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## Editorial Note on *Mycobacterium tuberculosis* Structure

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## Editorial

*Mycobacterium tuberculosis* is a pathogenic bacteria in the *Mycobacteriaceae* family that causes tuberculosis. *M. tuberculosis*, discovered by Robert Koch in 1882, has an uncommon, waxy coating on its cell surface, unsettled to the presence of mycolic acid. As a result of this coating, the cells are impenetrable to Gram staining and *Mycobacterium tuberculosis* can appear either Gramnegative or Gram-positive. To identify *M. tuberculosis* under a microscope, acid-fast stains such as Ziehl–Neelsen or fluorescent stains such as auramine are used. *M. tuberculosis*' physiology is highly aerobic and requires a lot of oxygen.

Mycobacterium tuberculosis is a clonal pathogen that has been proposed to have co-evolved with its human host for millennia, but our understanding of its genomic diversity and biogeography is still limited. We re-examine the population structure of Mycobacterium tuberculosis using phylogenetics and dimensionality reduction, providing an in-depth analysis of the ancient Indo-Oceanic Lineage 1 and the modern Central Asian Lineage 3, and expanding our understanding of Lineages 2 and 4. Using genomic sequences from 4939 pan-susceptible strains, we identify 30 new genetically distinct clades and certify them in a dataset of 4645 independent isolates. For 20 groups, including three Lineage 1 groups, we find a consistent geographically restricted or unrestricted pattern. The distribution of terminal branch lengths across the *M. tuberculosis* phylogeny supports the hypothesis that Lineages 2 and 4 are more transmissible than Lineages 3 and 1 on a global scale. We define an expanded barcode of 95 single nucleotide substitutions that allows us to quickly identify 69 *M. tuberculosis* sub-lineages and 26 additional internal groups. Our findings provide a more detailed picture of *M. tuberculosis* phylogeny and biogeography.

Tuberculosis (TB) is one of the top ten causes of death in the world. In 2018, more than ten million people became ill with tuberculosis (TB), and 1.5 million died as a result of the disease. Serious efforts have been made over the last two decades to understand strain-level genetic diversity in the TB bacillus *Mycobacterium tuberculosis* and its geographic distribution. A robust classification of Mtb strains into evolutionarily meaningful sub-lineages is censorious for taxonomic purposes as well as because sublineages can differ in virulence or antibiotic resistance. In 1997, Mtb was classified into three major genetic groups based on two

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neutral single nucleotide substitutions (SNSs) in the antibiotic resistance genes katG (codon 463) and gyrA. (codon 95). Various studies have attempted higher resolution classification since then, employing large genomic deletions, spoligotyping, and SNSs. There are currently nine recognised Mtb lineages (L1-9), with two (L2, L4) well represented in taxonomic and phylogeographic evaluations, and two others (L1 and L3) the subject of more recent work. Within the major lineages, 53 sub-lineages have been described and are definable with an SNS "barcode": seven for L1, six for L2, four for L3, and thirty-six for L4. These 53 sub-lineages best characterise L2 and L4 diversity. Because these lineages are most common in countries where pathogen sequencing is less widely used, the population structure of L1 and L3 is less well understood. Recently, studies in high-burden TB settings have begun to assess the evolutionary history of L1 and L3, including the role of migration and dispersal in driving their universality in different parts of the world.

Host-pathogen co-evolution, as well as more recent host-related selective pressures, have been suggest to drive Mtb genetic diversity. This genetic diversity is thought to support observed differences in Mtb sub-lineage transmissibility or host specificity, which is extremely important for public health. One modern L2 sub-lineage, for example, was found to be more transmissible than other L2 sub-lineages, L4 or L1, among the Mtb sub-lineages prevalent in Ho Chi Minh City, Vietnam. Another study found that L3 was less transmissible than the other Mtb major lineages in Montreal, Canada. Finally, the phylogeography of L5 and L6 (also known as *M. africanum*), L7, L8, and even some L4 sub-lineages has shown that these groups are more geographically limited than L2 and other L4 sub-lineages. These geographically restricted groups are related with lower variation in Mtb T-cell

epitopes, supporting the idea that Mtb sub-lineages have a range of pathogenic strategies and may be niche specialists infecting humans of a specific population or ancestry8. However, given the moderately few genetic differences that define Mtb sub-lineages or human ancestry, more evidence is needed to support this hypothesis.

We direct to raise our understanding of Mtb population structure by analysing 9584 genomes from 49 countries, including 738 L1 and 1104 L3 isolates. We recognize and certify 22 novel sub-lineages and 8 additional internal groups (i.e., genetically divergent groups found in sub-lineages that cannot be further divide hierarchically according to our criteria), including 7 in L1 and 4 in L3, and we enlarge the SNS typing barcode to 95 sites. L3 and L2 have similar phylogenetic structures, but L2 and L4 show a phylogenetic signal of increased transmissibility when compared to L1 or L3. These findings, together with our observations of new geographically restricted sub-lineages, add to the evidence supporting the Mtb human co-evolution hypothesis.