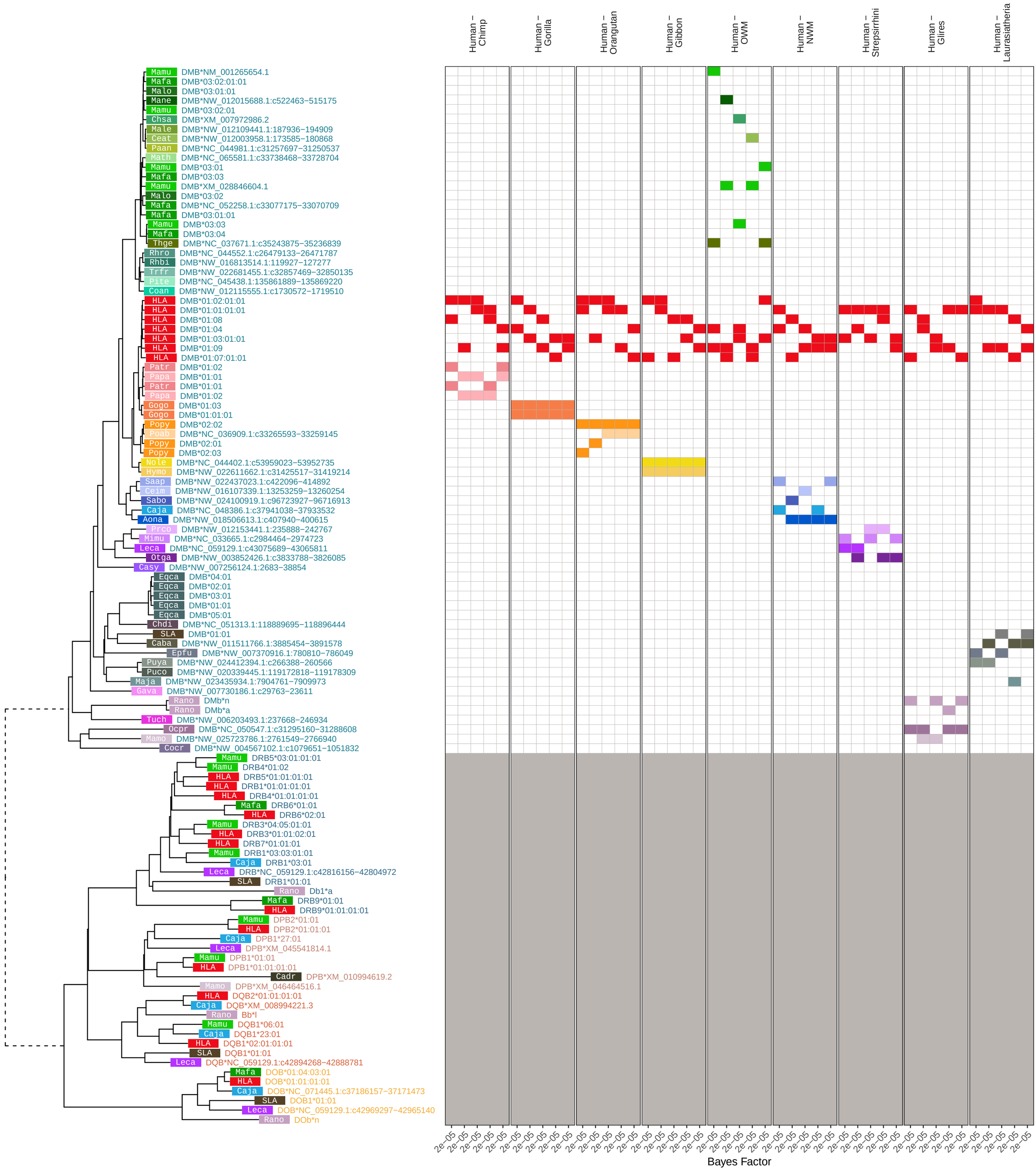
Bayes Factor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Human – Gorilla
Human – Orangutan
Human – Gibbon
Human – OWM
Human – NWM
Human – Strepsirrhini
Human – Glires
Human – Laurasiatheria
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Rhro DMB*NC_044552.1:c26479133−26471787
Rhbi DMB*NW_016813514.1:119927−127277
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Papa DMB*01:02
Gogo DMB*01:03
Gogo DMB*01:01:01
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Saap DMB*NW_022437023.1:c422096−414892
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Sabo DMB*NW_024100919.1:c96723927−96716913
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Aona DMB*NW_018506613.1:c407940−400615
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Mimu DMB*NC_033665.1:c2984464−2974723
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Otga DMB*NW_003852426.1:c3833788−3826085
Casy DMB*NW_007256124.1:2683−38854
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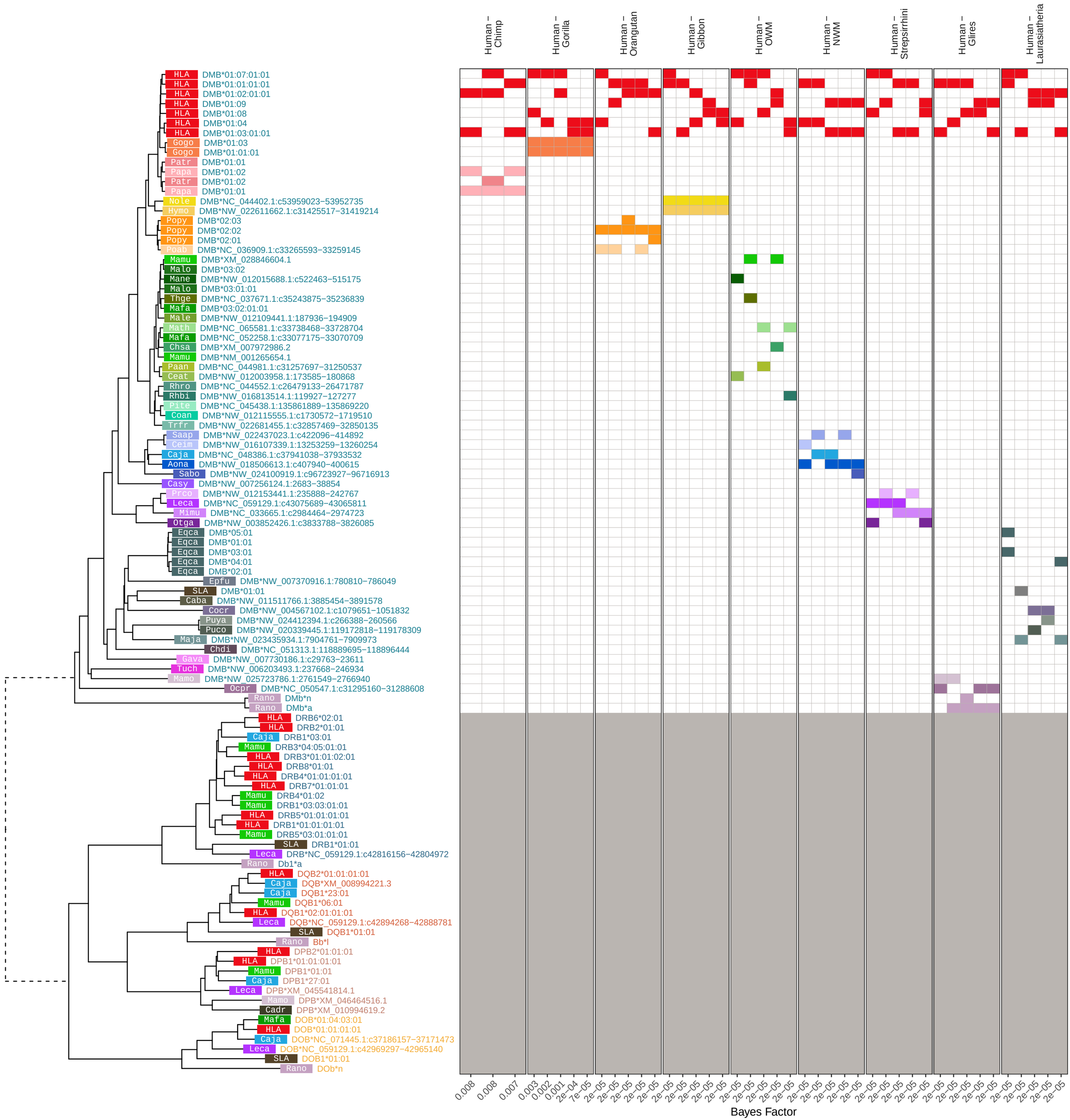
Bayes Factor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Human – Gorilla
Human – Orangutan
Human – Gibbon
Human – OWM
Human – NWM
Human – Strepsirrhini
Human – Glires
Human – Laurasiatheria
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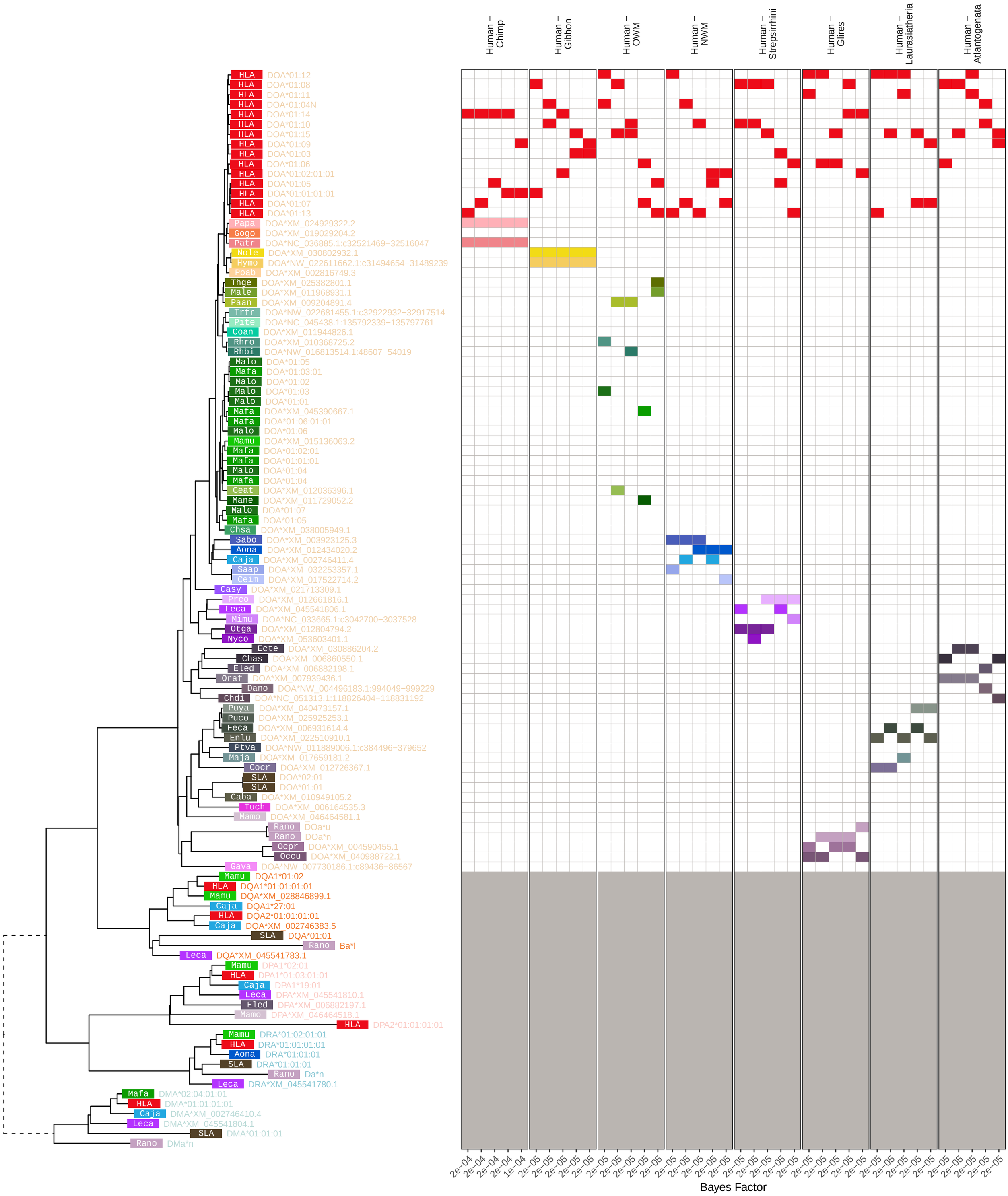
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Human – Gibbon
Human – OWM
Human – NWM
Human – Strepsirrhini
Human – Glires
Human – Laurasiatheria
Human – Atlantogenata
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Rano Da*n
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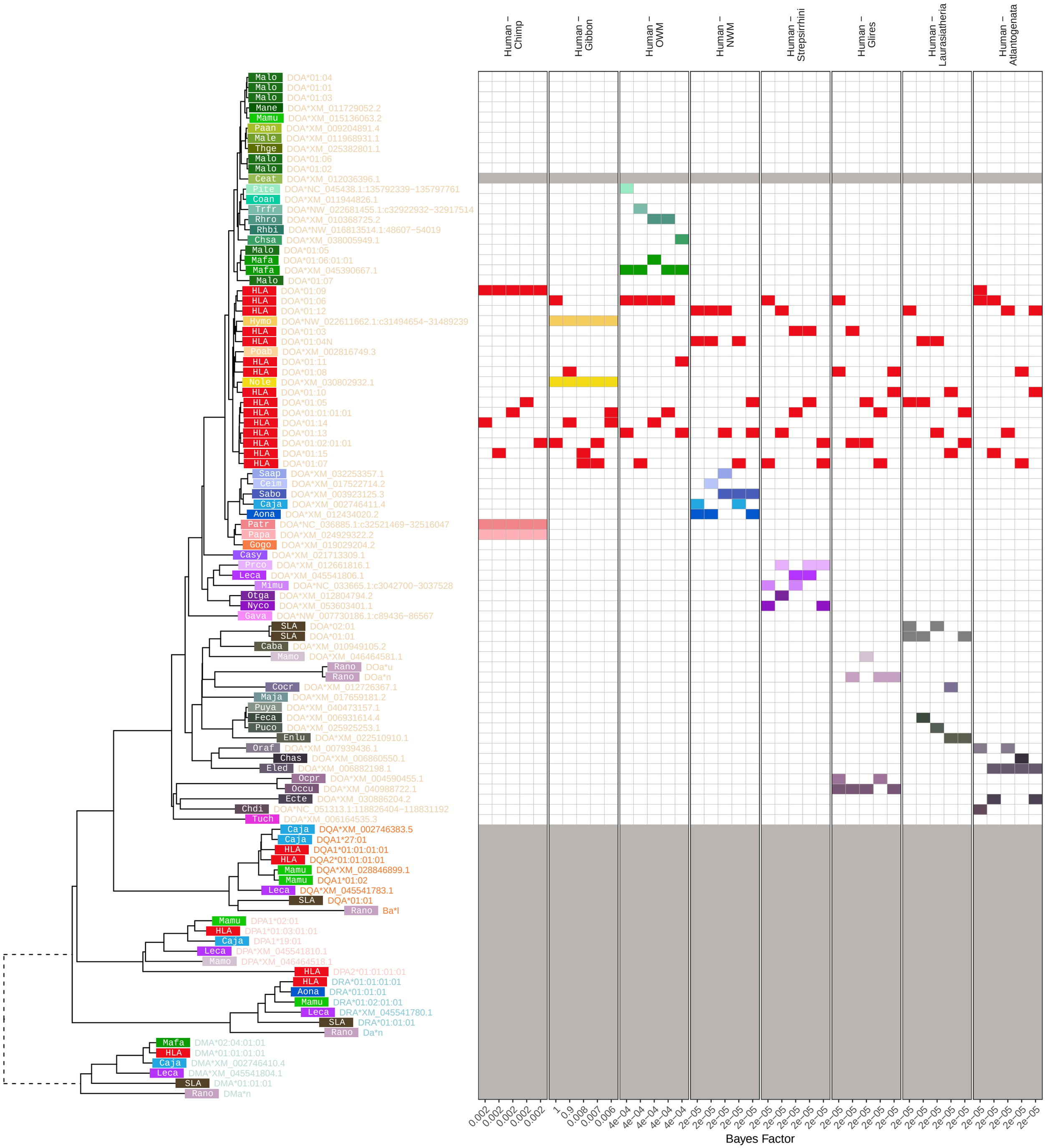
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Human – OWM
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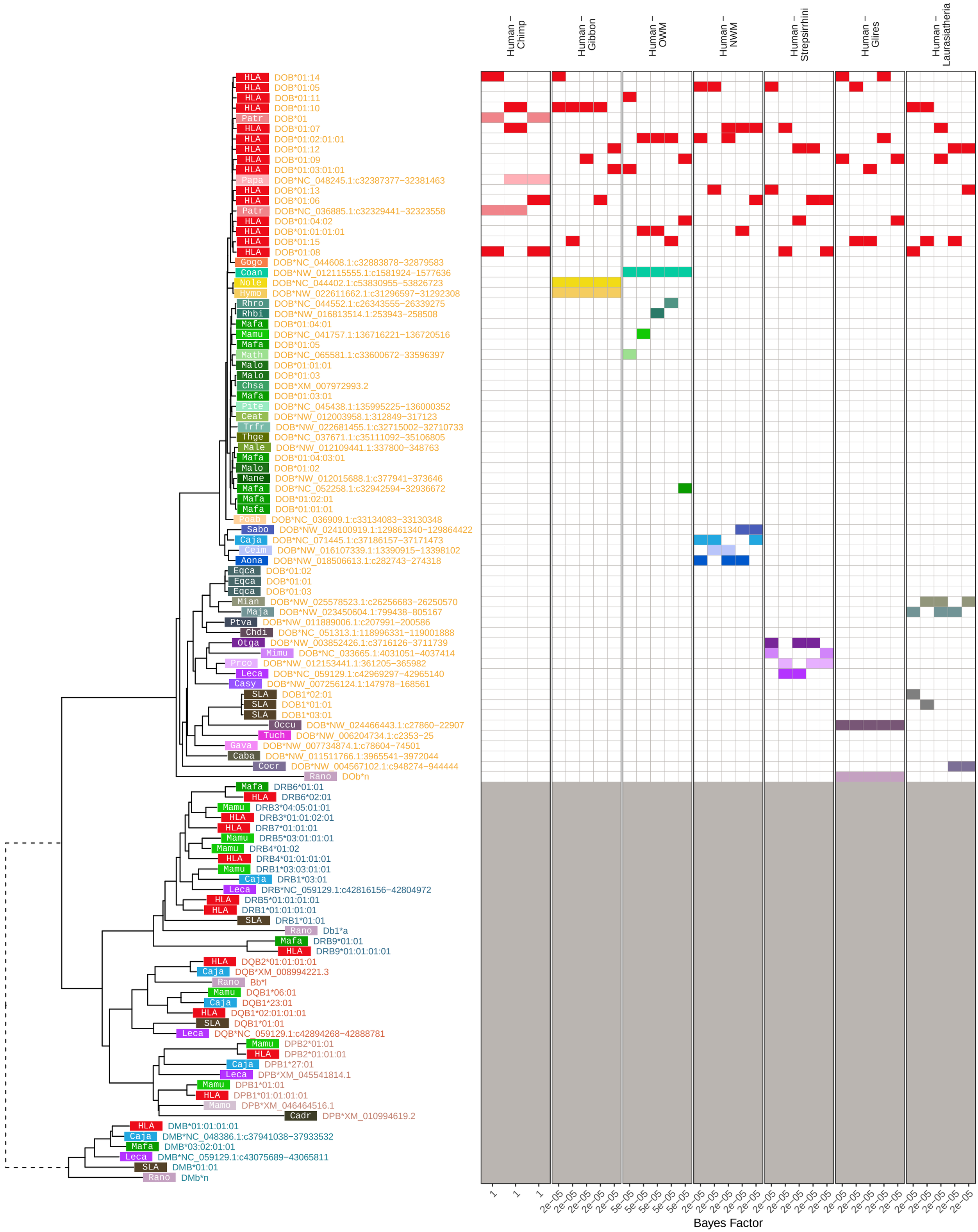
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Human – Gibbon
Human – OWM
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Rhro DOB*NC_044552.1:c26343555−26339275
Rhbi DOB*NW_016813514.1:253943−258508
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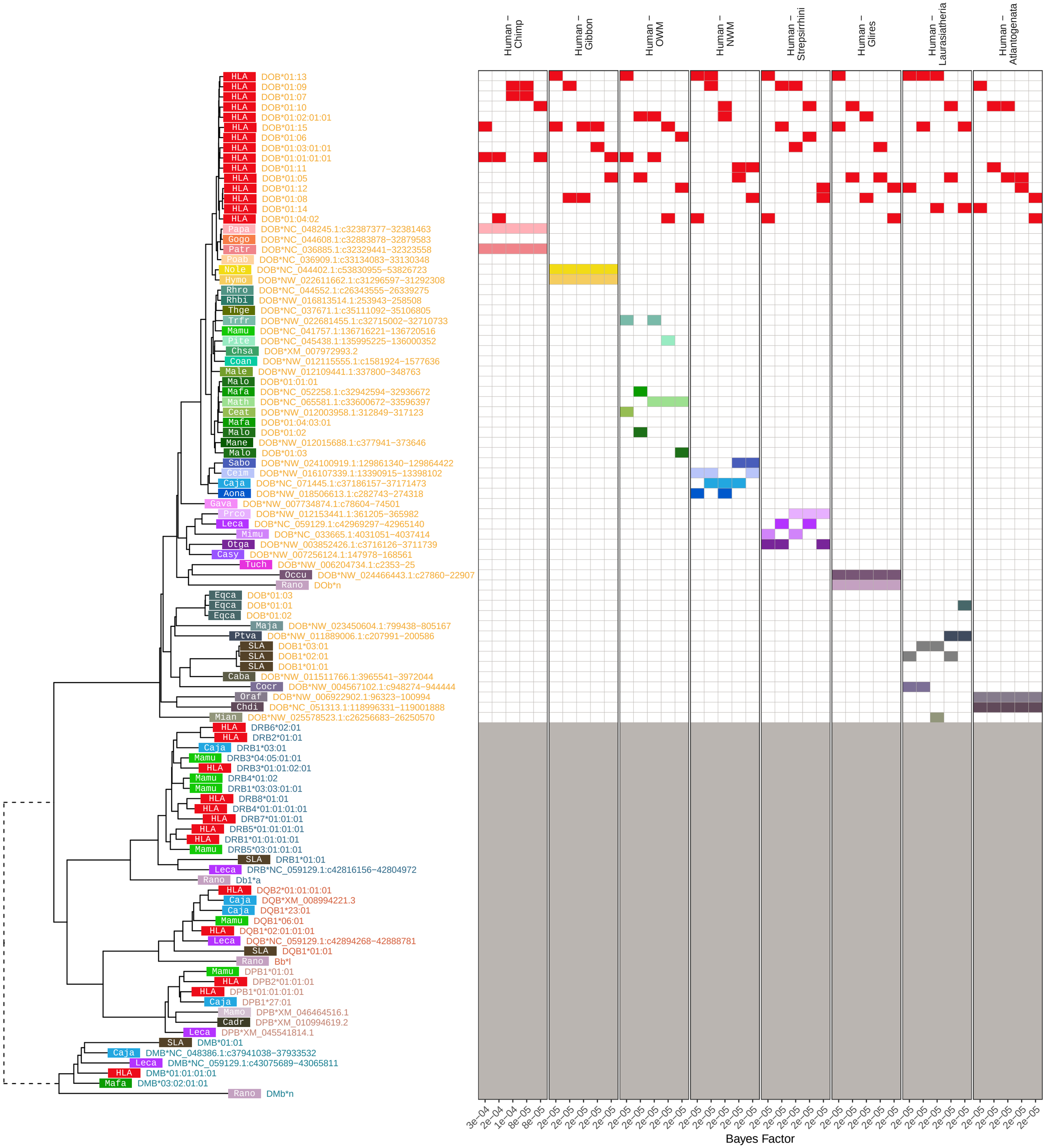
Bayes Factor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Human – Gibbon
Human – OWM
Human – NWM
Human – Strepsirrhini
Human – Glires
Human – Laurasiatheria
Human – Atlantogenata
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Papa DOB*NC_048245.1:c32387377−32381463
Gogo DOB*NC_044608.1:c32883878−32879583
Patr DOB*NC_036885.1:c32329441−32323558
Poab DOB*NC_036909.1:c33134083−33130348
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Hymo DOB*NW_022611662.1:c31296597−31292308
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Coan DOB*NW_012115555.1:c1581924−1577636
Male DOB*NW_012109441.1:337800−348763
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Rano Db1*a
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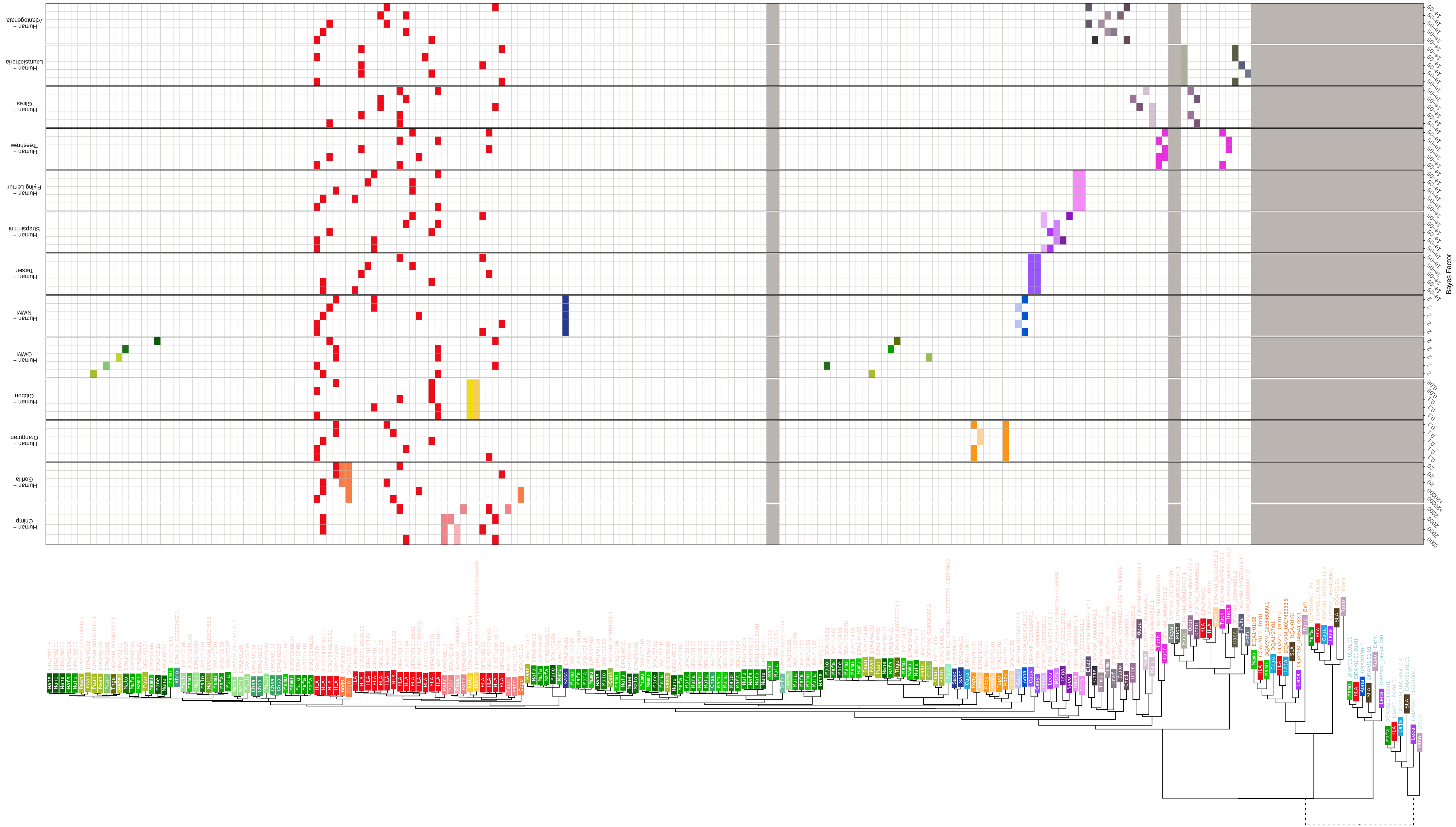
Human – Chimp
Human – Gorilla
Human – Orangutan
Human – Gibbon
Human – OWM
Human – NWM
Human – Tarsier
Human – Strepsirrhini
Human – Flying Lemur
Human – Treeshrew
Human – Glires
Human – Laurasiatheria
Human – Afrotheria
Bayes Factor

Human – Chimp
Human – Gorilla
Human – Orangutan
Human – Gibbon
Human – OWM
Human – NWM
Human – Strepsirrhini
Human – Flying Lemur
Human – Treeshrew
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Human – Laurasiatheria
Human – Atlantogenata
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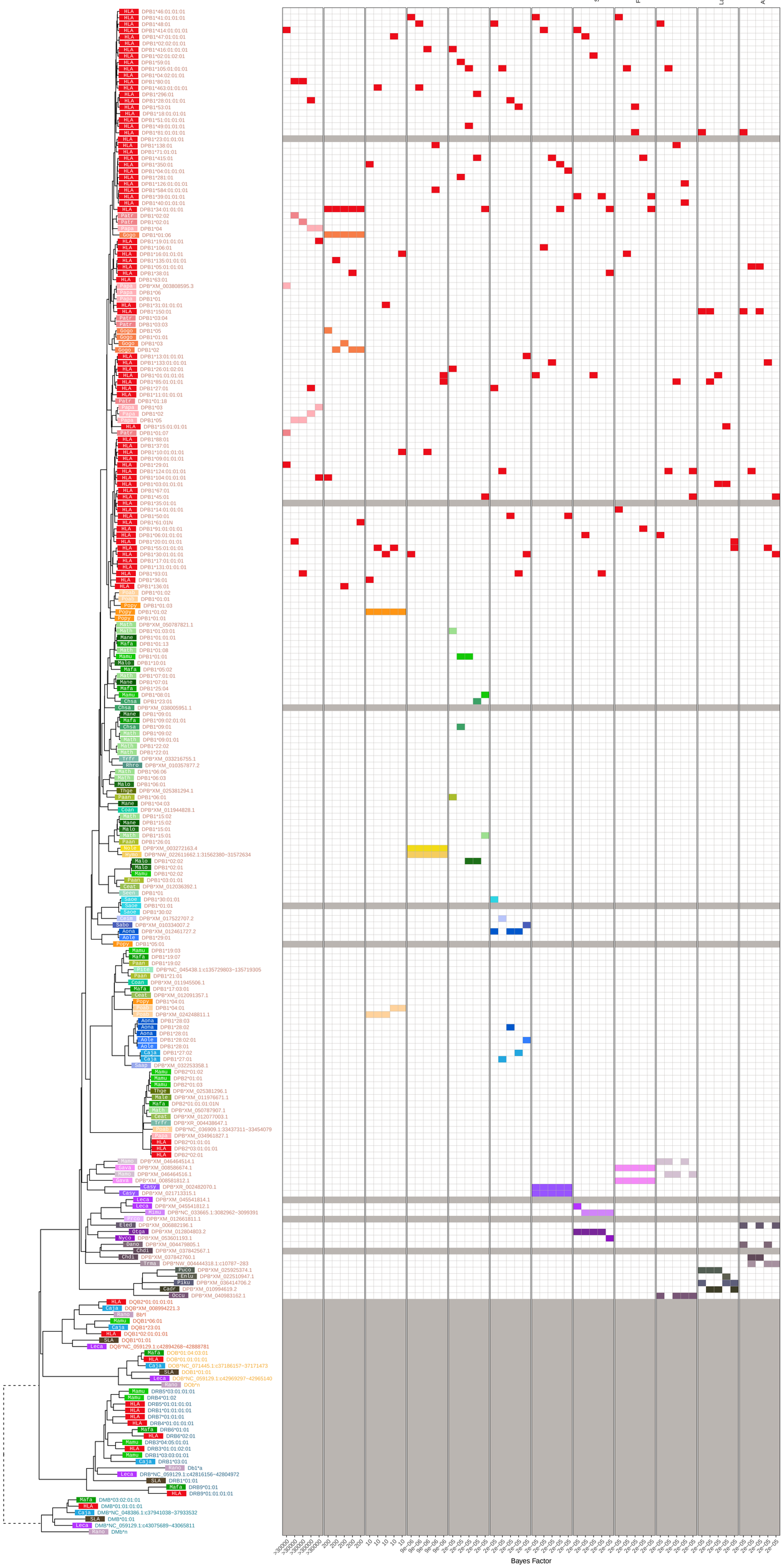
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Human – Gorilla
Human – Orangutan
Human – Gibbon
Human – OWM
Human – NWM
Human – Tarsier
Human – Strepsirrhini
Human – Flying Lemur
Human – Glires
Human – Laurasiatheria
Human – Afrotheria
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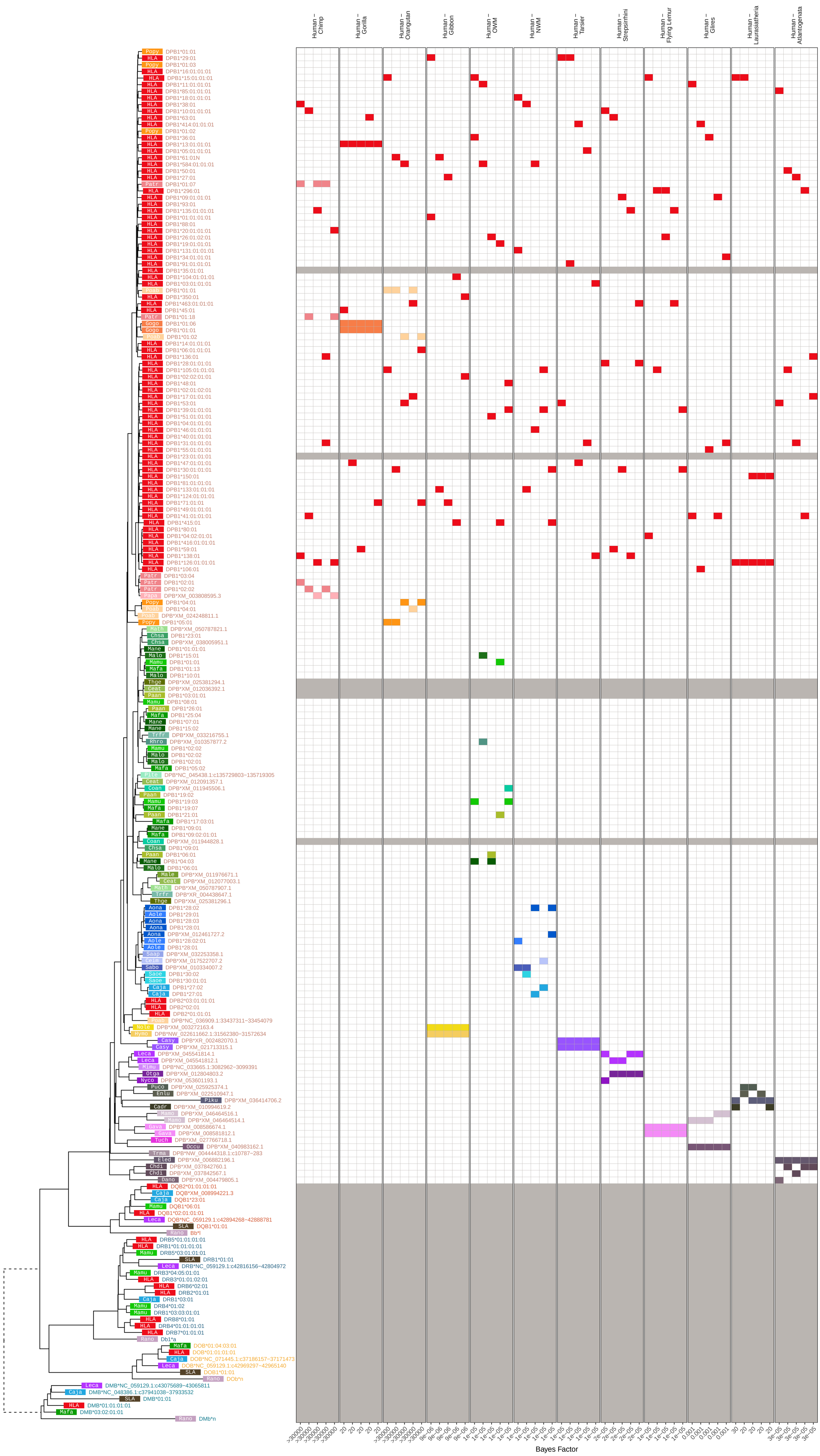
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Human – Glires
Human – Laurasiatheria
Human – Atlantogenata
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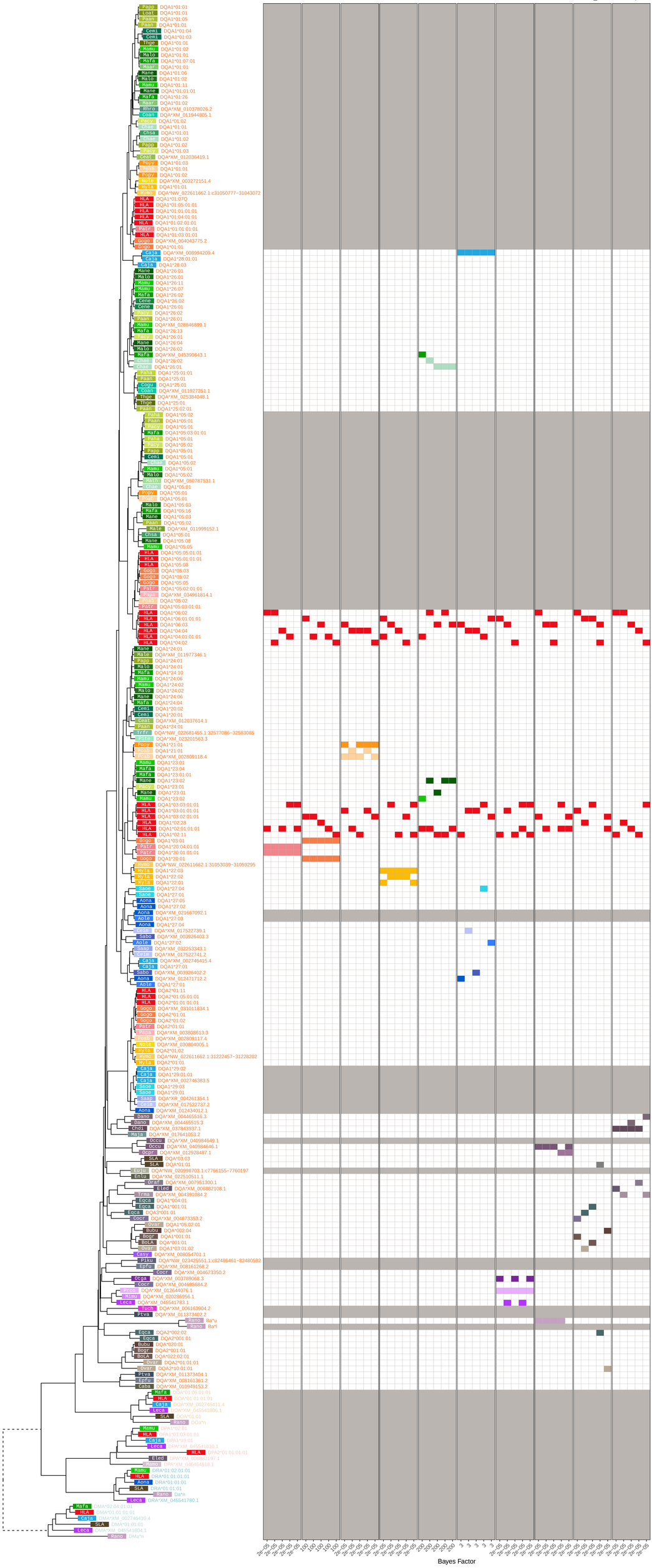
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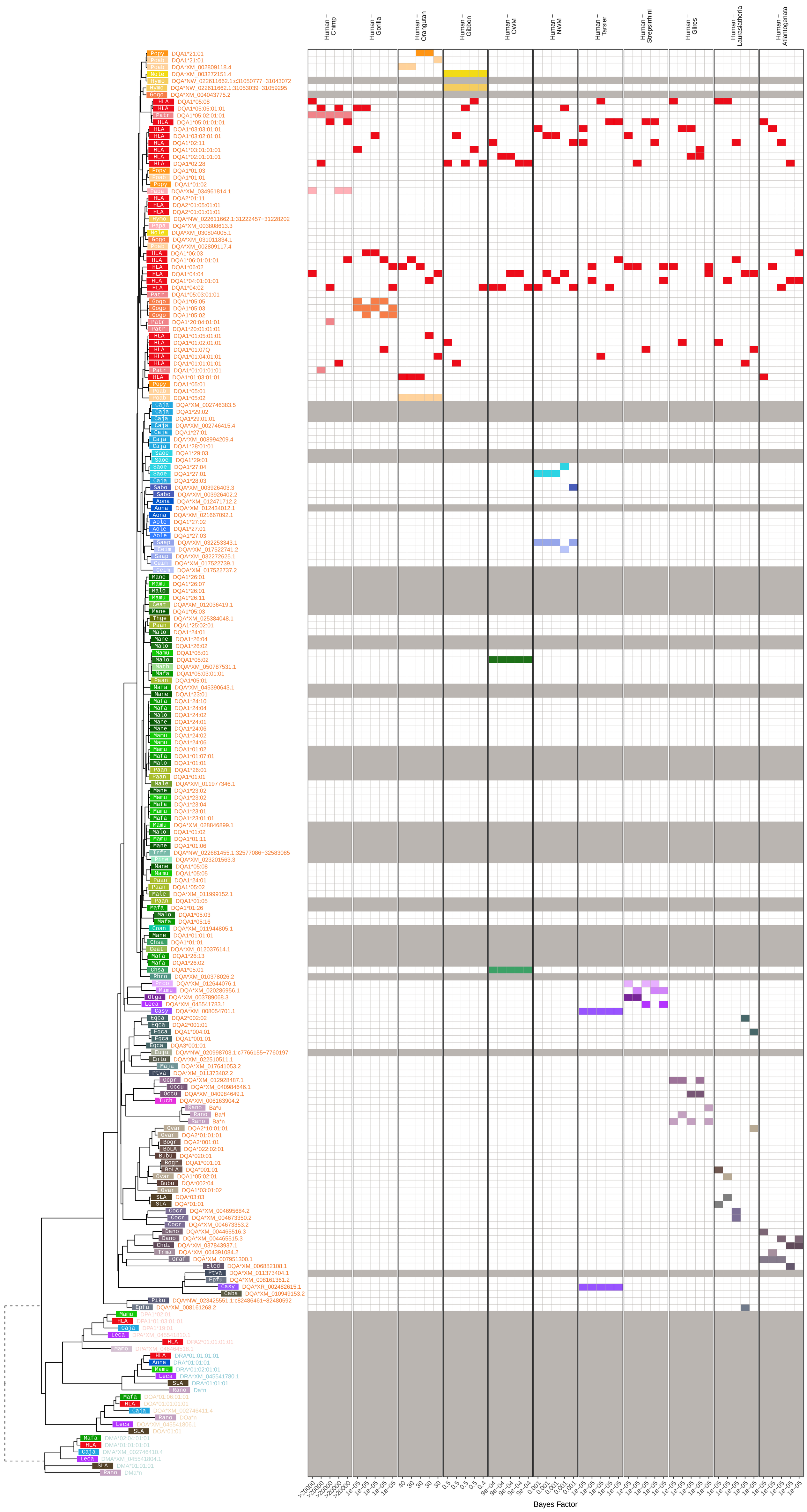
Bayes Factor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Human – Glires
Human – Laurasiatheria
Human – Afrotogenata
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Malo DQA1*24:02
Mane DQA1*24:01
Mane DQA1*24:06
Mamu DQA1*24:02
Mamu DQA1*24:06
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Rano Ba*l
Rano Ba*n
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BoLA DQA*022:02:01
Bubu DQA*020:01
Bogr DQA1*001:01
BoLA DQA*001:01
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Rano Da*n
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Caja DMA*XM_002746410.4
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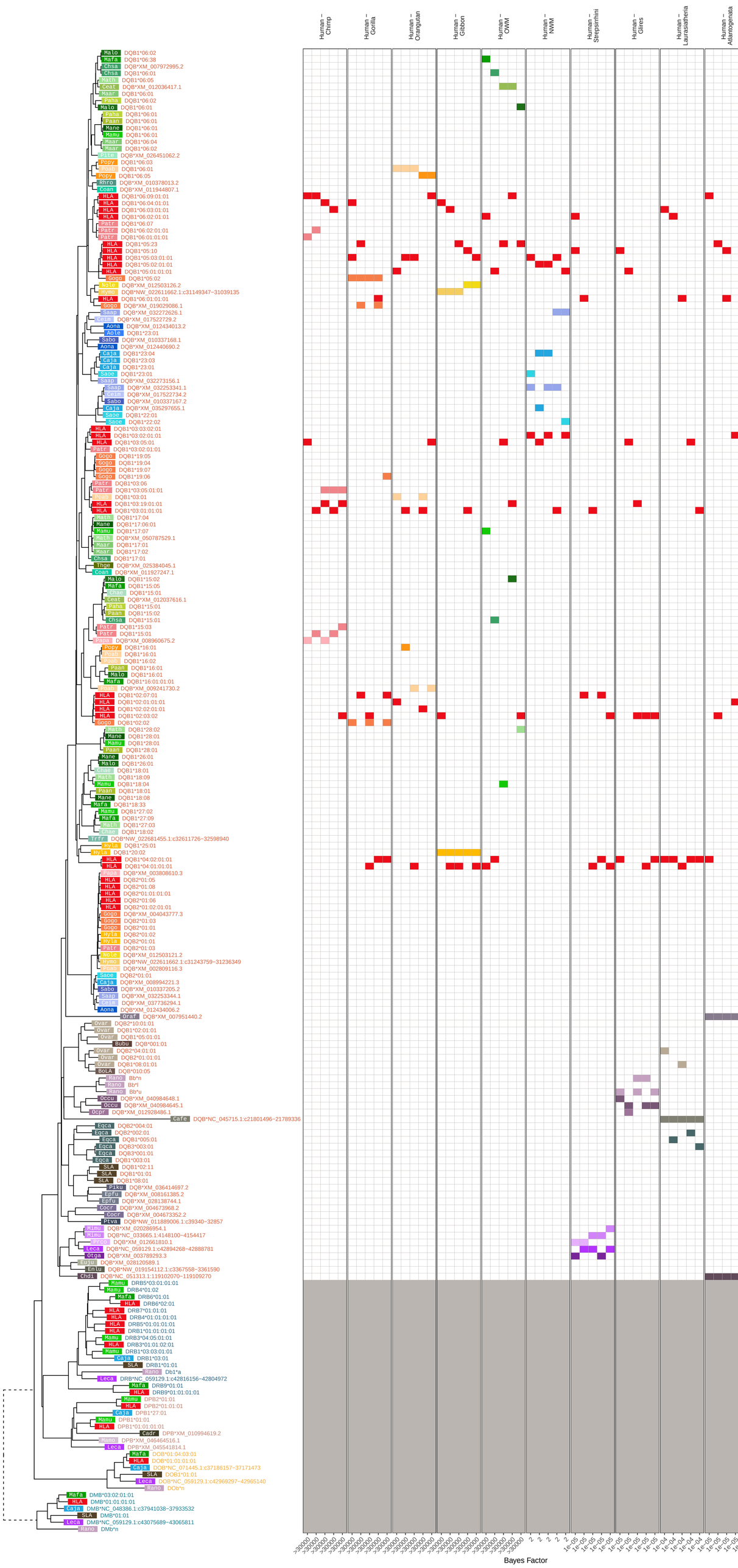
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Human – Gorilla
Human – Orangutan
Human – Gibbon
Human – OWM
Human – NWM
Human – Strepsirrhini
Human – Glires
Human – Laurasiatheria
Human – Atlantogenata
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Coan DQB*XM_011944807.1
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Gogo DQB1*02:02
Math DQB1*28:02
Mane DQB1*28:01
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Paan DQB1*28:01
Mane DQB1*26:01
Malo DQB1*26:01
Chae DQB1*18:01
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Mamu DQB1*18:04
Paan DQB1*18:01
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Bubu DQB*001:01
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Ovar DQB1*08:01:01
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Ranc Bb*l
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SLA DQB1*08:01
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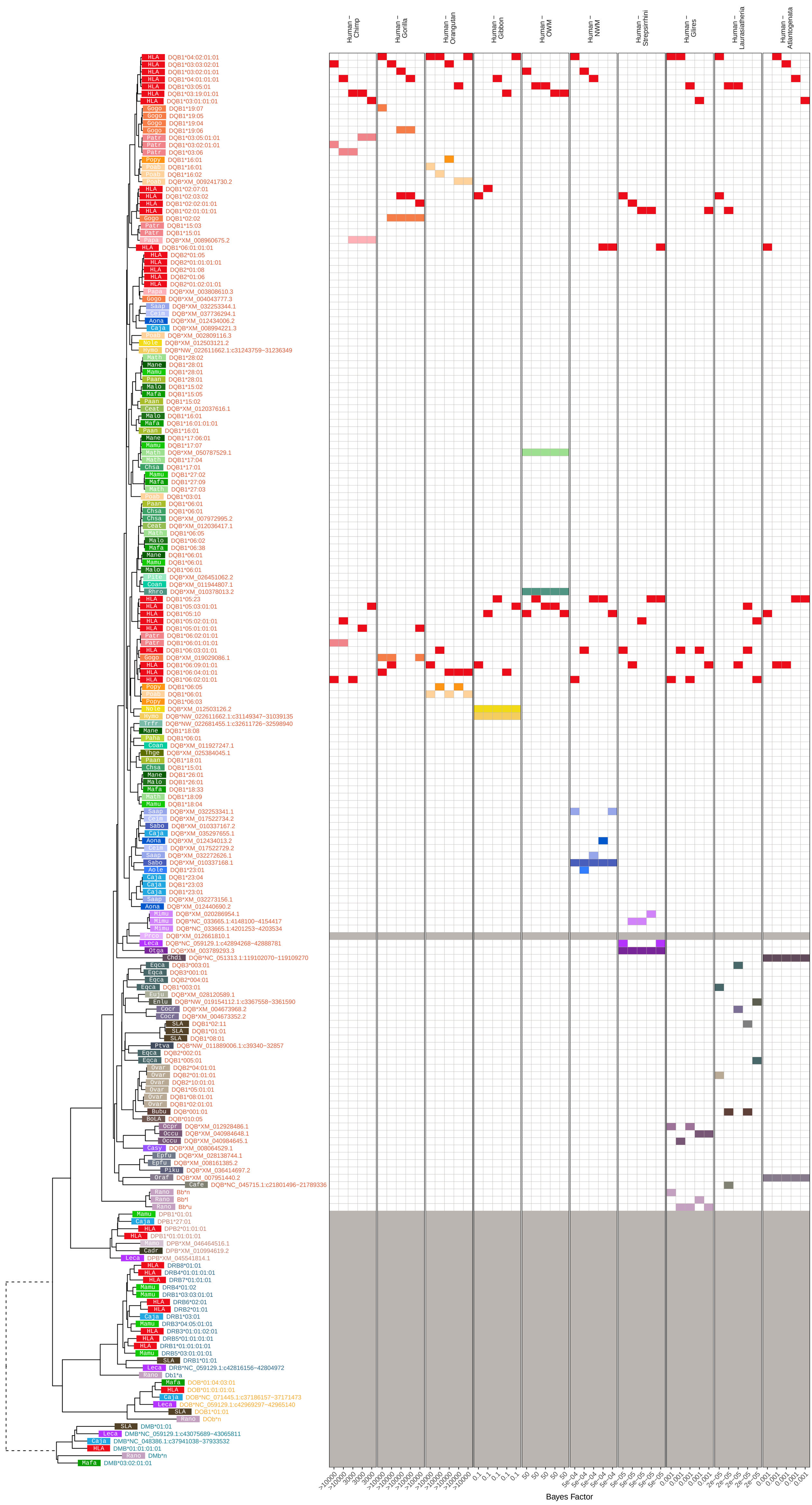
Human – Chimp
Human – Gorilla
Human – Orangutan
Human – Gibbon
Human – OWM
Human – NWM
Human – Strepsirrhini
Human – Glires
Human – Laurasiatheria
Human – Atlantogenata
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Gogo DQB1*19:07
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Gogo DQB1*02:02
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Saap DQB*XM_032253344.1
Ceim DQB*XM_037736294.1
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Chdi DQB*NC_051313.1:119102070−119109270
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Rano Bb*l
Rano Bb*u
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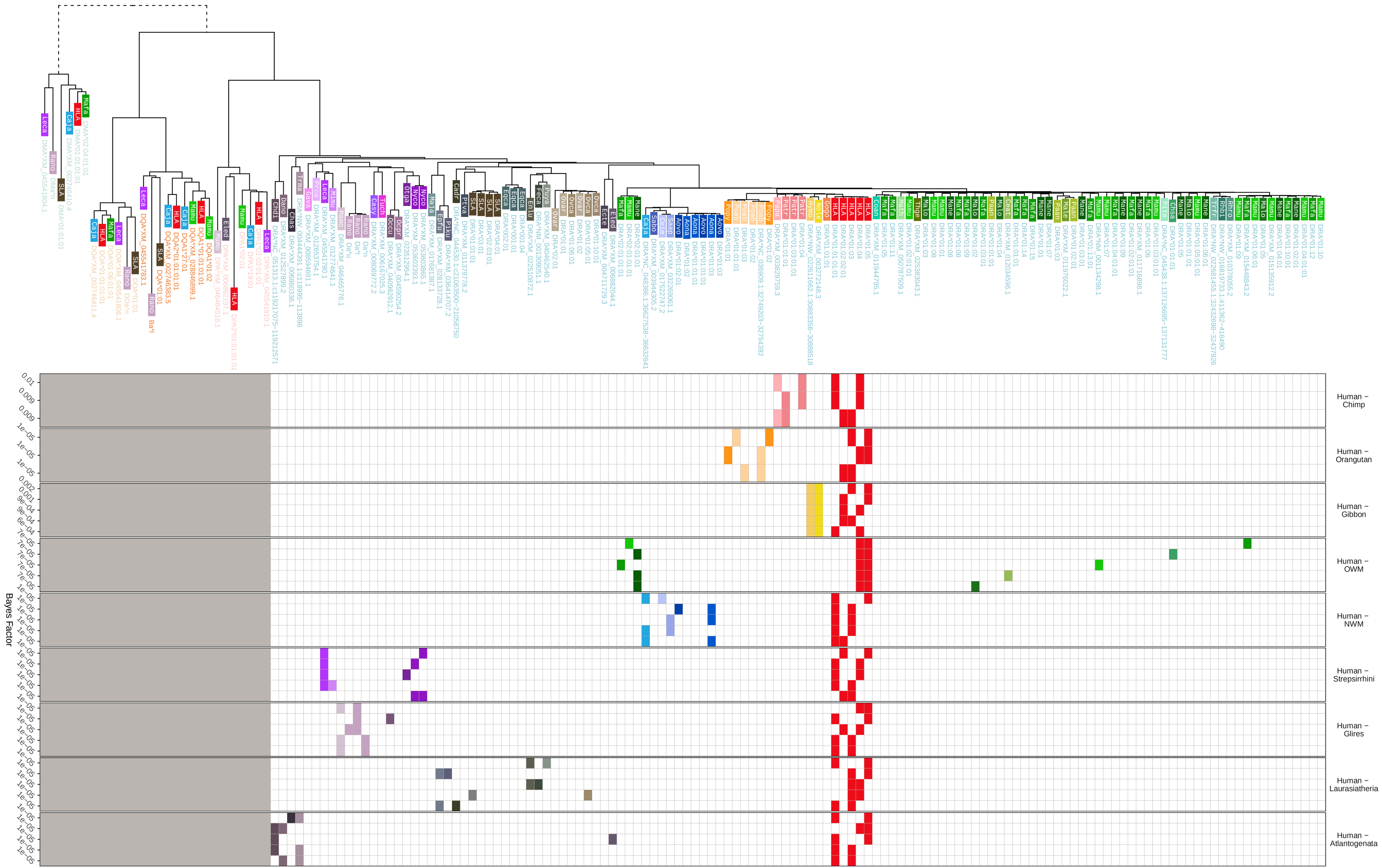
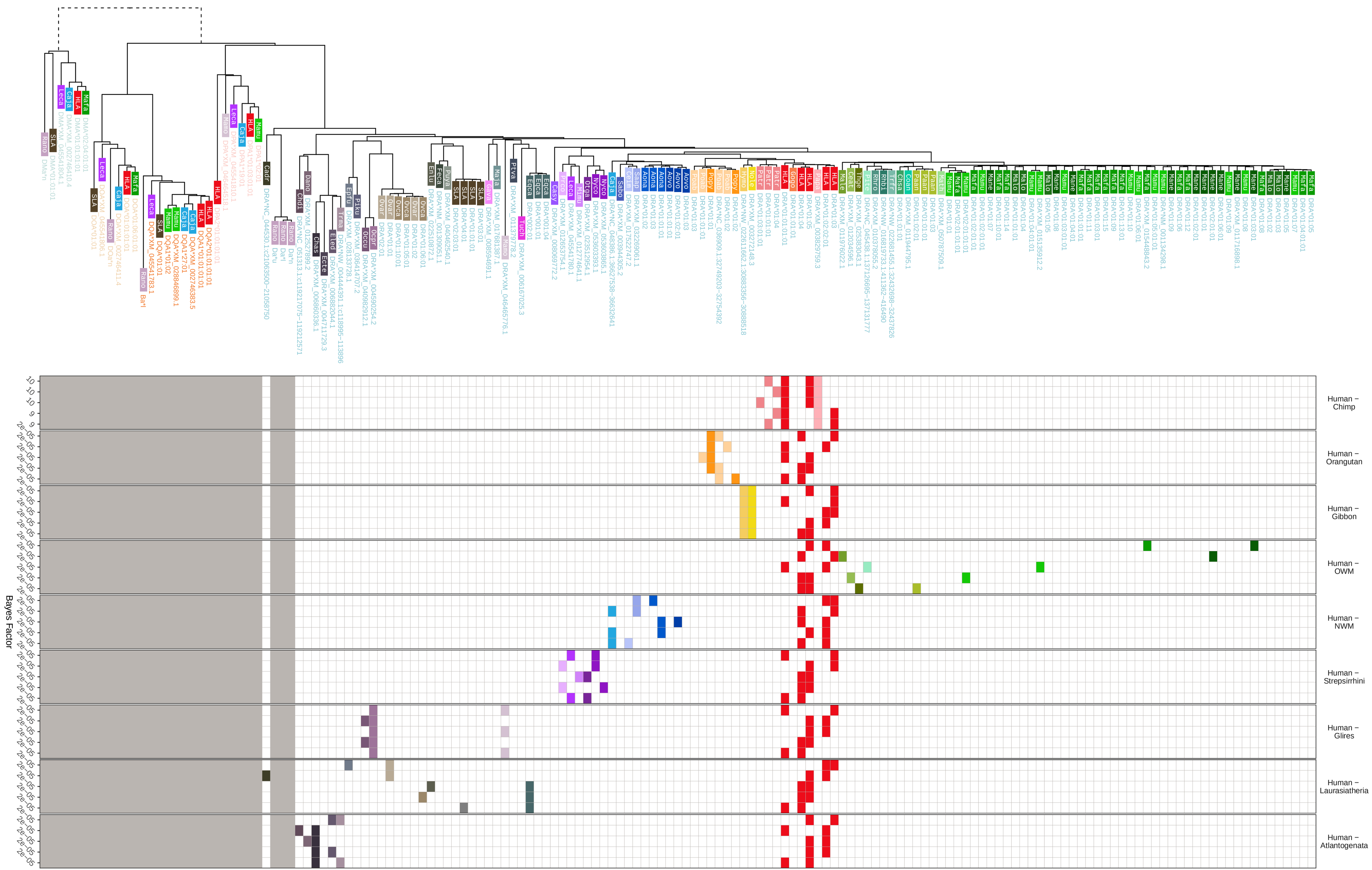
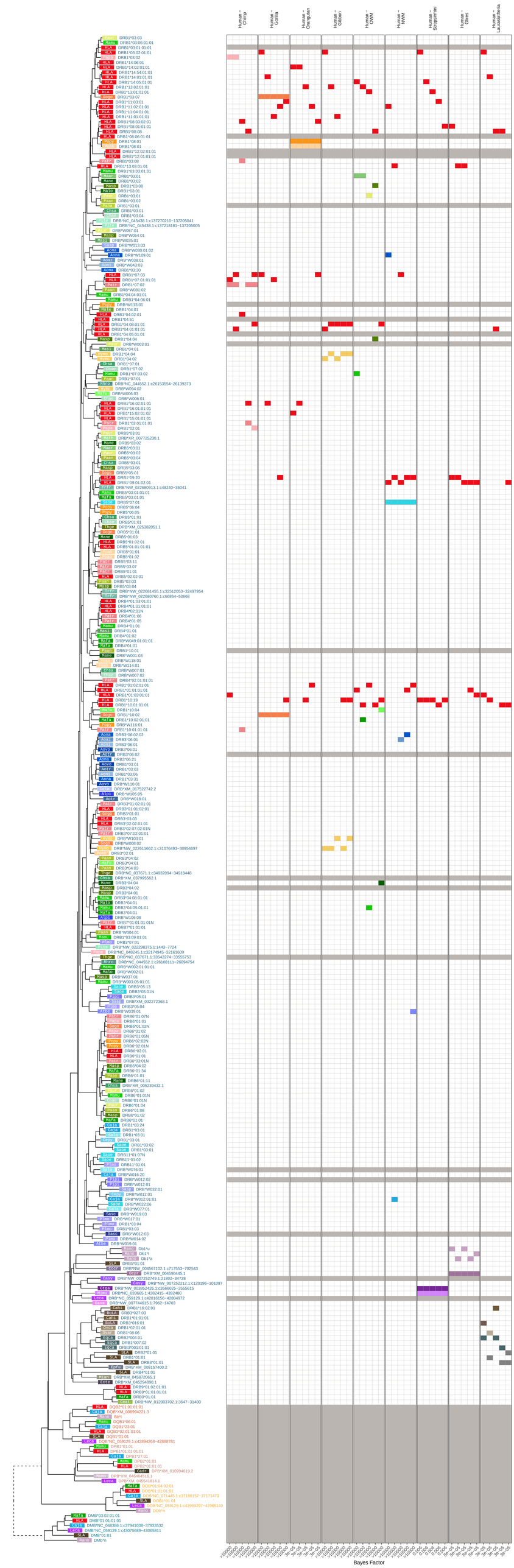
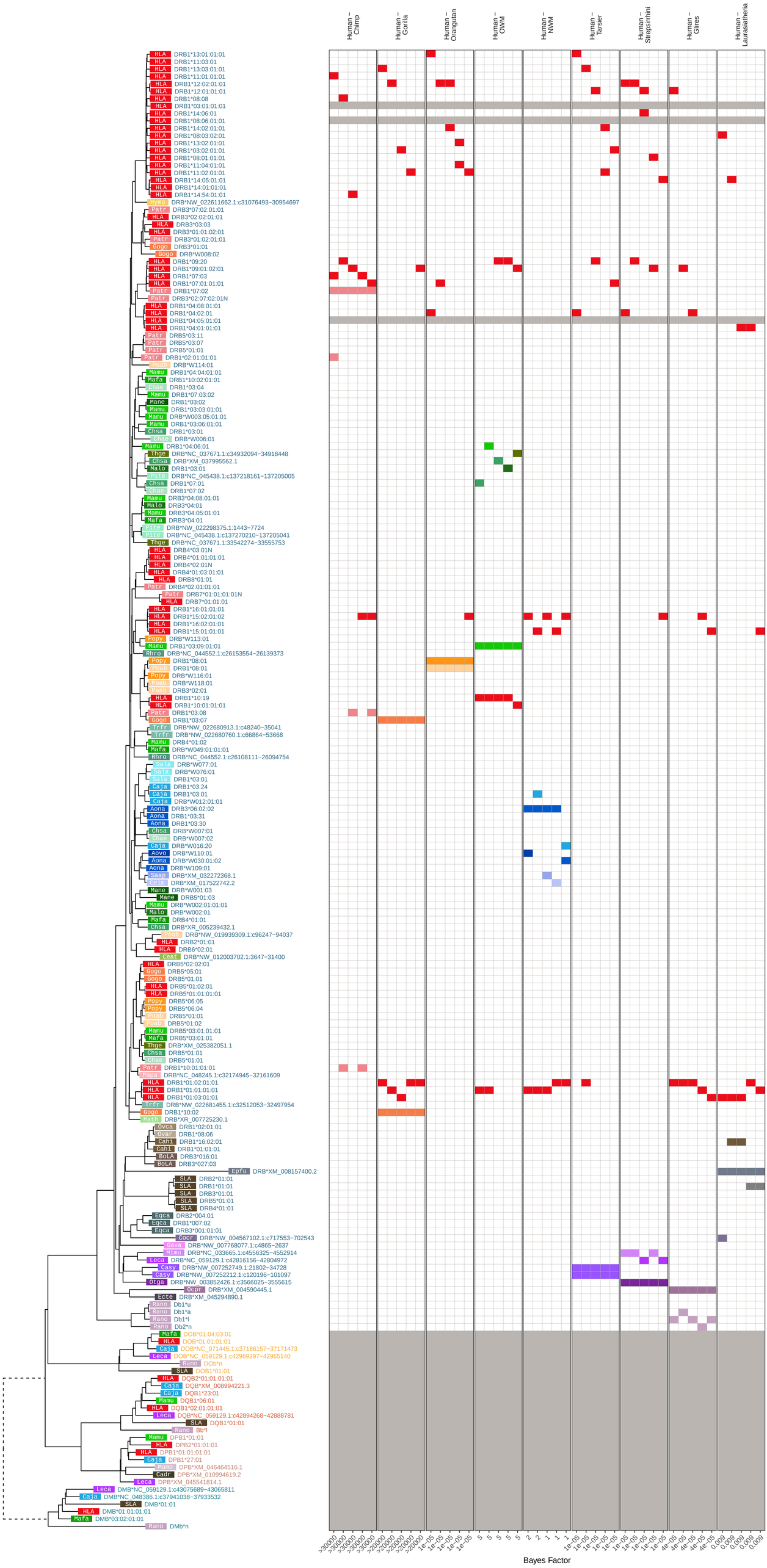
Bayes Factor


Bayes Factor
Human − Chimp
Human − Orangutan
Human − Gibbon
Human − OWM
Human − NWM
Human − Strepsirrhini
Human − Glires
Human − Laurasiatheria
Human − Atlantogenata


Bayes Factor
Human − Chimp
Human − Orangutan
Human − Gibbon
Human − OWM
Human − NWM
Human − Strepsirrhini
Human − Glires
Human − Laurasiatheria
Human − Atlantogenata


Human – Chimp
Human – Gorilla
Human – Orangutan
Human – Gibbon
Human – OWM
Human – NWM
Human – Strepsirrhini
Human – Chiro
Human – Laurasiatheria
Bayes Factor


Human – Chimp
Human – Gorilla
Human – Orangutan
Human – OWM
Human – NWM
Human – Tarsier
Human – Strepsirrhini
Human – Gibres
Human – Laurasiatheria
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Gogo DRB3*01:01
Gogo DRB*W008:02
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Patr DRB1*07:02
Patr DRB3*02:07:02:01N
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Patr DRB5*03:11
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Poab DRB*W114:01
Mamu DRB1*04:04:01:01
Mafa DRB1*10:02:01:01
Chae DRB1*03:04
Mamu DRB1*07:03:02
Mane DRB1*03:02
Mamu DRB1*03:03:01:01
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Chae DRB*W006:01
Mamu DRB1*04:06:01
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Pite DRB*NC_045438.1:c137218161–137205005
Chsa DRB1*07:01
Chae DRB1*07:02
Mamu DRB3*04:08:01:01
Malo DRB3*04:01
Mamu DRB3*04:05:01:01
Mafa DRB3*04:01
Pite DRB*NW_022298375.1:1443–7724
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Thge DRB*NC_037671.1:33542274–33555753
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Aona DRB1*03:30
Chsa DRB*W007:01
Chae DRB*W007:02
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Aona DRB*W109:01
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Poab DRB5*01:01
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Chae DRB5*01:01
Patr DRB1*10:01:01:01
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Math DRB*XR_007725230.1
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Ovar DRB1*08:06
Cahi DRB1*16:02:01
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BoLA DRB3*016:01
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Casy DRB*NW_007252749.1:21802–34728
Casy DRB*NW_007252212.1:c120196–101097
Otga DRB*NW_003852426.1:c3566025–3555615
Ocpr DRB*XM_004590445.1
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Rano Db1*a
Rano Db1*l
Rano Db2*n
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5 5 5 5 5
2 2 1 1 1
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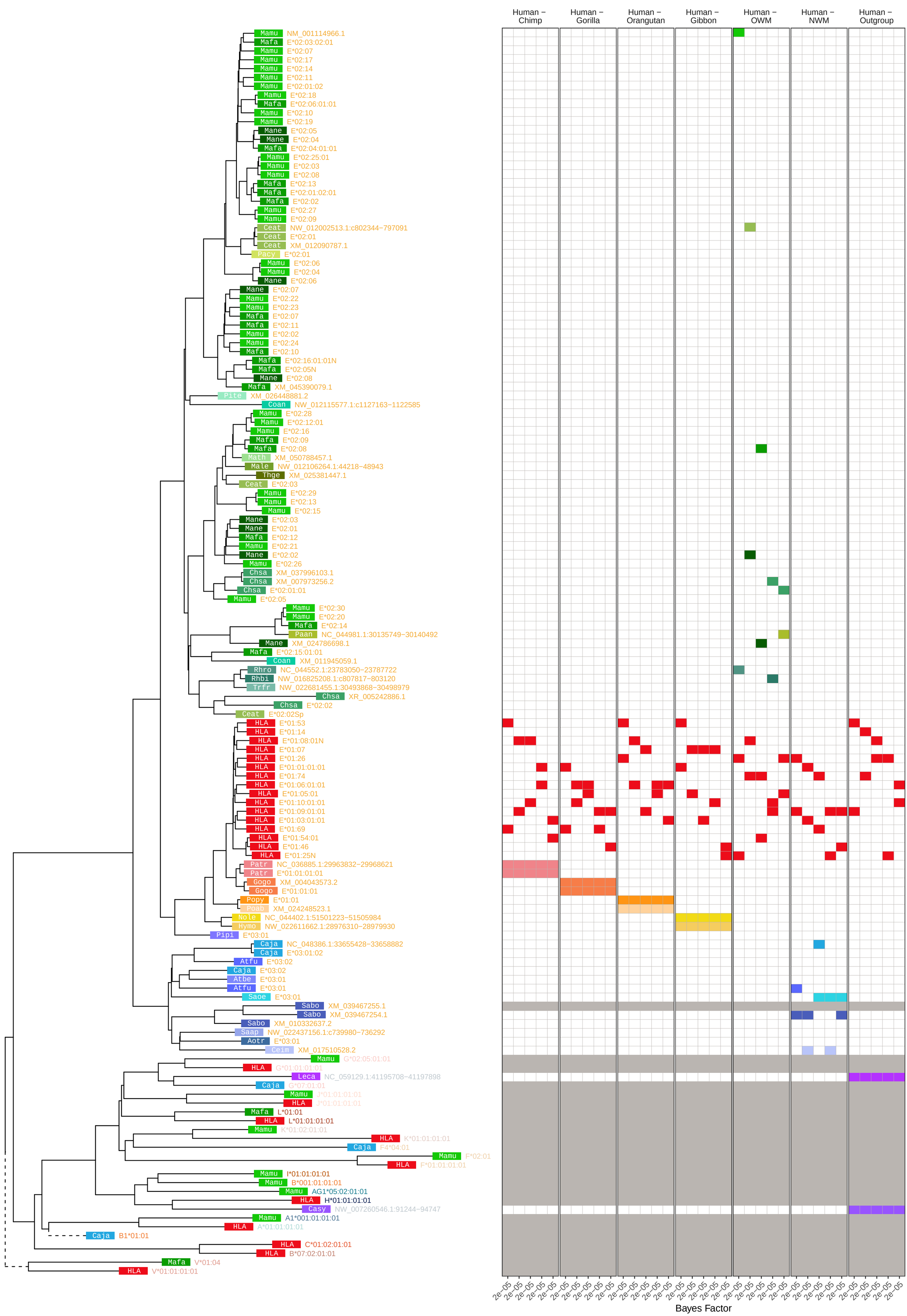
Bayes Factor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Human − Gorilla
Human − Orangutan
Human − Gibbon
Human − OWM
Human − NWM
Human − Outgroup
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Mamu E*02:11
Mamu E*02:01:02
Mamu E*02:18
Mafa E*02:06:01:01
Mamu E*02:10
Mamu E*02:19
Mane E*02:05
Mane E*02:04
Mafa E*02:04:01:01
Mamu E*02:25:01
Mamu E*02:03
Mamu E*02:08
Mafa E*02:13
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Mafa E*02:02
Mamu E*02:27
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Ceat XM_012090787.1
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Mamu E*02:04
Mane E*02:06
Mane E*02:07
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Mamu E*02:23
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Mafa E*02:09
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Mafa E*02:12
Mamu E*02:21
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Pipi E*03:01
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Sabo XM_010332637.2
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Mamu B*001:01:01:01
Mamu AG1*05:02:01:01
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Caja B1*01:01
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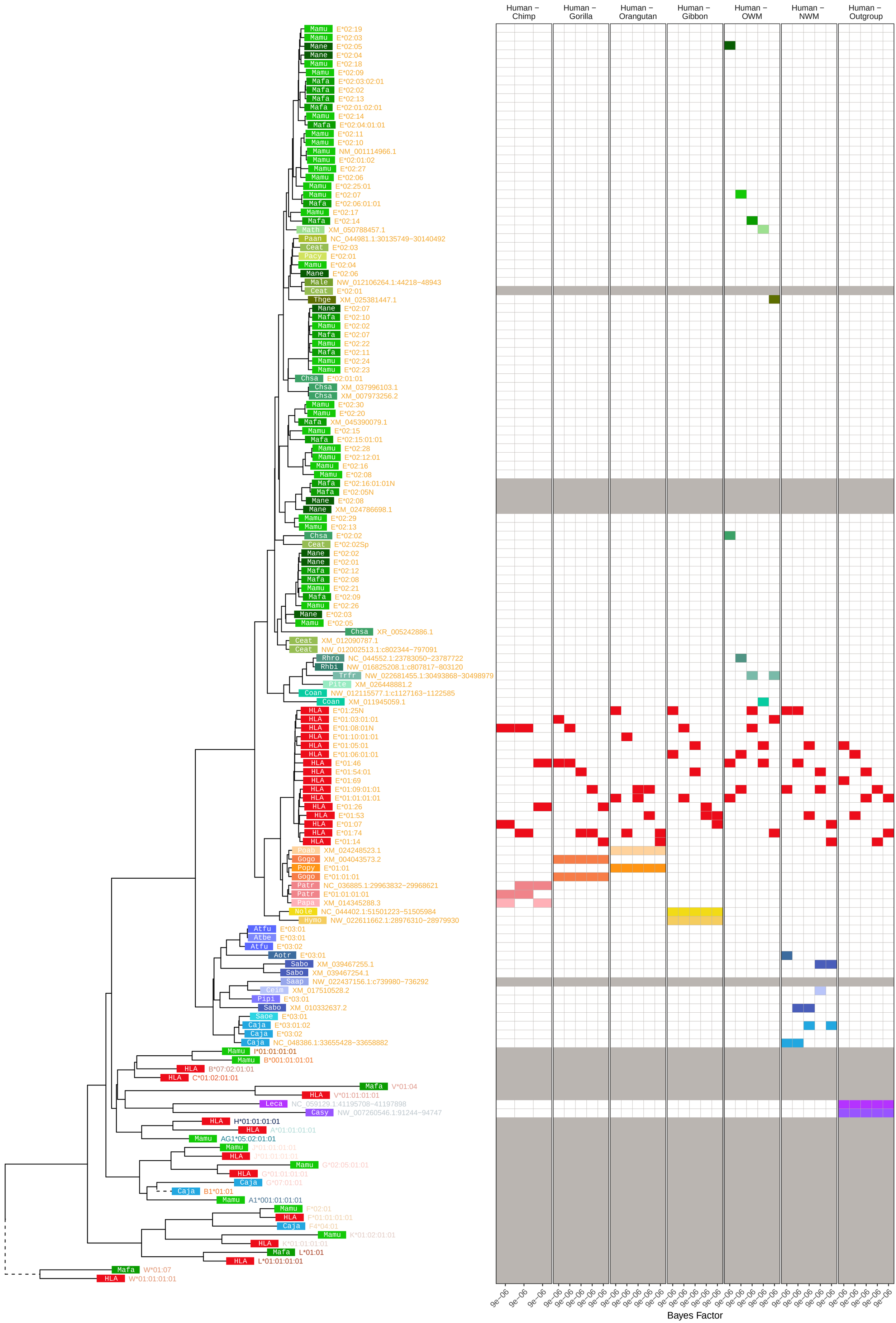
Bayes Factor


Human − Chimp
Human − Gorilla
Human − Orangutan
Human − Gibbon
Human − OWM
Human − NWM
Human − Outgroup
Mamu E*02:19
Mamu E*02:03
Mane E*02:05
Mane E*02:04
Mamu E*02:18
Mamu E*02:09
Mafa E*02:03:02:01
Mafa E*02:02
Mafa E*02:13
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Mamu E*02:14
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Mamu E*02:10
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Mamu E*02:27
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Ceat E*02:03
Pacy E*02:01
Mamu E*02:04
Mane E*02:06
Male NW_012106264.1:44218−48943
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Trfr NW_022681455.1:30493868−30498979
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Aotr E*03:01
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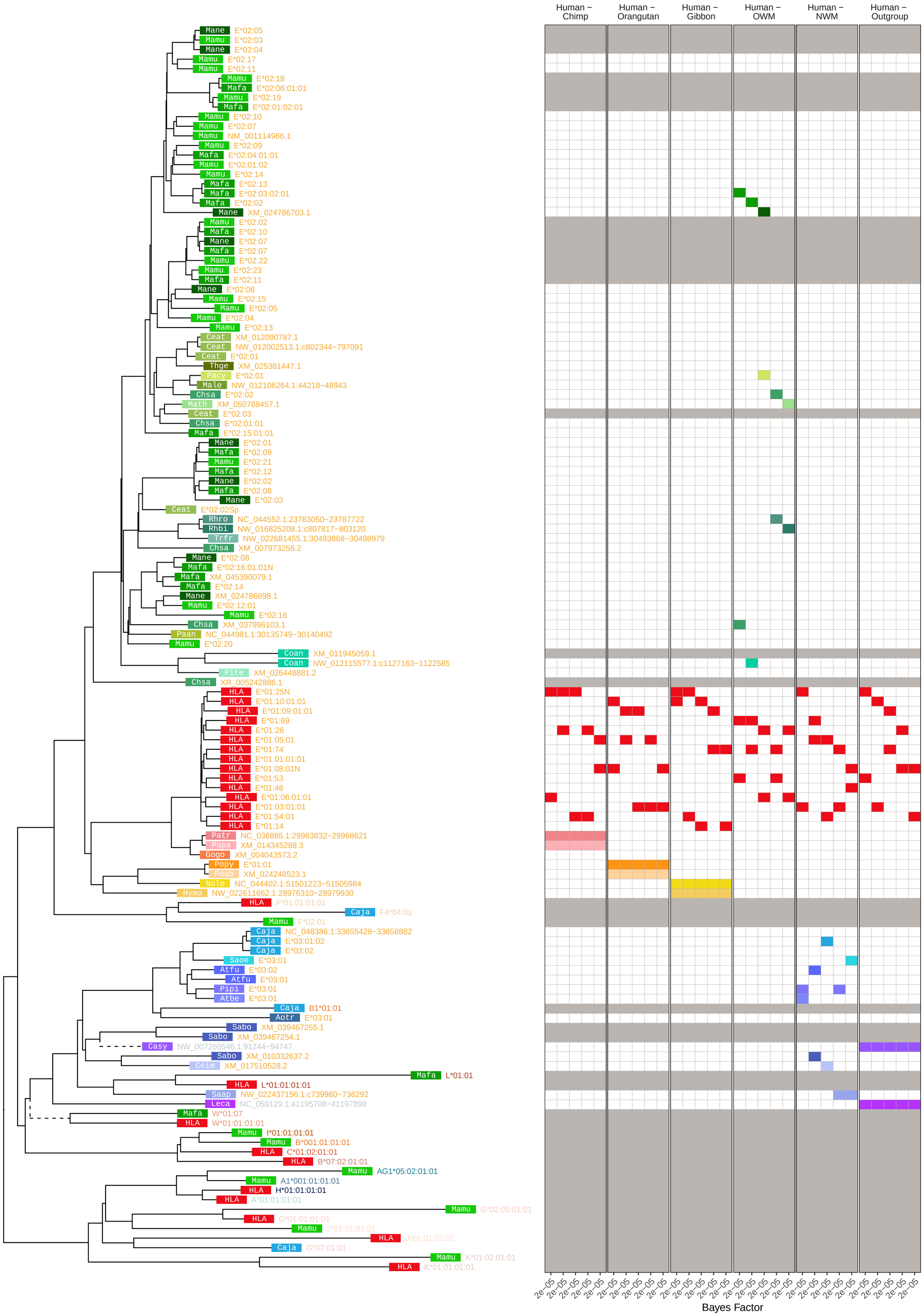
Bayes Factor


Human − Chimp
Human − Orangutan
Human − Gibbon
Human − OWM
Human − NWM
Human − Outgroup
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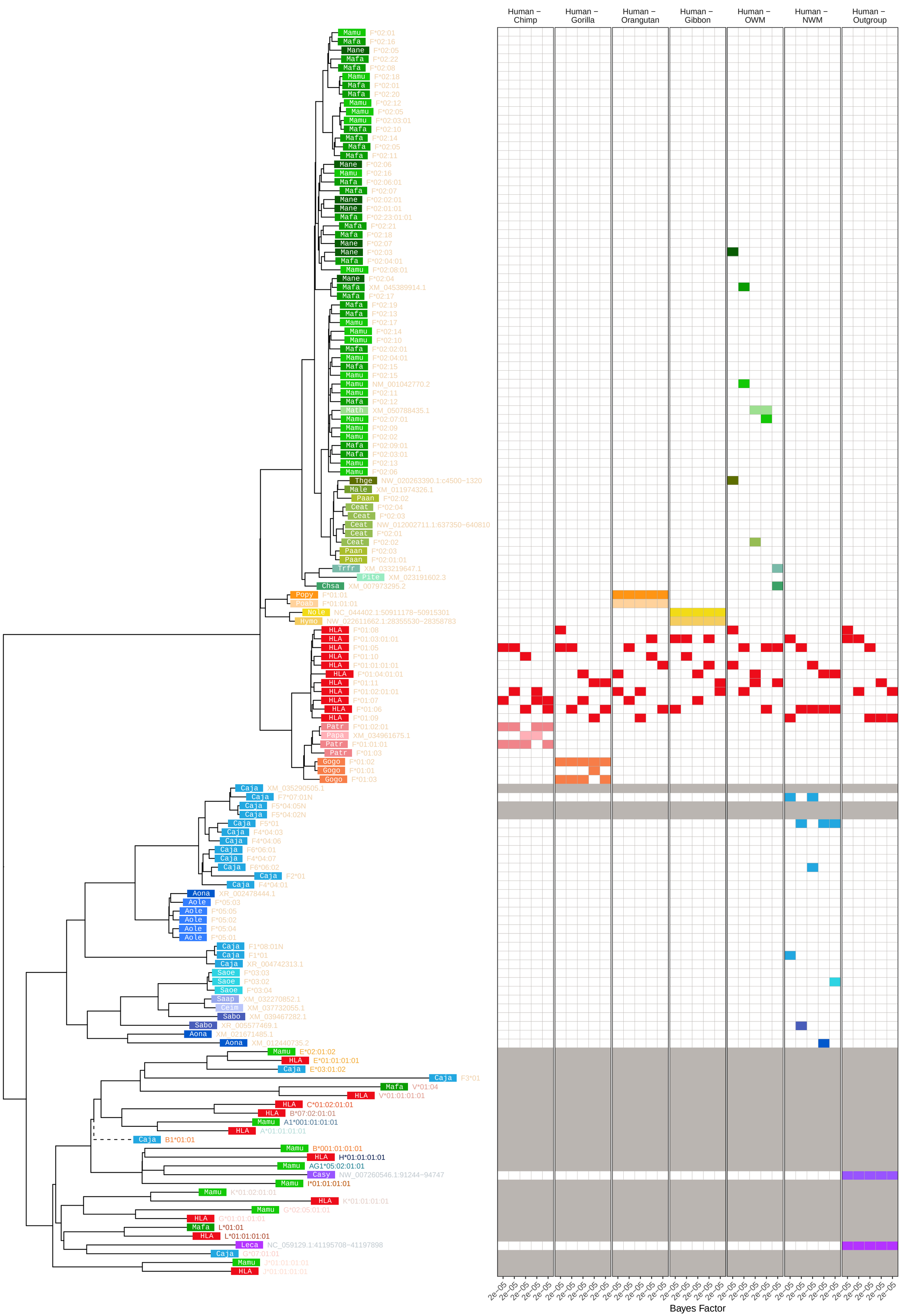
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Human − OWM
Human − NWM
Human − Outgroup
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Sabo XR_005577469.1
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Aona XM_012440735.2
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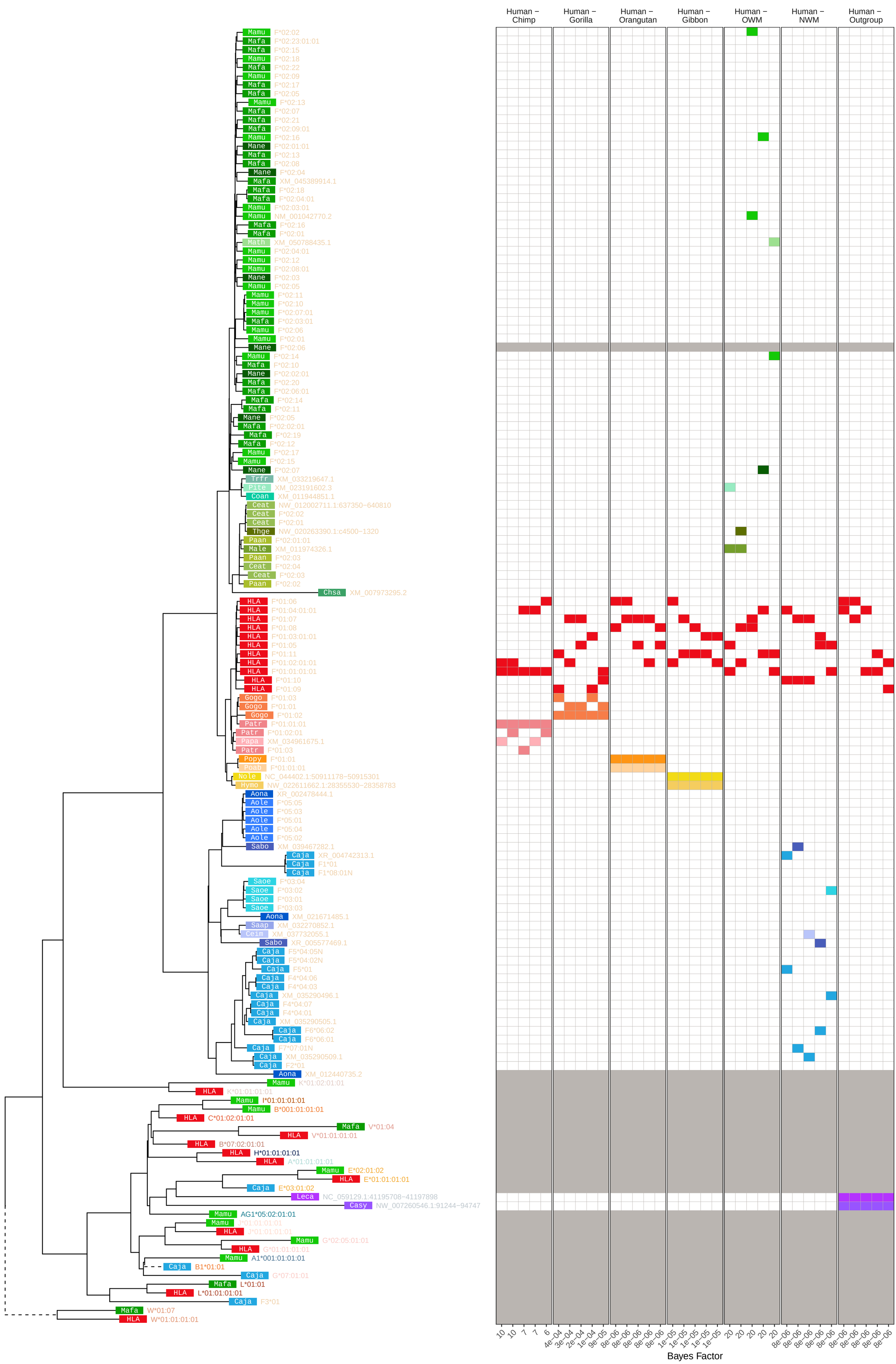
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Human − Outgroup
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Mamu F*02:07:01
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Mamu G*02:05:01:01
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Mamu A1*001:01:01:01
Caja B1*01:01
Caja G*07:01:01
Mafa L*01:01
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Caja F3*01
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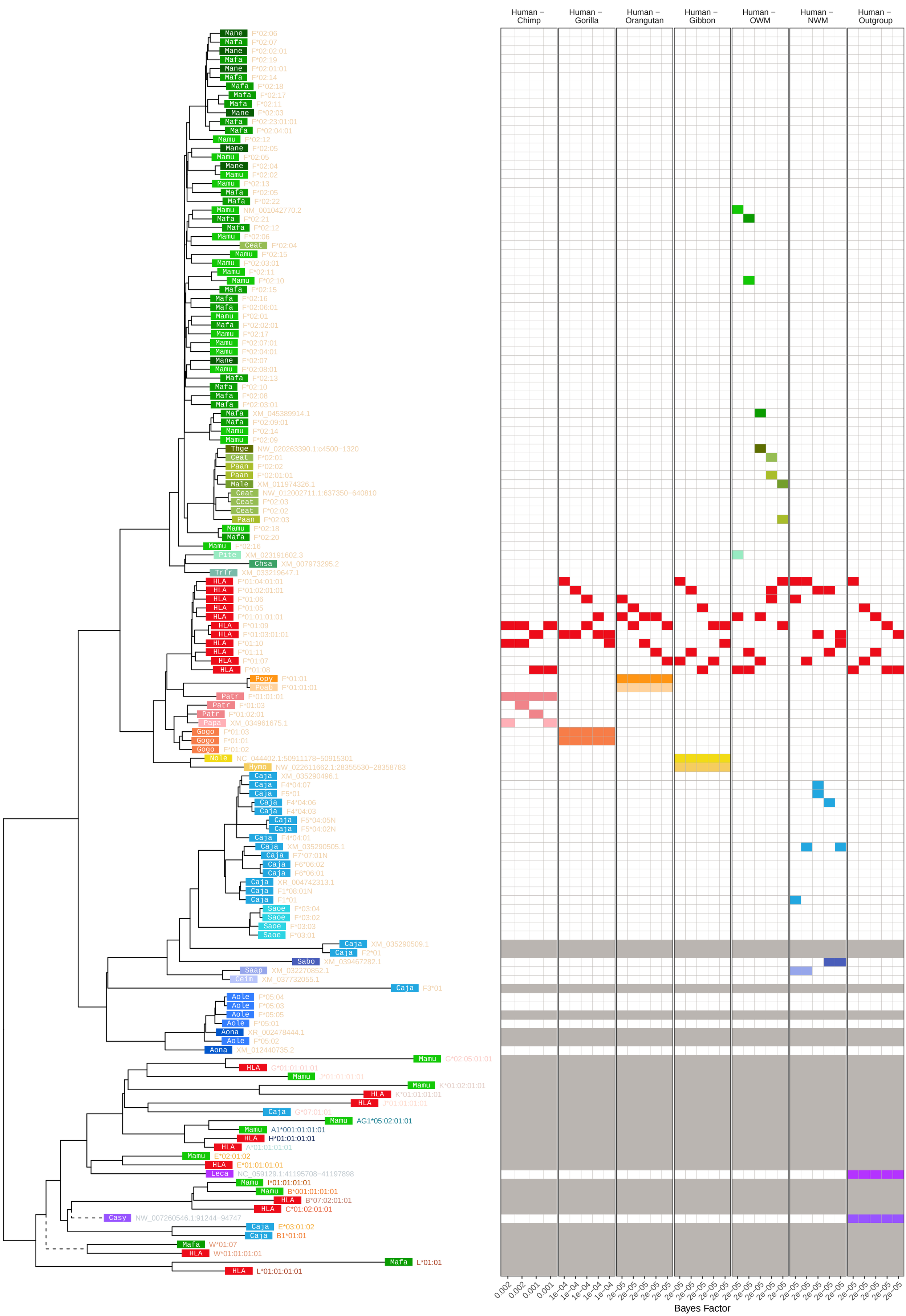
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Human − Orangutan
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Human − OWM
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Human − Outgroup
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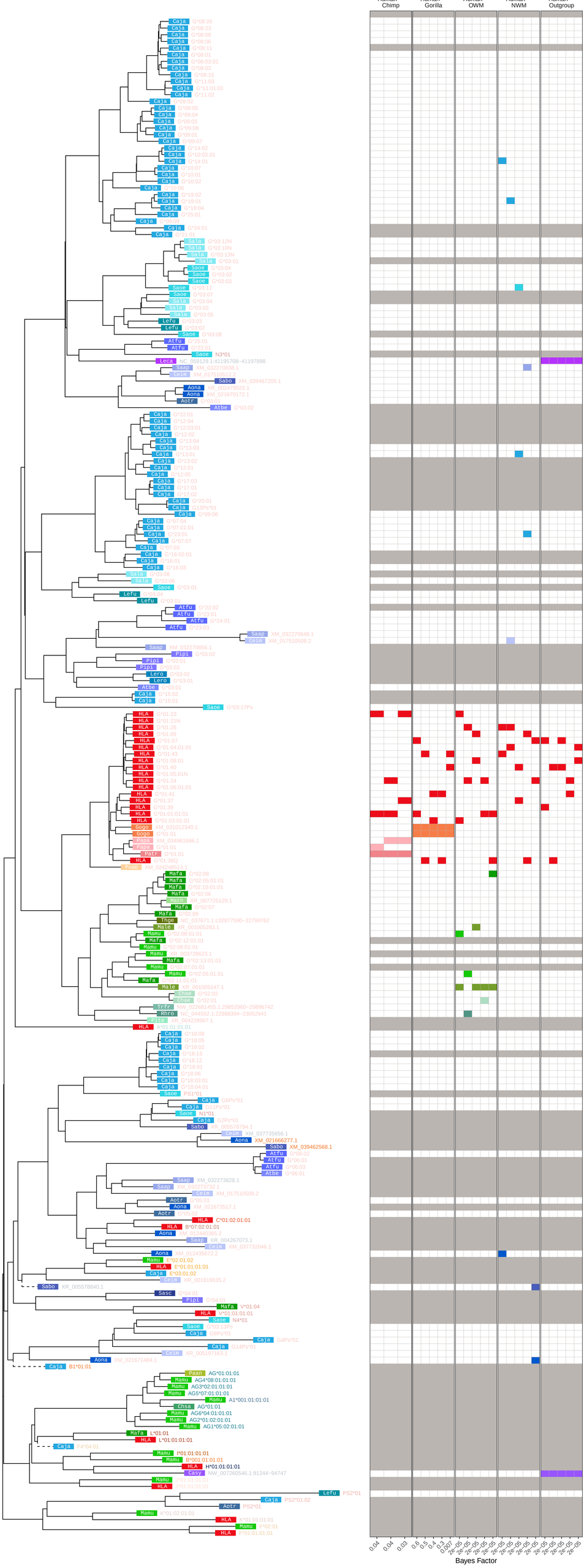
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Human − OWM
Human − NWM
Human − Outgroup
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Caja G*18:06
Caja G*18:03:01
Caja G*18:04:01
Saoe PS1*01
Caja G6Ps*01
Caja G11Ps*01
Saoe N1*01
Caja G2Ps*01
Sabo XR_005578794.1
Ceim XM_037735656.1
Aona XM_021666277.1
Sabo XM_039462568.1
Atfu G*06:02
Atfu G*06:01
Atfu G*06:03
Atbe G*06:01
Saap XM_032273828.1
Saap XM_032273732.1
Ceim XM_017510509.2
Aotr G*05:01
Aona XM_021673517.1
Aotr G*05:02
HLA C*01:02:01:01
HLA B*07:02:01:01
Aona XM_010369265.2
Saap XR_004267073.1
Ceim XM_037732046.1
Aona XM_012435672.2
Mamu A*02:01:02
HLA E*01:01:01:01
Caja E*03:01:02
Ceim XR_001819635.2
Sabo XR_005578840.1
Sasc G*04:01
Pipi G*04:01
Mafa V*01:04
HLA V*01:01:01:01
Saoe N4*01
Saoe PS3*01
Caja G8Ps*01
Caja G4Ps*01
Caja G14Ps*01
Ceim XR_005197163.1
Aona XM_021671484.1
Caja B1*01:01
Paan AG*01:01:01
Mamu AG4*08:01:01:01
Mamu AG3*02:01:01:01
Mamu AG5*07:01:01:01
Mamu A1*001:01:01:01
Chsa AG*01:01
Mamu AG6*04:01:01:01
Mamu AG2*01:02:01:01
Mamu AG1*05:02:01:01
Mafa L*01:01
HLA L*01:01:01:01
Caja F4*04:01
Mamu I*01:01:01:01
Mamu B*001:01:01:01
HLA H*01:01:01:01
Gaby NW_007260546.1:91244−94747
Mamu
HLA P*01:01:01:01
Lefu PS2*01
Caja PS2*01:02
Aotr PS2*01
Mamu K*01:02:01:01
HLA K*01:01:01:01
Mamu F*02:01
HLA F*01:01:01:01
0.04
0.04
0.03
0.6
0.5
0.4
0.3
0.007
2e−05
2e−05
2e−05
2e−05
2e−05
2e−05
2e−05
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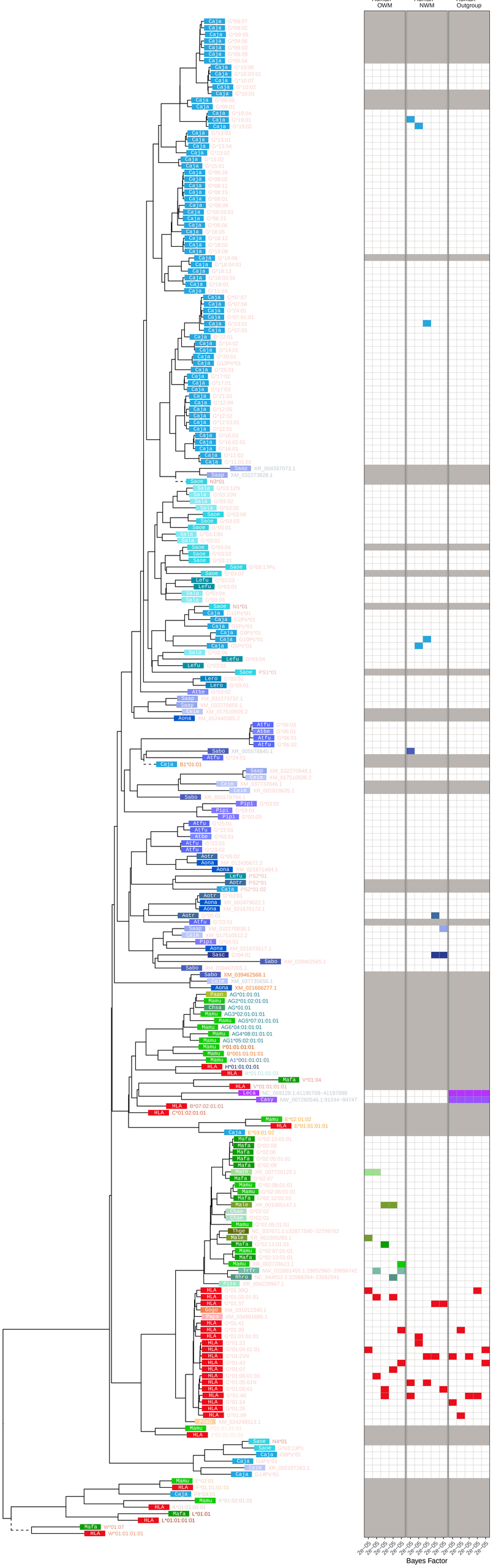
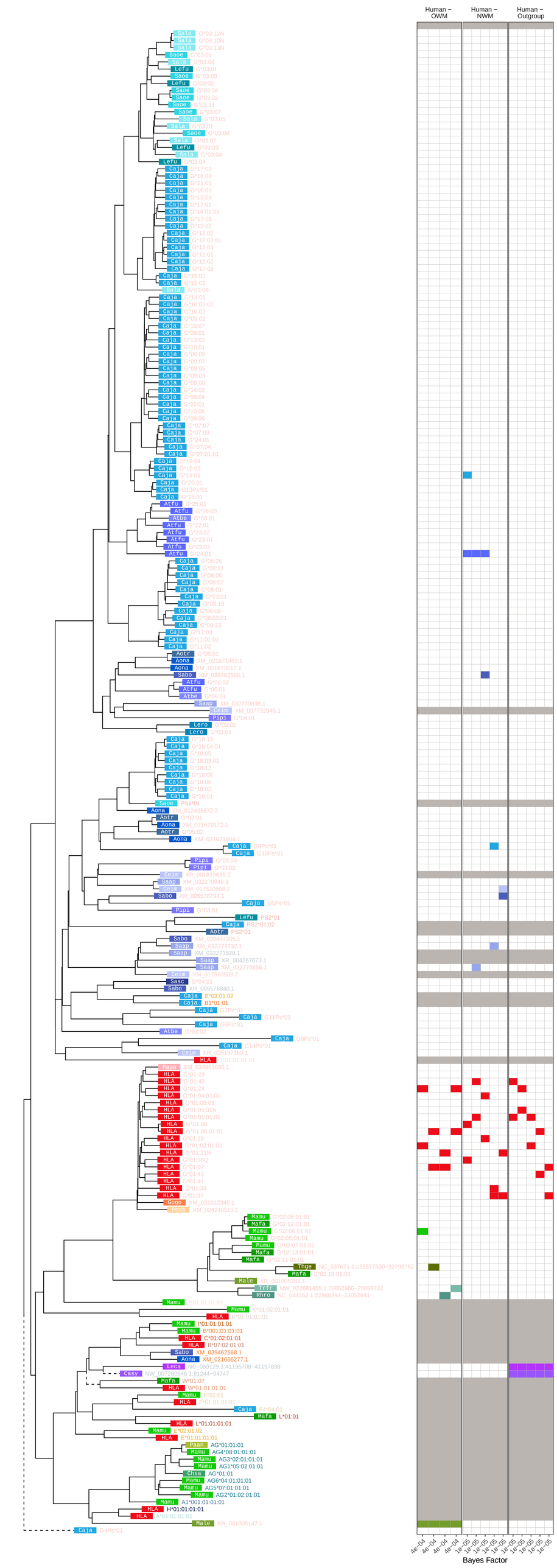
Bayes Factor


Human – OVM
Human – NWM
Human – Outgroup
Caja G*09:07
Caja G*09:02
Caja G*09:05
Caja G*09:06
Caja G*09:03
Caja G*09:09
Caja G*09:04
Caja G*10:06
Caja G*10:03:01
Caja G*10:07
Caja G*10:02
Caja G*10:01
Caja G*09:08
Caja G*09:01
Caja G*19:04
Caja G*19:01
Caja G*19:02
Caja G*13:01
Caja G*13:04
Caja G*13:02
Caja G*15:02
Caja G*15:01
Caja G*08:26
Caja G*08:02
Caja G*08:11
Caja G*08:15
Caja G*08:01
Caja G*08:08
Caja G*08:03:01
Caja G*08:23
Caja G*08:06
Caja G*18:05
Caja G*18:12
Caja G*18:02
Caja G*18:08
Caja G*18:06
Caja G*18:04:01
Caja G*18:11
Caja G*18:03:01
Caja G*18:01
Caja G*18:07
Caja G*07:07
Caja G*07:04
Caja G*24:01
Caja G*07:01:01
Caja G*23:01
Caja G*07:03
Caja G*22:01
Caja G*14:02
Caja G*14:01
Caja G*20:01
Caja G13Ps*01
Caja G*25:01
Caja G*17:02
Caja G*17:01
Caja G*17:03
Caja G*21:01
Caja G*12:04
Caja G*12:05
Caja G*12:02
Caja G*12:03:01
Caja G*12:01
Caja G*16:03
Caja G*16:02:01
Caja G*16:01
Caja G*11:02
Caja G*11:01:01
Saap XR_004267073.1
Saap XM_032273828.1
Saoe N3*01
Sala G*03:12N
Sala G*03:10N
Sala G*03:02
Sala G*03:05
Saoe G*03:08
Saoe G*03:03
Saoe G*03:01
Sala G*03:13N
Sala G*03:01
Saoe G*03:04
Saoe G*03:02
Saoe G*03:11
Saoe G*03:17Ps
Saoe G*03:07
Lefu G*03:03
Lefu G*03:01
Sala G*03:04
Sala G*03:06
Saoe N1*01
Caja G11Ps*01
Caja G2Ps*01
Caja G8Ps*01
Caja G6Ps*01
Caja G10Ps*01
Caja G5Ps*01
Sala G*03:05
Lefu G*03:04
Lefu G*03:12
Saoe PS1*01
Lero G*03:02
Lero G*03:01
Athe G*06:04
Saap XM_032273732.1
Saap XM_032270856.1
Ceim XM_017510509.2
Aona XM_012440365.2
Atfu G*06:03
Atbe G*06:01
Atfu G*06:01
Atfu G*06:02
Sabo XR_005573840.1
Atfu G*24:01
Caja B1*01:01
Saap XM_032270848.1
Ceim XM_017510508.2
Ceim XM_037732046.1
Ceim XR_001819635.2
Sabo XR_005573841.1
Pipi G*03:02
Pipi G*03:01
Pipi G*03:03
Atfu G*25:01
Atfu G*22:01
Atbe G*03:01
Atfu G*23:03
Atfu G*23:02
Aotr G*05:02
Aona XM_012435672.2
Aona XM_021671484.1
Lefu PS2*01
Aotr PS2*01
Caja PS2*01:02
Aotr G*03:01
Aona XR_002479022.1
Aona XM_021670172.1
Aotr G*03:02
Atfu G*23:01
Saap XM_032270838.1
Ceim XM_017510512.2
Pipi G*04:01
Aona XM_021673517.1
Sasc G*04:01
Sabo XR_005573839.1
Sabo XM_039462565.1
Sabo XM_039462568.1
Ceim XM_037735656.1
Aona XM_021666277.1
Paan AG*01:01:01
Mamu AG2*01:02:01:01
Chsa AG*01:01
Mamu AG3*02:01:01:01
Mamu AG5*07:01:01:01
Mamu AG6*04:01:01:01
Mamu AG4*08:01:01:01
Mamu AG1*05:02:01:01
Mamu I*01:01:01:01
Mamu B*001:01:01:01
Mamu A1*001:01:01:01
HLA H*01:01:01:01
HLA A*01:01:01:01
Mafa V*01:04
HLA V*01:01:01:01
Leca NC_059129.1:41195708–41197898
Casy NW_007260546.1:91244–94747
HLA B*07:02:01:01
HLA C*01:02:01:01
Mamu E*02:01:02
HLA E*01:01:01:01
Caja E*03:01:02
Mafa G*02:10:01:01
Mafa G*02:08
Mafa G*02:06
Mafa G*02:05:01:01
Mafa G*02:09
Sata XR_007725129.1
Mafa G*02:07
Mamu G*02:08:01:01
Mamu G*02:06:01:01
Mafa G*02:12:01:01
Male XR_001005147.1
Chae G*02:02
Gogo G*02:01
Mamu G*02:05:01:01
Thge NC_037671.1:c32877590–32799762
Mate XR_001005283.1
Mafa G*02:11:01:01
Mamu G*02:07:01:01
Mafa G*02:13:01:01
Mamu XR_003728623.1
Trfr NW_022681455.1:29852960–29896742
Rhro NC_044552.1:22988394–23052941
Ptro XR_004228867.1
HLA G*01:38Q
HLA G*01:03:01:01
HLA G*01:37
Gogo XM_031012340.1
Papa XM_034961686.1
HLA G*01:41
HLA G*01:39
HLA G*01:01:01:01
HLA G*01:23
HLA G*01:04:01:01
HLA G*01:21N
HLA G*01:43
HLA G*01:07
HLA G*01:06:01:01
HLA G*01:05:01N
HLA G*01:08:01
HLA G*01:40
HLA G*01:24
HLA G*01:26
HLA G*01:09
Pata XM_024248513.1
Mamu I*01:01:01:01
HLA J*01:01:01:01
Saoe N4*01
Saoe G*03:13Ps
Caja G8Ps*01
Caja G4Ps*01
Ceim XR_005197163.1
Caja G14Ps*01
Mamu F*02:01
HLA F*01:01:01:01
Caja E*04:01
Mamu K*01:02:01:01
HLA K*01:01:01:01
Mafa L*01:01
HLA L*01:01:01:01
Mafa W*01:07
HLA W*01:01:01:01
Bayes Factor


Human – OWM
Human – NWM
Human – Outgroup
Sala G*03:12N
Sala G*03:10N
Sala G*03:13N
Saoe G*03:01
Sala G*03:08
Lefu G*03:01
Saoe G*03:03
Lefu G*03:02
Saoe G*03:04
Saoe G*03:02
Saoe G*03:11
Saoe G*03:07
Sala G*03:05
Sala G*03:01
Saoe G*03:08
Sala G*03:02
Lefu G*03:03
Sala G*03:04
Lefu G*03:04
Caja G*17:03
Caja G*16:03
Caja G*21:01
Caja G*16:01
Caja G*13:04
Caja G*17:01
Caja G*16:02:01
Caja G*13:01
Caja G*13:02
Caja G*12:05
Caja G*12:03:01
Caja G*12:04
Caja G*12:01
Caja G*12:02
Caja G*17:02
Caja G*15:02
Caja G*15:01
Sala G*03:06
Caja G*14:01
Caja G*10:03:01
Caja G*10:02
Caja G*09:02
Caja G*10:07
Caja G*09:01
Caja G*13:03
Caja G*10:01
Caja G*09:09
Caja G*09:07
Caja G*09:05
Caja G*09:03
Caja G*09:08
Caja G*14:02
Caja G*09:04
Caja G*22:01
Caja G*10:06
Caja G*09:06
Caja G*07:07
Caja G*07:03
Caja G*24:01
Caja G*07:04
Caja G*07:01:01
Caja G*19:04
Caja G*19:02
Caja G*19:01
Caja G*20:01
Caja G13Ps*01
Caja G*25:01
Atfu G*25:01
Atfu G*06:03
Atbe G*03:01
Atfu G*22:01
Atfu G*23:02
Atfu G*23:01
Atfu G*23:03
Atfu G*24:01
Caja G*08:26
Caja G*08:11
Caja G*08:06
Caja G*08:02
Caja G*08:01
Caja G*23:01
Caja G*08:15
Caja G*08:08
Caja G*08:03:01
Caja G*08:23
Caja G*11:03
Caja G*11:01:01
Caja G*11:02
Aotr G*05:01
Aona XM_021671483.1
Aona XM_021673517.1
Sabo XM_039462565.1
Atfu G*06:02
Atfu G*06:01
Atbe G*06:01
Saap XM_032270838.1
Ceim XM_037732046.1
Pipi G*04:01
Lero G*03:02
Lero G*03:01
Caja G*18:13
Caja G*18:04:01
Caja G*18:05
Caja G*18:03:01
Caja G*18:12
Caja G*18:08
Caja G*18:06
Caja G*18:02
Caja G*18:01
Saoe PS1*01
Aona XM_012435672.2
Aotr G*03:01
Aona XM_021670172.1
Aotr G*05:02
Aona XM_021671484.1
Caja G9Ps*01
Caja G10Ps*01
Pipi G*03:03
Pipi G*03:02
Ceim XR_001819635.2
Saap XM_032270848.1
Ceim XM_017510508.2
Sabo XR_005578794.1
Caja G5Ps*01
Pipi G*03:01
Lefu PS2*01
Caja PS2*01:02
Aotr PS2*01
Sabo XM_039467205.1
Saap XM_032273732.1
Saap XM_032273828.1
Saap XR_004267073.1
Saap XM_032270856.1
Ceim XM_017510509.2
Sasc G*04:01
Sabo XR_005578840.1
Caja E*03:01:02
Caja B1*01:01
Caja G2Ps*01
Caja G11Ps*01
Caja G6Ps*01
Atbe G*03:02
Caja G8Ps*01
Caja G14Ps*01
Ceim XR_005197163.1
HLA J*01:01:01:01
Papa XM_034961686.1
HLA G*01:23
HLA G*01:40
HLA G*01:24
HLA G*01:04:01:01
HLA G*01:08:01
HLA G*01:05:01N
HLA G*01:01:01:01
HLA G*01:09
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HLA G*01:26
HLA G*01:03:01:01
HLA G*01:21N
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HLA G*01:07
HLA G*01:43
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HLA G*01:39
HLA G*01:37
Gogo XM_031012340.1
Poab XM_024248513.1
Mamu G*02:08:01:01
Mafa G*02:12:01:01
Mamu G*02:06:01:01
Mamu G*02:05:01:01
Mamu G*02:07:01:01
Mafa G*02:13:01:01
Mafa G*02:11:01:01
Thge NC_037671.1:c32877590-32799762
Mafa G*02:10:01:01
Male XR_001005283.1
Trfr NW_022681455.1:29852960-29896742
Rhro NC_044552.1:22988394-23052941
Mamu J*01:01:01:01
Mamu K*01:02:01:01
HLA K*01:01:01:01
Mamu I*01:01:01:01
Mamu B*001:01:01:01
HLA C*01:02:01:01
HLA B*07:02:01:01
Sabo XM_039462568.1
Aona XM_021666277.1
Leca NC_059129.1:41195708-41197898
Casy NW_007260546.1:91244-94747
Mafa W*01:07
HLA W*01:01:01:01
Mamu F*02:01
HLA F*01:01:01:01
Caja F4*04:01
Mafa L*01:01
HLA L*01:01:01:01
Mamu E*02:01:02
HLA E*01:01:01:01
Paan AG*01:01:01
Mamu AG4*08:01:01:01
Mamu AG3*02:01:01:01
Mamu AG1*05:02:01:01
Chsa AG*01:01
Mamu AG6*04:01:01:01
Mamu AG5*07:01:01:01
Mamu AG2*01:02:01:01
Mamu A1*001:01:01:01
HLA H*01:01:01:01
HLA A*01:01:01:01
Male XR_001005147.1
Caja G4Ps*01
4e−04
4e−04
4e−04
4e−04
1e−05
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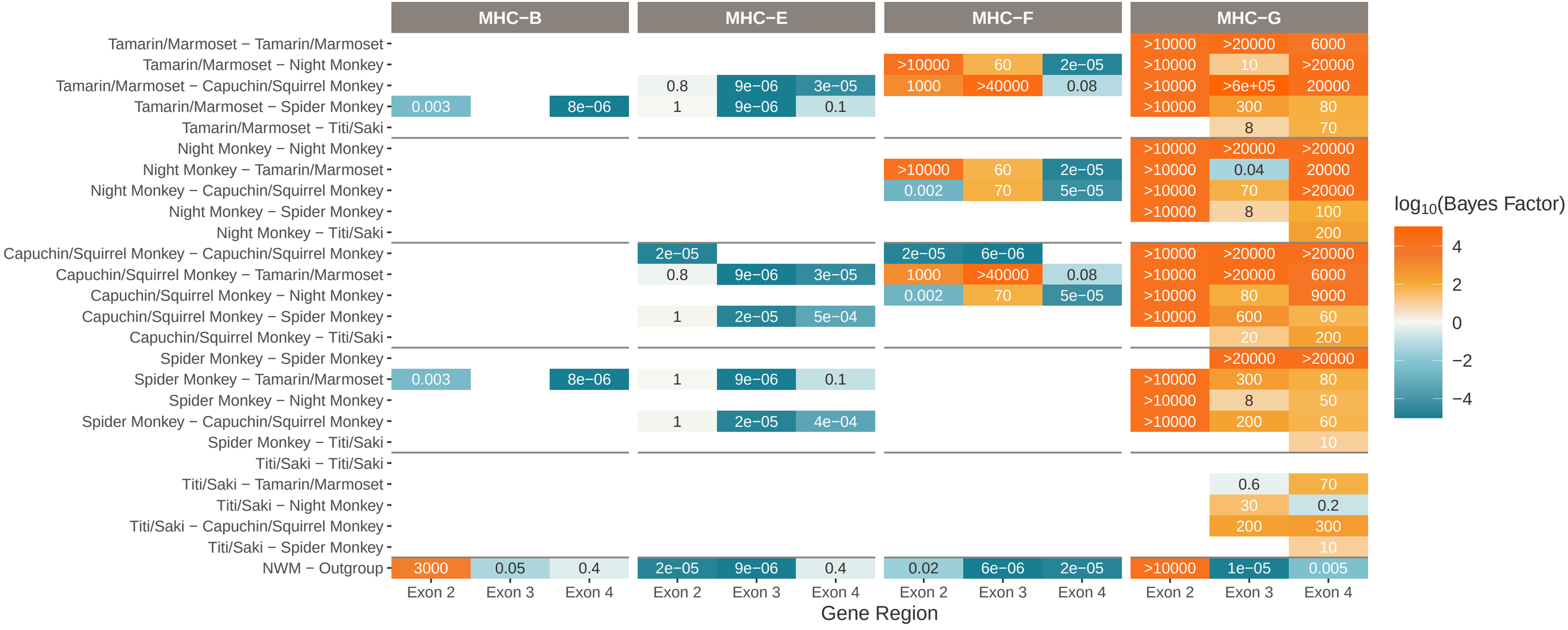
Bayes Factor


MHC−B
MHC−E
MHC−F
MHC−G
Tamarin/Marmoset − Tamarin/Marmoset
Tamarin/Marmoset − Night Monkey
Tamarin/Marmoset − Capuchin/Squirrel Monkey
Tamarin/Marmoset − Spider Monkey
Tamarin/Marmoset − Titi/Saki
Night Monkey − Night Monkey
Night Monkey − Tamarin/Marmoset
Night Monkey − Capuchin/Squirrel Monkey
Night Monkey − Spider Monkey
Night Monkey − Titi/Saki
Capuchin/Squirrel Monkey − Capuchin/Squirrel Monkey
Capuchin/Squirrel Monkey − Tamarin/Marmoset
Capuchin/Squirrel Monkey − Night Monkey
Capuchin/Squirrel Monkey − Spider Monkey
Capuchin/Squirrel Monkey − Titi/Saki
Spider Monkey − Spider Monkey
Spider Monkey − Tamarin/Marmoset
Spider Monkey − Night Monkey
Spider Monkey − Capuchin/Squirrel Monkey
Spider Monkey − Titi/Saki
Titi/Saki − Titi/Saki
Titi/Saki − Tamarin/Marmoset
Titi/Saki − Night Monkey
Titi/Saki − Capuchin/Squirrel Monkey
Titi/Saki − Spider Monkey
NWM − Outgroup
>10000 >20000 6000
>10000 60 2e−05 >10000 10 >20000
0.8 9e−06 3e−05 1000 >40000 0.08 >10000 >6e+05 20000
0.003 8e−06 1 9e−06 0.1 >10000 300 80
8 70
>10000 >20000 >20000
>10000 60 2e−05 >10000 0.04 20000
0.002 70 5e−05 >10000 70 >20000
>10000 8 100
200
2e−05 2e−05 6e−06 >10000 >20000 >20000
0.8 9e−06 3e−05 1000 >40000 0.08 >10000 >20000 6000
0.002 70 5e−05 >10000 80 9000
1 2e−05 5e−04 >10000 600 60
20 200
>20000 >20000
0.003 8e−06 1 9e−06 0.1 >10000 300 80
>10000 8 50
1 2e−05 4e−04 >10000 200 60
10
0.6 70
30 0.2
200 300
10
3000 0.05 0.4 2e−05 9e−06 0.4 0.02 6e−06 2e−05 >10000 1e−05 0.005
Exon 2 Exon 3 Exon 4 Exon 2 Exon 3 Exon 4 Exon 2 Exon 3 Exon 4 Exon 2 Exon 3 Exon 4
Gene Region
log10(Bayes Factor)
4
2
0
−2
−4

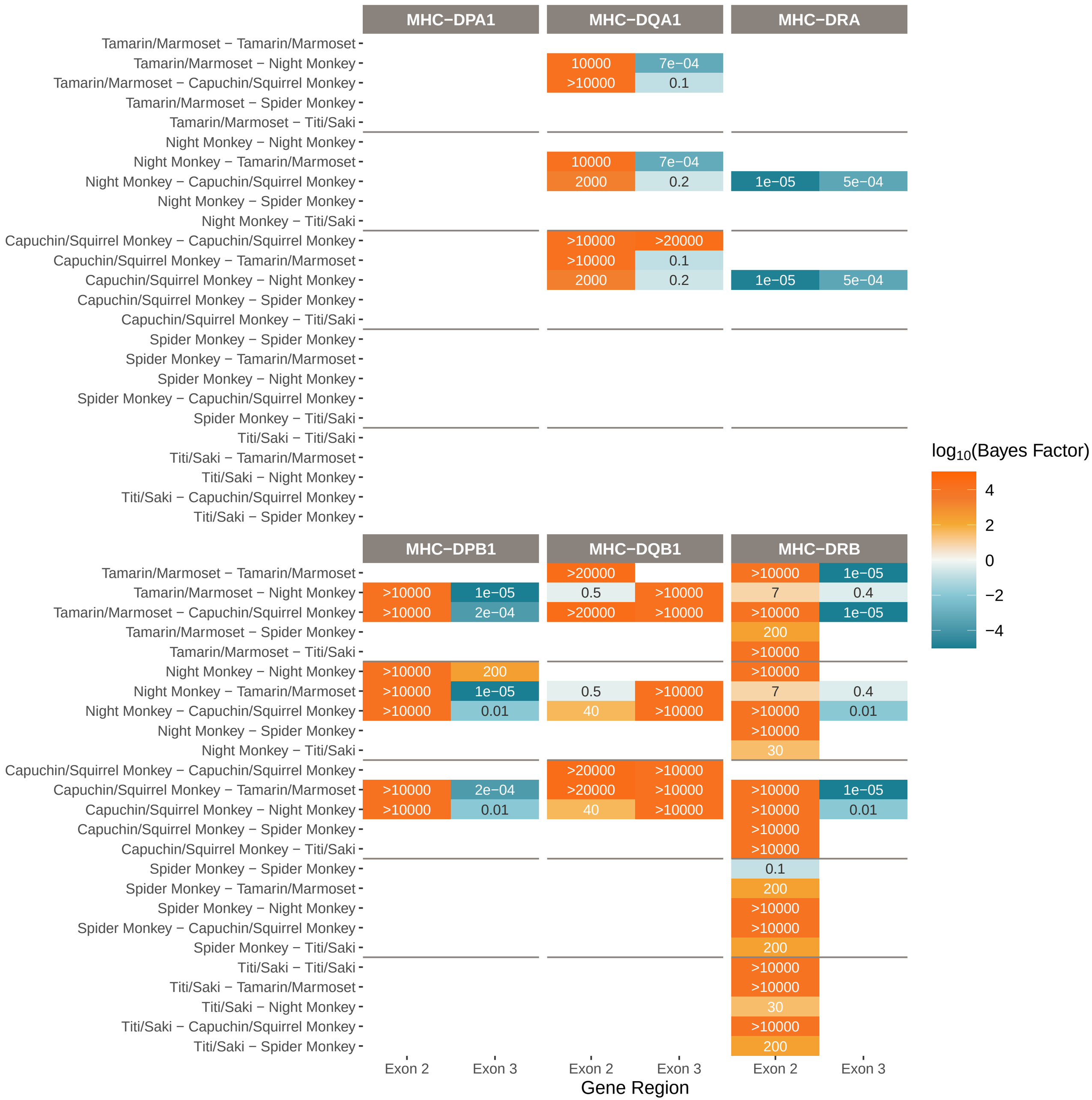
	MHC−A			MHC−B			MHC−E		
	Exon 2	Exon 3	Exon 4	Exon 2	Exon 3	Exon 4	Exon 2	Exon 3	Exon 4
Baboon/Gelada/Drill − Baboon/Gelada/Drill	2000	>10000	>10000	400	1		>10000	2	1000
Baboon/Gelada/Drill − Macaque	>30000	>10000	>10000	>10000	>10000	2	>10000	400	7000
Baboon/Gelada/Drill − Vervet/Guenon		>10000	>10000	>10000	>10000	0.2	500	800	>10000
Baboon/Gelada/Drill − Colobus/Langur/Snub−Nosed	>30000	2000	>10000				3	7e−04	5
Macaque − Macaque				>10000	>10000	>30000	>10000	>30000	>10000
Macaque − Baboon/Gelada/Drill	>30000	>10000	>10000	>10000	>10000	2	>10000	1000	7000
Macaque − Vervet/Guenon		>10000	>10000	>10000	6000	200	40	1000	4000
Macaque − Colobus/Langur/Snub−Nosed	>30000	>10000	>10000				3	8e−04	3
Vervet/Guenon − Vervet/Guenon				>10000	70				
Vervet/Guenon − Baboon/Gelada/Drill		>10000	>10000	>10000	>10000	0.2	100	800	>10000
Vervet/Guenon − Macaque		>10000	>10000	>10000	6000	200	4	1000	4000
Vervet/Guenon − Colobus/Langur/Snub−Nosed		200	>10000				3	8e−04	5
Colobus/Langur/Snub−Nosed − Colobus/Langur/Snub−Nosed	0.1	>10000	>10000				3	0.01	
Colobus/Langur/Snub−Nosed − Baboon/Gelada/Drill	>30000	2000	>10000				3	7e−04	5
Colobus/Langur/Snub−Nosed − Macaque	>30000	>10000	>10000				2	8e−04	3
Colobus/Langur/Snub−Nosed − Vervet/Guenon		200	>10000				3	8e−04	5
OWM − NWM				>10000	70	100	0.03	9e−06	3e−04
OWM − Outgroup	0.2	2e−05	2e−05	2000	0.1	0.2	2e−05	9e−06	0.003

	MHC−F			MHC−G		
	Exon 2	Exon 3	Exon 4	Exon 2	Exon 3	Exon 4
Baboon/Gelada/Drill − Baboon/Gelada/Drill	0.8	100	1			
Baboon/Gelada/Drill − Macaque	0.002	0.005	1	3	50	0.3
Baboon/Gelada/Drill − Vervet/Guenon						
Baboon/Gelada/Drill − Colobus/Langur/Snub−Nosed	2e−05	1e−05	2e−05	2e−05	0.01	1e−05
Macaque − Macaque	10	1	10		1e−05	
Macaque − Baboon/Gelada/Drill	0.002	0.005	1	0.9	100	>20000
Macaque − Vervet/Guenon						
Macaque − Colobus/Langur/Snub−Nosed	2e−05	0.003	0.2	2e−05	0.009	1e−05
Vervet/Guenon − Vervet/Guenon						
Vervet/Guenon − Baboon/Gelada/Drill						
Vervet/Guenon − Macaque						
Vervet/Guenon − Colobus/Langur/Snub−Nosed						
Colobus/Langur/Snub−Nosed − Colobus/Langur/Snub−Nosed						
Colobus/Langur/Snub−Nosed − Baboon/Gelada/Drill	2e−05	1e−05	2e−05	2e−05	0.01	1e−05
Colobus/Langur/Snub−Nosed − Macaque	2e−05	0.003	0.03	2e−05	0.009	1e−05
Colobus/Langur/Snub−Nosed − Vervet/Guenon						
OWM − NWM	2e−05	6e−06	2e−05	2e−05	1e−05	0.1
OWM − Outgroup	2e−05	6e−06	2e−05	2e−05	1e−05	0.01

Gene Region

$\log_{10}$(Bayes Factor)

4
2
0
−2
−4


MHC−DPA1
MHC−DQA1
MHC−DRA
MHC−DPB1
MHC−DQB1
MHC−DRB
Tamarin/Marmoset − Tamarin/Marmoset
Tamarin/Marmoset − Night Monkey
Tamarin/Marmoset − Capuchin/Squirrel Monkey
Tamarin/Marmoset − Spider Monkey
Tamarin/Marmoset − Titi/Saki
Night Monkey − Night Monkey
Night Monkey − Tamarin/Marmoset
Night Monkey − Capuchin/Squirrel Monkey
Night Monkey − Spider Monkey
Night Monkey − Titi/Saki
Capuchin/Squirrel Monkey − Capuchin/Squirrel Monkey
Capuchin/Squirrel Monkey − Tamarin/Marmoset
Capuchin/Squirrel Monkey − Night Monkey
Capuchin/Squirrel Monkey − Spider Monkey
Capuchin/Squirrel Monkey − Titi/Saki
Spider Monkey − Spider Monkey
Spider Monkey − Tamarin/Marmoset
Spider Monkey − Night Monkey
Spider Monkey − Capuchin/Squirrel Monkey
Spider Monkey − Titi/Saki
Titi/Saki − Titi/Saki
Titi/Saki − Tamarin/Marmoset
Titi/Saki − Night Monkey
Titi/Saki − Capuchin/Squirrel Monkey
Titi/Saki − Spider Monkey
10000 7e−04
>10000 0.1
10000 7e−04
2000 0.2
1e−05 5e−04
>10000 >20000
>10000 0.1
2000 0.2
1e−05 5e−04
>10000 1e−05
>10000 2e−04
>20000
0.5 >10000
>20000 >10000
>10000 1e−05
7 0.4
>10000 1e−05
200
>10000
>10000 200
>10000 1e−05
>10000 0.01
0.5 >10000
40 >10000
7 0.4
>10000 0.01
>10000
30
>20000 >10000
>10000 2e−04
>20000 >10000
>10000 1e−05
>10000 0.01
40 >10000
>10000 0.01
>10000
>10000
0.1
200
>10000
>10000
200
>10000
>10000
30
>10000
200
Exon 2
Exon 3
Exon 2
Exon 3
Exon 2
Exon 3
Gene Region
log10(Bayes Factor)
4
2
0
−2
−4

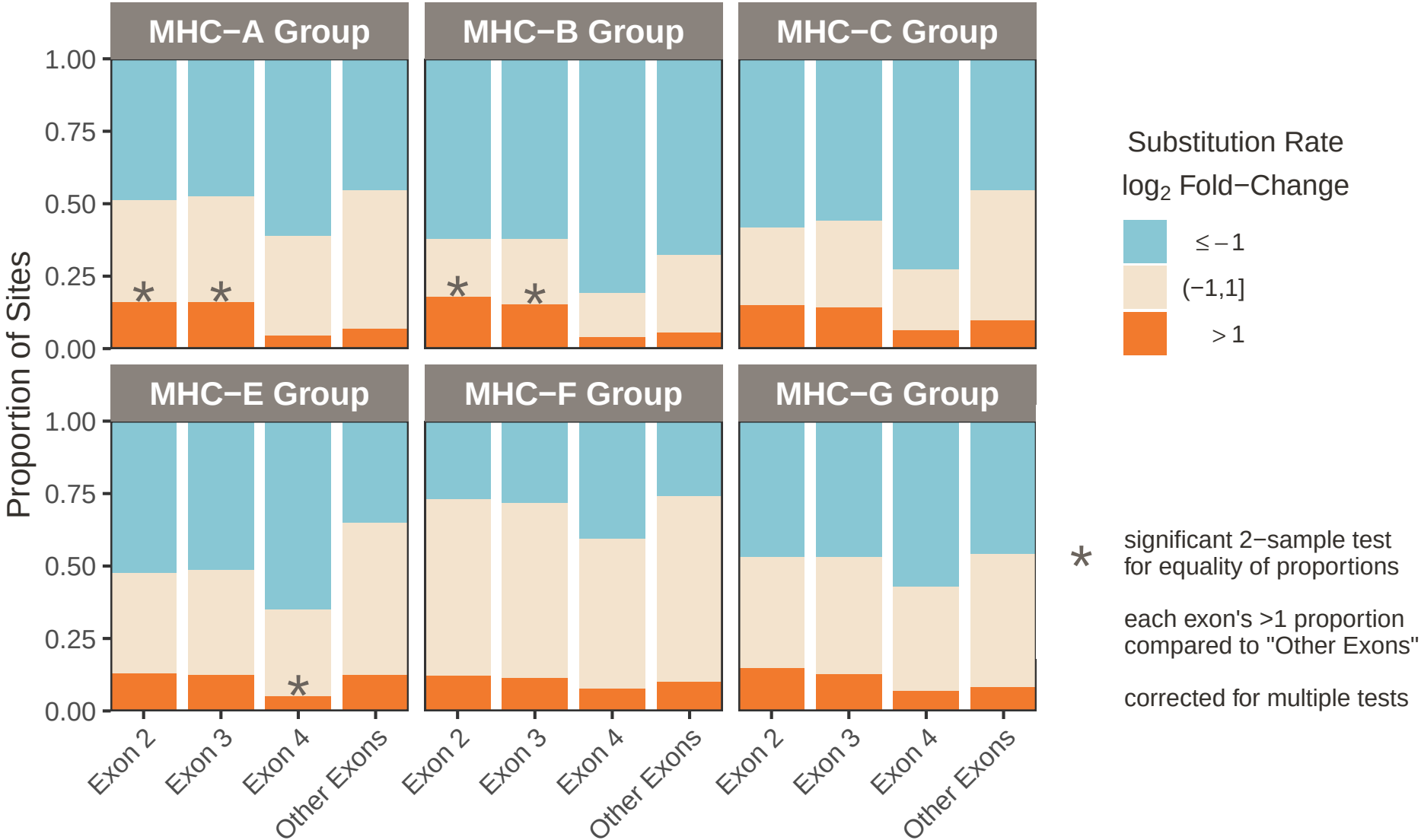
	MHC−DMA		MHC−DOA		MHC−DPA1		MHC−DQA1		MHC−DRA	
	Exon 2	Exon 3	Exon 2	Exon 3	Exon 2	Exon 3	Exon 2	Exon 3	Exon 2	Exon 3
Baboon/Gelada/Drill − Baboon/Gelada/Drill					>20000	>10000	>10000	100		
Baboon/Gelada/Drill − Macaque	1	2	30	5e−04	>20000	>10000	>10000	>20000	1	0.1
Baboon/Gelada/Drill − Vervet/Guenon					>20000	90	>10000			
Baboon/Gelada/Drill − Colobus/Langur/Snub−Nosed	1e−05	0.01	0.07	2e−05	>20000	>10000	>10000		1	20
Macaque − Macaque	9	1	40	0.06	>20000	>10000	>10000	>20000	>20000	>10000
Macaque − Baboon/Gelada/Drill	1	2	30	5e−04	>20000	>10000	>10000	>20000	1	0.1
Macaque − Vervet/Guenon					>20000	>10000	>10000			
Macaque − Colobus/Langur/Snub−Nosed	6e−04	0.01	0.01	0.1	>20000	>10000	500		20	0.06
Vervet/Guenon − Vervet/Guenon										
Vervet/Guenon − Baboon/Gelada/Drill					>20000	90	>10000			
Vervet/Guenon − Macaque					>20000	>10000	>10000			
Vervet/Guenon − Colobus/Langur/Snub−Nosed							20			
Colobus/Langur/Snub−Nosed − Colobus/Langur/Snub−Nosed										
Colobus/Langur/Snub−Nosed − Baboon/Gelada/Drill	1e−05	0.01	0.07	2e−05	>20000	>10000	>10000		1	20
Colobus/Langur/Snub−Nosed − Macaque	5e−04	0.01	0.01	0.1	>20000	>10000	500		20	0.06
Colobus/Langur/Snub−Nosed − Vervet/Guenon						>10000	20			
OWM − NWM	1e−05	2e−05	0.05	2e−05	5000	0.008	1	1e−05	1e−05	2e−05

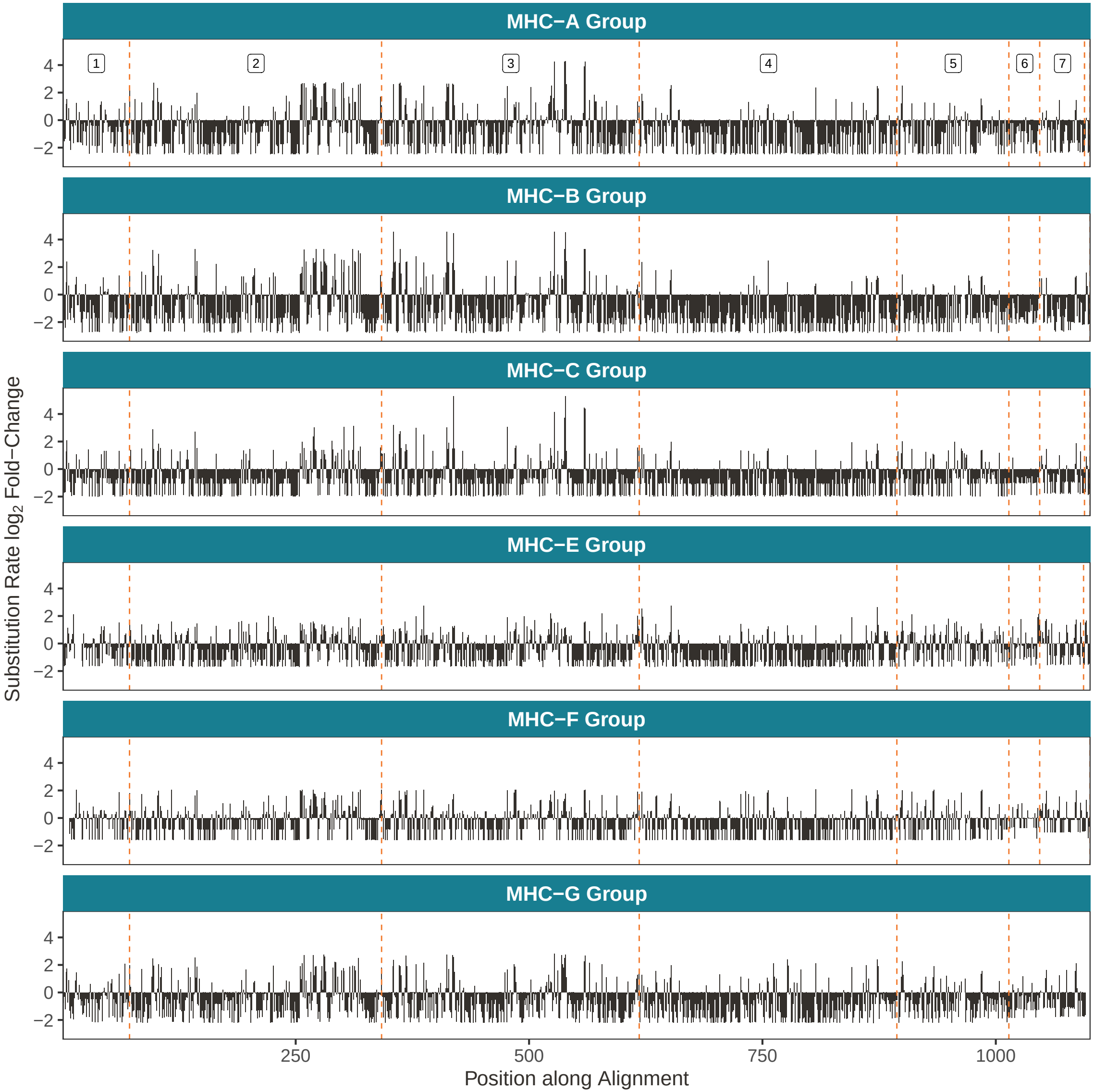
	MHC−DMB		MHC−DOB		MHC−DPB1		MHC−DQB1		MHC−DRB	
	Exon 2	Exon 3	Exon 2	Exon 3	Exon 2	Exon 3	Exon 2	Exon 3	Exon 2	Exon 3
Baboon/Gelada/Drill − Baboon/Gelada/Drill					>10000		>20000	>10000	>10000	
Baboon/Gelada/Drill − Macaque	>10000	100	200	>20000	>10000	>20000	>1e+06	>10000	>10000	
Baboon/Gelada/Drill − Vervet/Guenon					0.07	20000	>1e+06	>10000	>10000	
Baboon/Gelada/Drill − Colobus/Langur/Snub−Nosed	2e−05	3e−04	2	1	>10000	>20000	70000	>10000		
Macaque − Macaque	>10000	>10000	100	1	>10000	>20000	>1e+05	>10000	>10000	70000
Macaque − Baboon/Gelada/Drill	>10000	100	20	>20000	>10000	>20000	>1e+05	>10000	>10000	
Macaque − Vervet/Guenon					>10000	>20000	>2e+06	>10000	>10000	>20000
Macaque − Colobus/Langur/Snub−Nosed	2e−05	2e−04	2	2	>10000	>20000	>20000	>10000		
Vervet/Guenon − Vervet/Guenon									>10000	>20000
Vervet/Guenon − Baboon/Gelada/Drill					0.07	20000	>20000	>10000	>10000	
Vervet/Guenon − Macaque					>10000	>20000	>20000	>10000	>10000	>20000
Vervet/Guenon − Colobus/Langur/Snub−Nosed					10000	>20000	>20000	>10000		
Colobus/Langur/Snub−Nosed − Colobus/Langur/Snub−Nosed					>10000			>10000		
Colobus/Langur/Snub−Nosed − Baboon/Gelada/Drill	2e−05	3e−04	2	1	>10000	>20000	>20000	>10000		
Colobus/Langur/Snub−Nosed − Macaque	2e−05	2e−04	2	2	>10000	>20000	>2e+05	>10000		
Colobus/Langur/Snub−Nosed − Vervet/Guenon					10000	>20000	>20000	>10000		
OWM − NWM	2e−05	2e−05	2e−05	1e−05	>10000	1e−05	2	5e−04	>10000	10

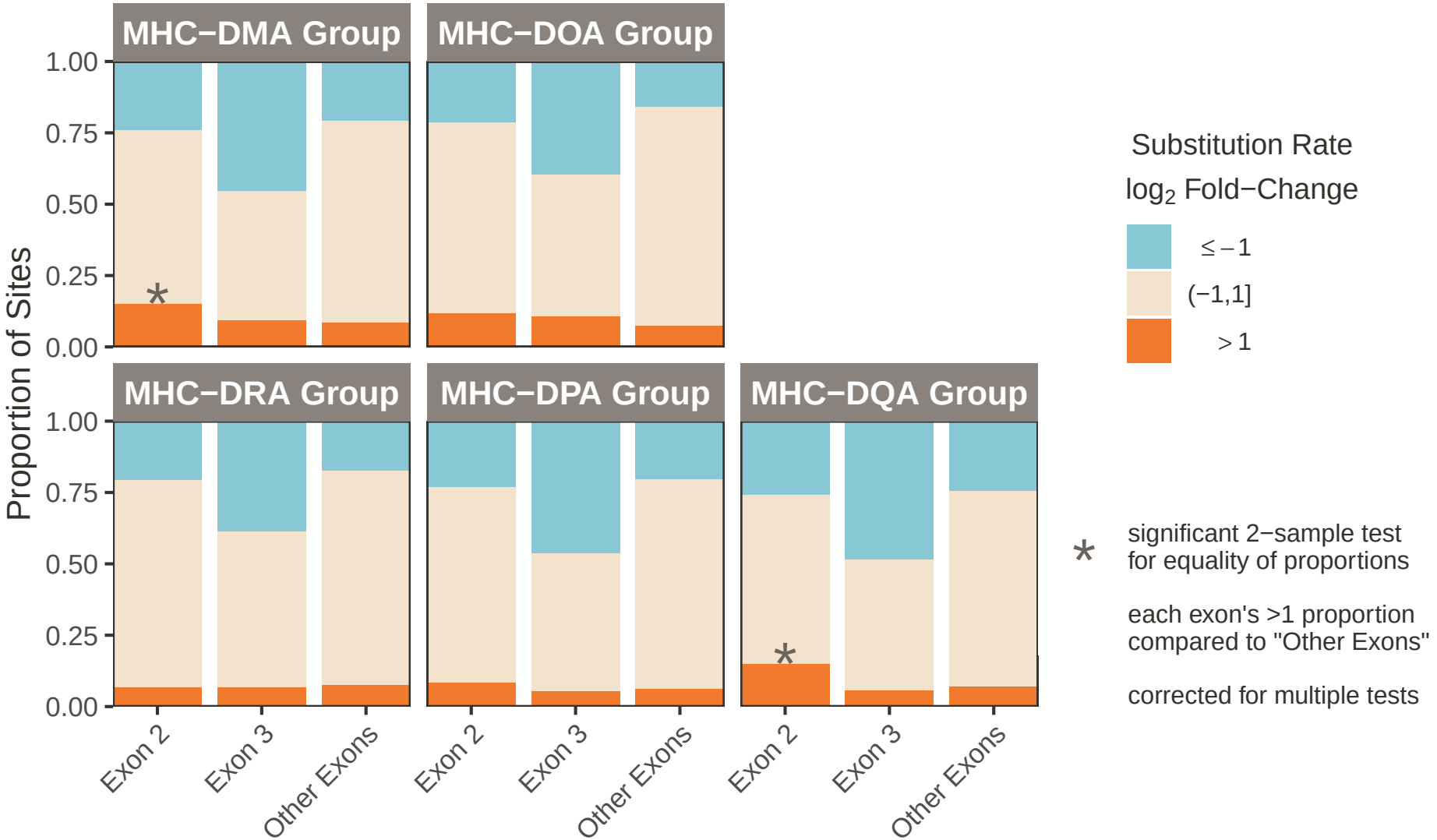
Gene Region

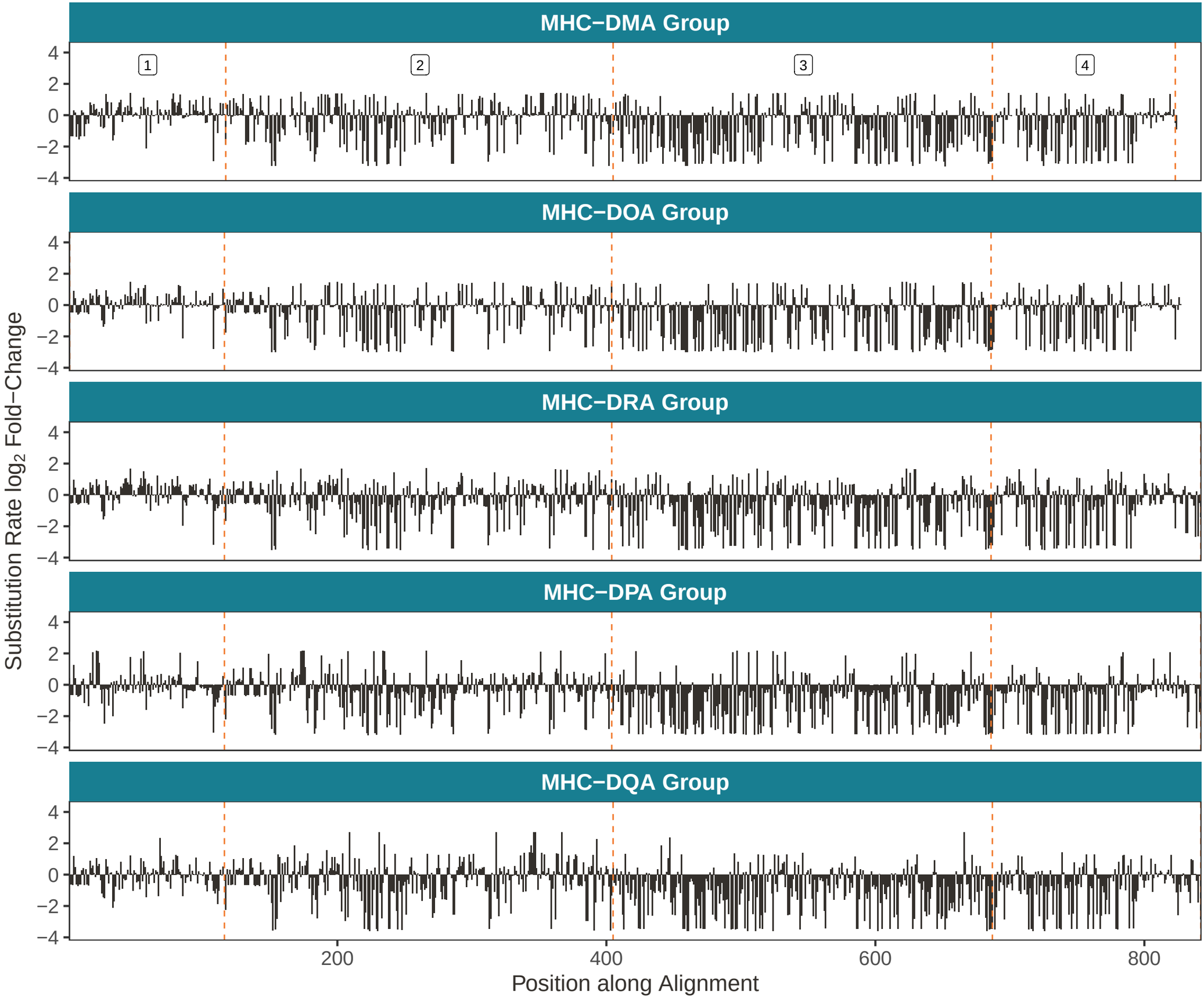
$\log_{10}$(Bayes Factor)

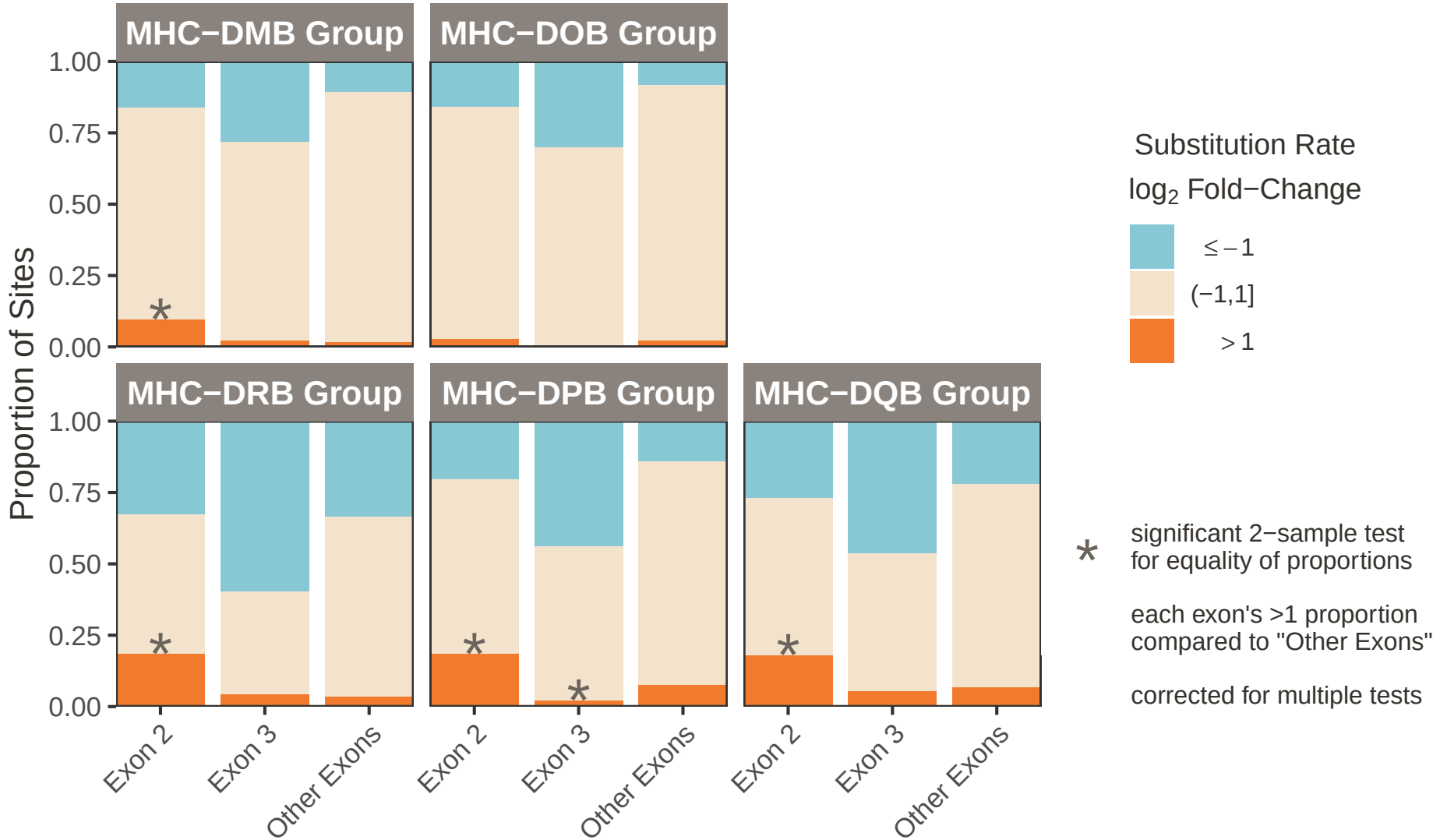
4
2
0
−2
−4

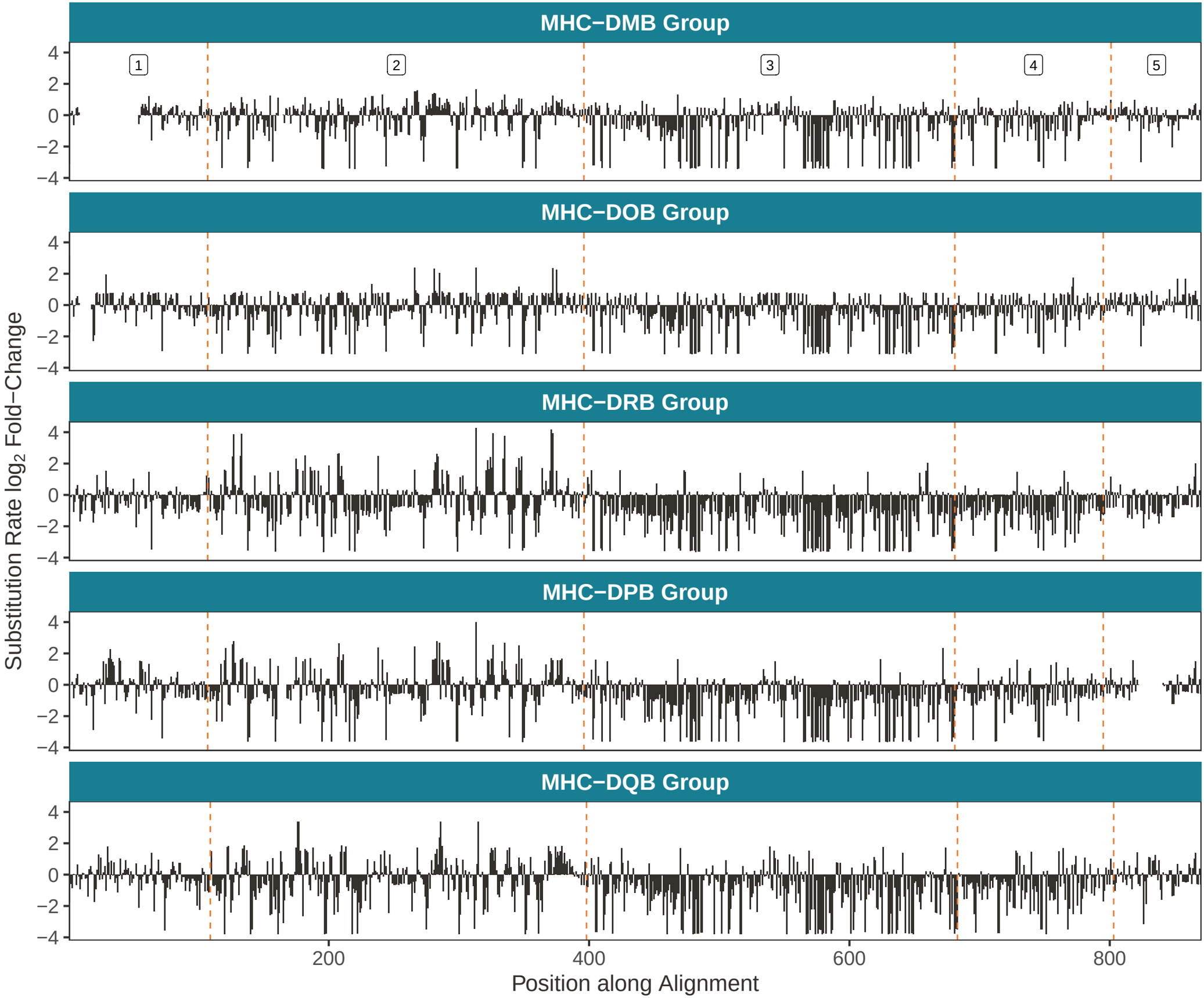

MHC−A Group
MHC−B Group
MHC−C Group
MHC−E Group
MHC−F Group
MHC−G Group
Proportion of Sites
1.00
0.75
0.50
0.25
0.00
Exon 2
Exon 3
Exon 4
Other Exons
Substitution Rate
log2 Fold−Change
≤ −1
(−1,1]
> 1
*
significant 2−sample test
for equality of proportions
each exon's >1 proportion
compared to "Other Exons"
corrected for multiple tests

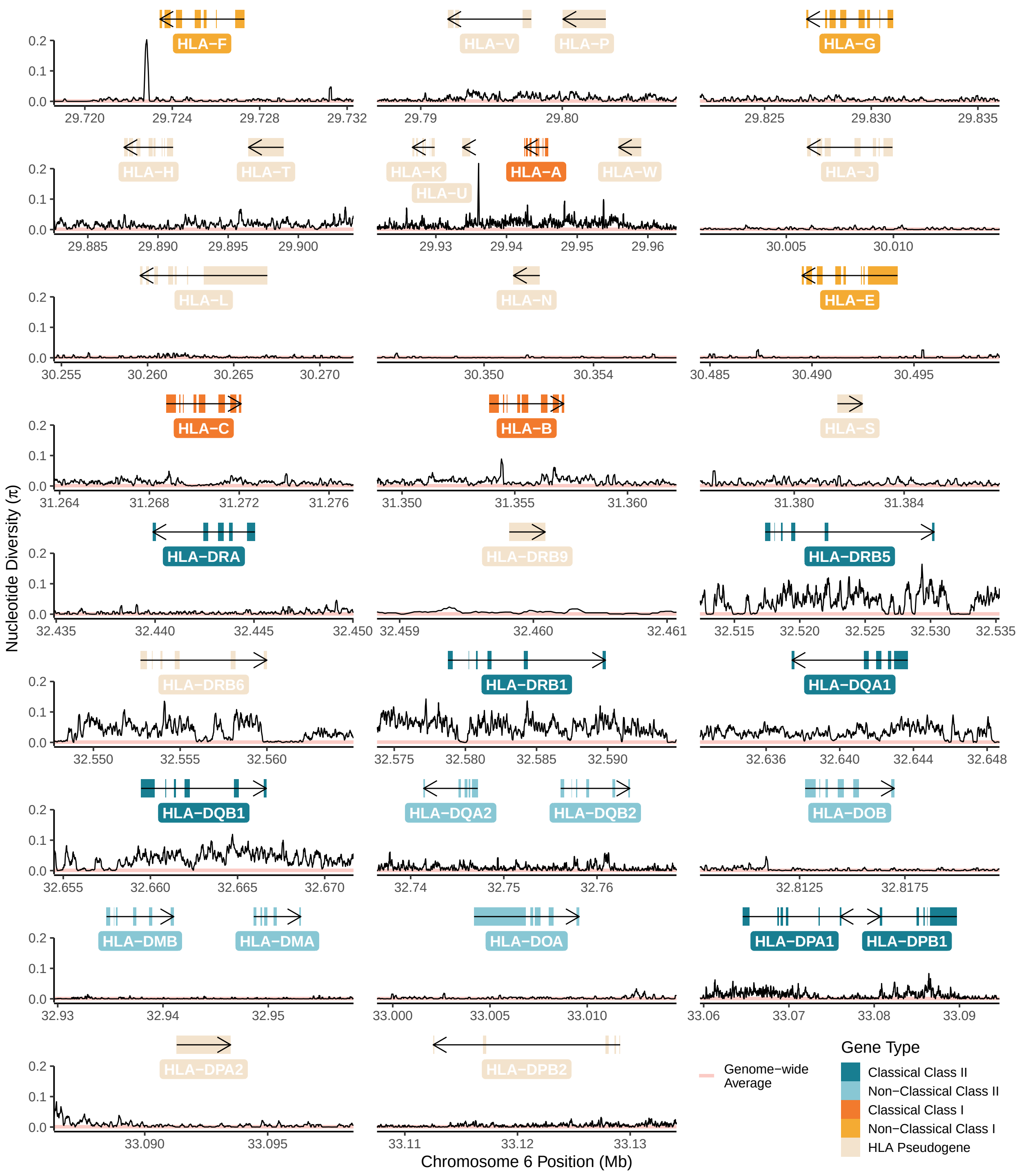

MHC−A Group
MHC−B Group
MHC−C Group
MHC−E Group
MHC−F Group
MHC−G Group
1
2
3
4
5
6
7
4
2
0
−2
Substitution Rate log2 Fold−Change
250
500
750
1000
Position along Alignment

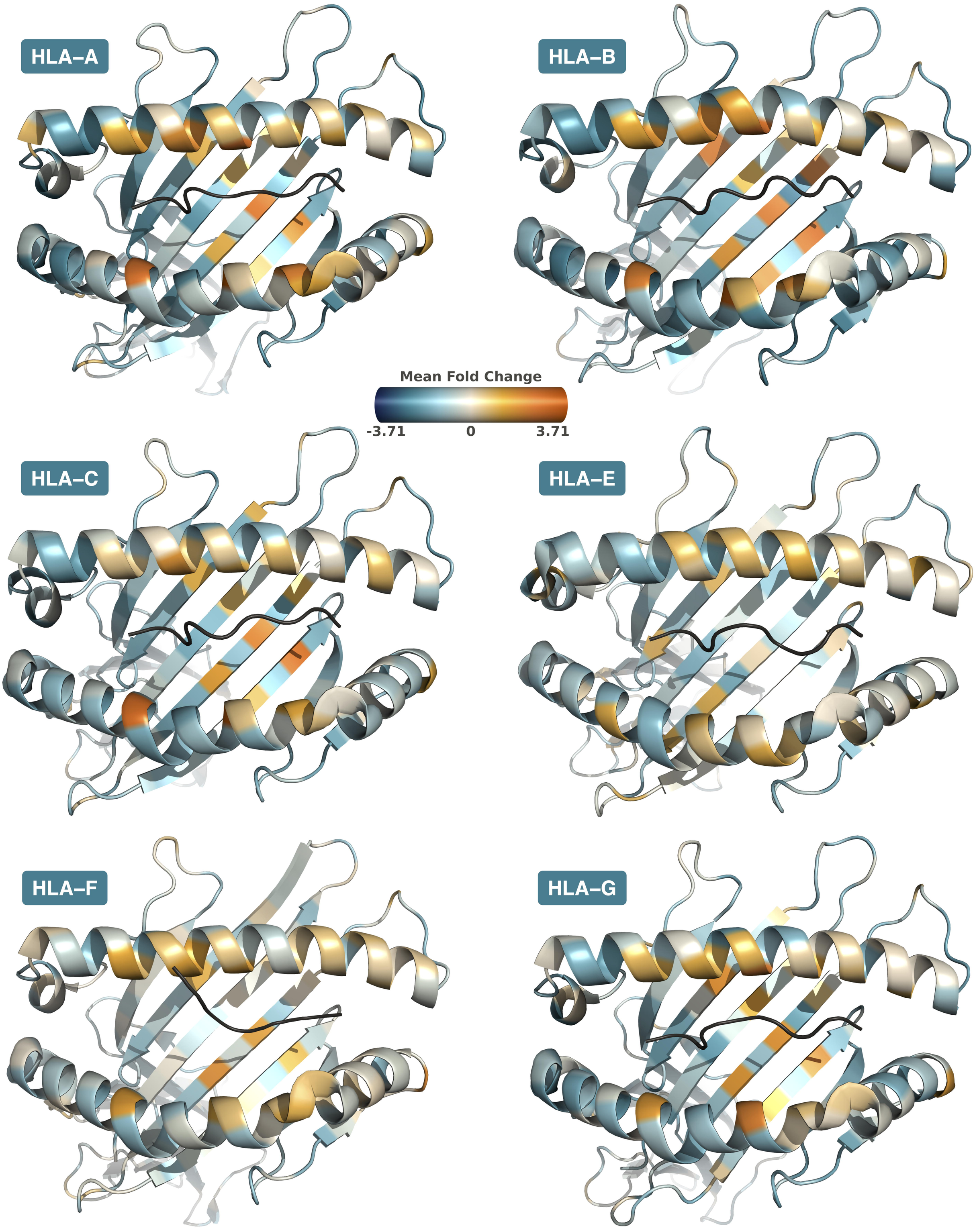

MHC−DMA Group
MHC−DOA Group
MHC−DRA Group
MHC−DPA Group
MHC−DQA Group
Proportion of Sites
1.00
0.75
0.50
0.25
0.00
*
Exon 2
Exon 3
Other Exons
Substitution Rate
log2 Fold−Change
≤ −1
(−1,1]
> 1
* significant 2−sample test for equality of proportions
each exon's >1 proportion compared to "Other Exons"
corrected for multiple tests

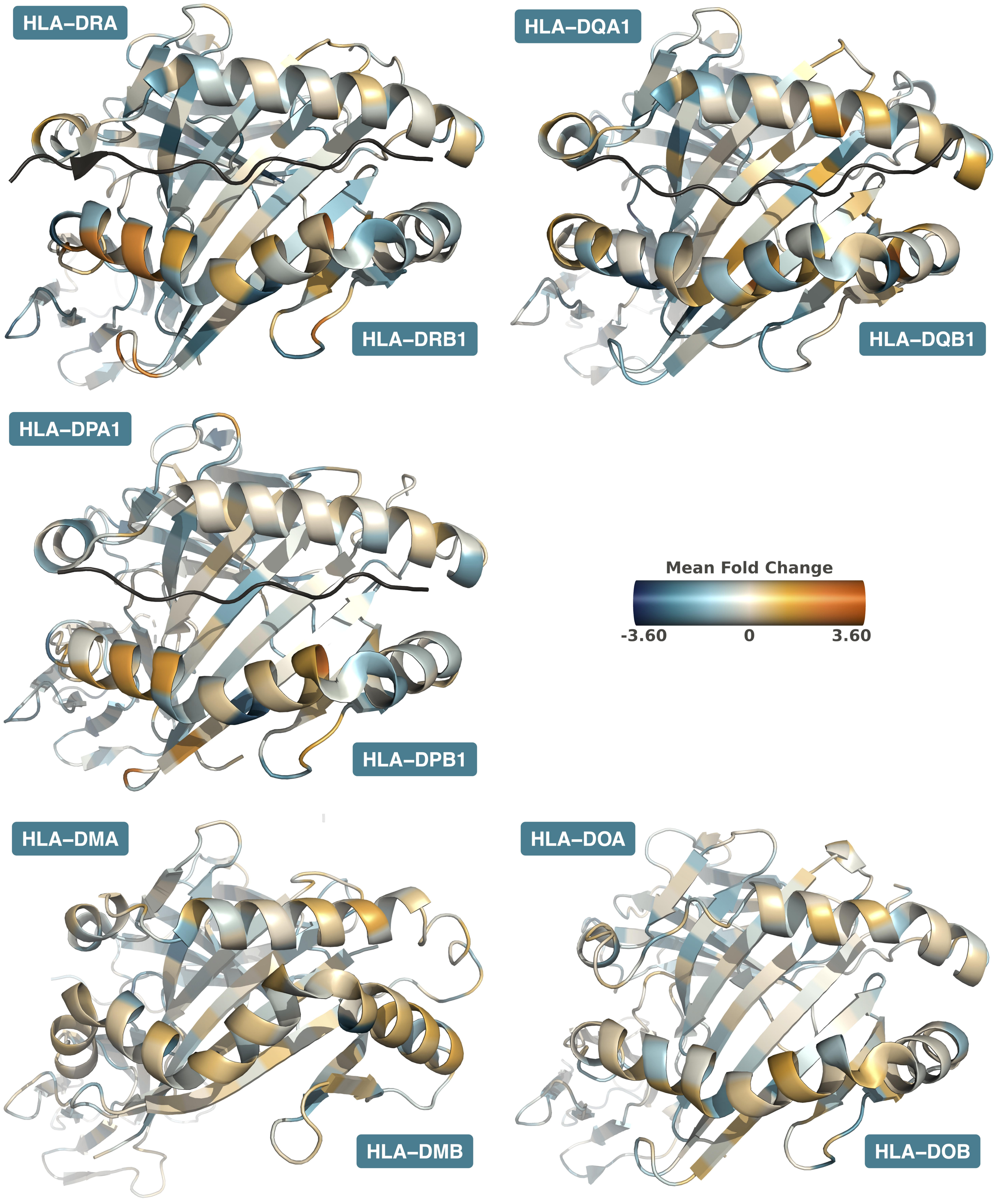

MHC−DMA Group
MHC−DOA Group
MHC−DRA Group
MHC−DPA Group
MHC−DQA Group
1
2
3
4
4
2
0
−2
−4
Substitution Rate log2 Fold−Change
200
400
600
800
Position along Alignment


MHC−DMB Group
MHC−DOB Group
MHC−DRB Group
MHC−DPB Group
MHC−DQB Group
Proportion of Sites
1.00
0.75
0.50
0.25
0.00
Exon 2
Exon 3
Other Exons
Substitution Rate
log2 Fold−Change
≤ −1
(−1,1]
> 1
*
significant 2−sample test
for equality of proportions
each exon's >1 proportion
compared to "Other Exons"
corrected for multiple tests


MHC−DMB Group
MHC−DOB Group
MHC−DRB Group
MHC−DPB Group
MHC−DQB Group
1
2
3
4
5
4
2
0
−2
−4
Substitution Rate log2 Fold−Change
200
400
600
800
Position along Alignment


HLA−F
HLA−V
HLA−P
HLA−G
HLA−H
HLA−T
HLA−K
HLA−U
HLA−A
HLA−W
HLA−J
HLA−L
HLA−N
HLA−E
HLA−C
HLA−B
HLA−S
HLA−DRA
HLA−DRB9
HLA−DRB5
HLA−DRB6
HLA−DRB1
HLA−DQA1
HLA−DQB1
HLA−DQA2
HLA−DQB2
HLA−DOB
HLA−DMB
HLA−DMA
HLA−DOA
HLA−DPA1
HLA−DPB1
HLA−DPA2
HLA−DPB2
Nucleotide Diversity (π)
Chromosome 6 Position (Mb)
Genome−wide Average
Gene Type
Classical Class II
Non−Classical Class II
Classical Class I
Non−Classical Class I
HLA Pseudogene


HLA–A
HLA–B
Mean Fold Change
-3.71
0
3.71
HLA–C
HLA–E
HLA–F
HLA–G


HLA–DRA
HLA–DRB1
HLA–DQA1
HLA–DQB1
HLA–DPA1
HLA–DPB1
Mean Fold Change
-3.60
0
3.60
HLA–DMA
HLA–DMB
HLA–DOA
HLA–DOB