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Mapping the human genetic architecture of COVID-19

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TITLE

Mapping the human genetic architecture of COVID-19

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AUTHOR CONTRIBUTIONS STATEMENT

Author contributions are provided within the Authorship list.

ABSTRACT

The genetic makeup of an individual contributes to susceptibility and response to viral infection. While environmental, clinical and social factors play a role in exposure to SARS-CoV-2 and COVID-19 disease severity^{1,2}, host genetics may also be important. Identifying host-specific genetic factors may reveal biological mechanisms of therapeutic relevance and clarify causal relationships of modifiable environmental risk factors for SARS-CoV-2 infection and outcomes. We formed a global network of researchers to investigate the role of human genetics in SARS-CoV-2 infection and COVID-19 severity. We describe the results of three genome-wide association meta-analyses comprised of up to 49,562 COVID-19 patients from 46 studies across 19 countries. We reported 13 genome-wide significant loci that are associated with SARS-CoV-2 infection or severe manifestations of COVID-19. Several of these loci correspond to previously documented associations to lung or autoimmune and inflammatory diseases³⁻⁷. They also represent potentially actionable mechanisms in response to infection. Mendelian Randomization analyses support a causal role for smoking and body mass index for severe COVID-19 although not for type II diabetes. The identification of novel host genetic factors associated with COVID-19, with unprecedented speed, was made possible by the community of human genetic researchers coming together to prioritize sharing of data, results, resources and analytical frameworks. This working model of international collaboration underscores what is possible for future genetic discoveries in emerging pandemics, or indeed for any complex human disease.

INTRODUCTION

The coronavirus disease 2019 (COVID-19) pandemic, caused by infections with severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2), has resulted in enormous health and economic burden worldwide. One of the most remarkable features of SARS-CoV-2 infection is the variation in consequence ranging from asymptomatic to life-threatening, viral pneumonia and acute respiratory distress syndrome⁸. While established host factors correlate with disease severity (e.g., increasing age, being a man, and higher body mass index¹), these risk factors alone do not explain all variability in disease severity observed across individuals.

Genetic factors contributing to COVID-19 susceptibility and severity may provide novel biological insights into disease pathogenesis and identify mechanistic targets for therapeutic development or drug repurposing, as treating the disease remains a highly important goal despite the recent development of vaccines. Further suggesting this line of inquiry, rare loss-of-function variants in genes involved in type I interferon (*IFN*) response may be involved in severe forms of COVID-19⁹⁻¹². At the same time, several genome-wide association studies (GWAS) that investigate the contribution of common genetic variation¹³⁻¹⁶ to COVID-19 have provided robust support for the involvement of several genomic loci associated with COVID-19 severity and susceptibility, with the strongest and most robust finding for severity being at locus 3p21.31¹³⁻¹⁷. However, much remains unknown about the genetic basis of susceptibility to SARS-CoV-2 and severity of COVID-19.

The COVID-19 Host Genetics Initiative (COVID-19 HGI) (<https://www.covid19hg.org/>)¹⁸ is an international, open-science collaboration to share scientific methods and resources with research groups across the world with the goal to robustly map the host genetic determinants of SARS-CoV-2 infection and severity of the resulting COVID-19 disease. Here, we report the latest results of meta-analyses of 46 studies from 19 countries (**Fig. 1**) for COVID-19 host genetic effects.

RESULTS

Meta-analyses of COVID-19

Overall, the COVID-19 Host Genetics Initiative combined genetic data from 49,562 cases and two million controls across 46 distinct studies (**Fig. 1**). The data included studies from populations of different genetic ancestries, including European, Admixed American, African, Middle Eastern, South Asian and East Asian individuals (**Supplementary Table 1**). An overview of the study design is provided in **Extended Data Figure 1**. We performed case-control meta-analyses in three main categories of COVID-19 disease according to predefined and partially overlapping phenotypic criteria. These were (1) critically ill COVID-19 cases defined as those who required respiratory support in hospital or who were deceased due to the disease, (2) cases with moderate or severe COVID-19 defined as those hospitalized due to symptoms associated with the infection, and (3) all cases with reported SARS-CoV-2 infection regardless of symptoms (**Methods**). Controls for all three analyses were selected as genetically ancestry-matched samples without known SARS-CoV-2 infection, if that information was available (**Methods**). The average age of COVID-19 cases across studies was 55 years (**Supplementary Table 1**). We report quantile-quantile plots as **Supplementary Figure 1** and ancestry principal component plots for contributing studies in **Extended Data Figure 2**.

Across our three analyses, we reported a total of 13 independent genome-wide significant loci associated with COVID-19 ($P < 1.67 \times 10^{-8}$ threshold adjusted for multiple trait testing) (**Supplementary Table 2**),

most of which were shared between two or more COVID-19 phenotypes. Two of these loci are in very close proximity within the 3p21.31 region, which was previously reported as one single locus associated with COVID-19 severity^{13–17} (**Extended Data Figure 3**). Overall, we find six genome-wide significant associations for critical illness due to COVID-19, using data for 6,179 cases and 1,483,780 controls from 16 studies (**Extended Data Figure 4**). Nine genome-wide significant loci were detected for moderate to severe hospitalized COVID-19 (including five of the six critical illness loci), from an analysis of 13,641 COVID-19 cases and 2,070,709 controls, across 29 studies (**Fig. 2a top panel**). Finally, seven loci reached genome-wide significance in the analysis using data for all available 49,562 reported cases of SARS-CoV-2 infection and 1,770,206 controls, using data from a total of 44 studies (**Fig. 2a bottom panel**). The proportion of cases with non-European genetic ancestry for each of the three analyses was 23%, 29% and 22%, respectively. We report the results for the lead variants at the 13 loci in different ancestry-group meta-analyses in **Supplementary Table 3**. We note that two loci, tagged by lead variants rs1886814 and rs72711165, had higher allele frequencies in South East Asian (rs1886814, 15%) and East Asian genetic ancestry (rs72711165, 8%) whilst the minor allele frequencies in European populations were < 3%. This highlights the value of including data from diverse populations for genetic discovery. We discuss replication of previous findings and the new discoveries from these three analyses in our **Supplementary Note**.

Variant effects on severity vs. susceptibility

We found no genome-wide significant sex-specific effects at the 13 loci. However, we did identify significant heterogeneous effects ($P < 0.004$) across studies for 3 out of the 13 loci (**Methods**), likely reflecting differential ascertainment of cases (**Supplementary Table 2**). There was minor sample overlap ($n = 8,380$ EUR; $n = 745$ EAS) between controls from the genOMICC and the UK Biobank studies, but leave-one-out sensitivity analyses did not reveal any bias in the corresponding effect sizes or P -values (**Supplementary Information, Extended Data Figure 5**).

We next wanted to better understand whether the 13 significant loci were acting through mechanisms increasing susceptibility to infection or by affecting the progression of symptoms towards more severe disease. For all 13 loci, we compared the lead variant (strongest association P -value) odds ratios (ORs) for the risk-increasing allele across our different COVID-19 phenotype definitions.

Focusing on the two better powered analyses: all cases with reported infection and all cases hospitalized due to COVID-19, we find four of the loci have similar odds ratios between these two analyses (**Methods**) (**Supplementary Table 2**). Such consistency suggests a stronger link to susceptibility to SARS-CoV-2 infection rather than to the development of severe COVID-19. The strongest susceptibility signal was the previously reported *ABO* locus (rs912805253)^{13,14,16,17}. Interestingly, and in agreement with the report by Robert and colleagues¹⁶, we also report a locus within the 3p21.31 region that was more strongly associated with susceptibility to SARS-CoV-2 than progression to more severe COVID-19 phenotypes. Rs2271616 showed a stronger association with reported infection ($P=1.79 \times 10^{-34}$; OR[95%CI]= 1.15 [1.13-1.18]) than hospitalization ($P=1.05 \times 10^{-5}$; OR[95%CI]=1.12[1.06-1.19]). For this locus, which contains additional independent signals, the linkage-disequilibrium pattern is discordant with the P -value expectation (**Supplementary Note; Extended Data Figure 6**), pointing to a key missing causal variant or to a potentially undiscovered multi-allelic or structural variant in this locus.

In contrast, nine out of the 13 loci were associated with increased risk of severe symptoms with significantly larger ORs for hospitalized COVID-19 compared to the mildest phenotype of reported infection (eight loci below threshold $P < 0.004$ test for effect size difference, and additionally lead variant rs10774671 had a clear increase in ORs despite not passing this threshold) (**Supplementary Table 2**). We further compared the ORs for these nine loci for critical illness due to COVID-19 *vs.* hospitalized due to COVID-19, and found that these loci exhibited a general increase in effect risk for critical illness (**Methods**) (**Extended Data Figure 7a, Supplementary Table 4**), but the lower power for association analysis of critically ill COVID-19 means that these results should be considered as suggestive. Overall, these results indicated that these nine loci were more likely associated with progression of the disease and worse outcome from SARS-CoV-2 infection compared to being associated with susceptibility to SARS-CoV-2 infection.

For some of these analyses, the controls were simply existing population controls without knowledge of SARS-CoV-2 infection or COVID-19 status, which may bias effect size estimates as some of these individuals may have either become infected with SARS-CoV-2 or developed COVID-19. We perform several sensitivity analyses (**Supplementary Note; Extended Data Figure 7b; Supplementary Table 4**) showing that using population controls can be a valid and powerful strategy for host genetic discovery of infectious disease, and particularly those that are widespread and with rare severe outcomes.

Gene prioritization and PheWas

To better understand the potential biological mechanism of each locus, we applied several approaches to prioritize candidate causal genes and explore additional associations with other complex diseases and traits. Of the 13 genome-wide significant loci, we found nine loci to implicate biologically plausible genes (**Supplementary Table 2, Supplementary Table 5**). Protein-altering variants in LD with lead variants implicated genes at six loci, including *TYK2* (19p13.2) and *PPP1R15A* (19q13.33). The COVID-19 lead variant rs74956615:T>A in *TYK2*, which confers risk for critical illness (OR[95%] = 1.43 [1.29, 1.59]; $P = 9.71 \times 10^{-12}$) and hospitalization due to COVID-19 (OR [95%CI] = 1.27 [1.18, 1.36]; $P = 5.05 \times 10^{-10}$) is correlated with the missense variant rs34536443:G>C (p.Pro1104Ala; $r^2 = 0.82$). This is consistent with the primary immunodeficiency described with complete *TYK2* loss of function³ as this variant is known to reduce function^{19,20}. In contrast, this missense variant was previously reported to be protective against autoimmune diseases (**Extended Data Figure 8; Supplementary Table 6**), including rheumatoid arthritis (OR = 0.74; $P = 3.0 \times 10^{-8}$; UKB SAIGE), and hypothyroidism (OR = 0.84; $P = 1.8 \times 10^{-10}$; UK Biobank). At the 19q13.33 locus, the lead variant rs4801778, that was significantly associated with reported infection (OR [95%CI] = 0.95 [0.93, 0.96]; $P = 2.1 \times 10^{-8}$), is in LD ($r^2 = 0.93$) with a missense variant rs11541192:G>A (p.Gly312Ser) in *PPP1R15A*.

Lung-specific *cis*-eQTL from GTEx v8²¹ ($n = 515$) and the Lung eQTL Consortium²² ($n = 1,103$) provided further support for a subset of loci (**Supplementary Table 7**), including *FOXP4* (6p21.1) and *ABO* (9q34.2), *OAS1/OAS3/OAS2* (12q24.13), and *IFNAR2/IL10RB* (21q22.11), where the COVID-19 associated variants modify gene expression in lung. Furthermore, our PheWAS analysis (**Supplementary Table 6**) implicated three additional loci related to lung function, with modest lung eQTL evidence, i.e. the lead variant was not fine-mapped but significantly associated. An intronic variant rs2109069:G>A in *DPP9* (19p13.3), positively associated with critical illness, was previously reported to be risk-increasing for interstitial lung disease (tag lead variant rs12610495:A>G [p.Leu8Pro], OR = 1.29, $P = 2.0 \times 10^{-12}$)⁵. The COVID-19 lead variant rs1886814:A>C in *FOXP4* locus is correlated ($r^2 = 0.64$) with a lead variant of lung adenocarcinoma (tag variant=rs7741164; OR=1.2, $P=6.0 \times 10^{-13}$)^{6,23} and similarly with a lead variant reporting in subclinical interstitial lung disease²⁴. In severe COVID, lung cancer and ILD, the minor, expression increasing allele is associated with increased risk. We also found that intronic variants (1q22) and rs1819040:T>A in *KANSL1* (17q21.31), associated protectively against hospitalization due to COVID-19, were previously reported for reduced lung function (e.g. tag lead variant rs141942982:G>T, OR [95%CI] = 0.96 [0.95, 0.97], $P = 1.00 \times 10^{-20}$)⁷. Notably, the 17q21.31 locus is a well-known locus for structural variants containing a megabase inversion polymorphism (H1 and inverted H2 forms) and complex copy-number variations, where the inverted H2 forms were shown to be positively selected in Europeans^{25,26}.

Lastly, there are two loci in the 3p21.31 region with varying genes prioritized by different methods for different independent signals. For the severity lead variant rs10490770:T>C, we prioritized *CXCR6* with the Variant2Gene (V2G) algorithm²⁷, although *LZTFL1* is the closest gene. The *CXCR6* plays a role in chemokine signaling²⁸, and *LZTFL1* has been implicated in lung cancer²⁹. Rs2271616:G>T, associated with susceptibility, tags a complex region including several independent signals (**Supplementary Note**) all located within a gene body of *SLC6A20* which is known to functionally interact with the SARS-CoV-2 receptor ACE2³⁰. However, none of the lead variants in the 3p21.31 region has been previously associated with other traits or diseases in our PheWAS analysis. While these results provide supporting *in-silico* evidence for candidate causal gene prioritization, further functional characterization is strongly needed. Detailed locus descriptions and LocusZoom plots are provided in **Supplementary Figure 2**.

Polygenic architecture of COVID-19

To further investigate the genetic architecture of COVID-19, we used results from meta-analyses including samples from European ancestries (sample sizes described in **Methods and Supplementary Table 1**) to estimate SNP heritability, i.e. proportion of variation in the two phenotypes that was attributable to common genetic variants, and to determine whether heritability for COVID-19 phenotypes was enriched in genes specifically expressed in certain tissues³¹ from GTEx dataset³². We detected a low, but significant heritability across all three analyses (<1% on observed scale, all *P*-values < 0.0001, LDSC intercept range 1.0024-1.0137; **Supplementary Table 8**). The values are low compared to previously published studies¹⁵ but may be explained by differences in reported estimate scale (observed vs. liability), the specific method used, disease prevalence estimates, phenotypic differences between patient cohorts or ascertainment of controls. Despite the low reported values, we found that heritability for reported infection was significantly enriched in genes specifically expressed in the lung ($P = 5.0 \times 10^{-4}$) (**Supplementary Table 9**). These findings, together with genome-wide significant loci identified in the meta-analyses, suggest that there is a significant polygenic architecture that can be better leveraged with future, larger, sample sizes.

Genetic correlation Mendelian Randomization

Genetic correlations (*rg*) between the three COVID-19 phenotypes was high, though lower correlations were observed between hospitalized COVID-19 and reported infection (critical illness vs. hospitalized: *rg* [95%CI] = 1.37 [1.08, 1.65], $P = 2.9 \times 10^{-21}$; critical illness vs. reported infection, *rg* [95%CI] = 0.96 [0.71, 1.20], $P = 1.1 \times 10^{-14}$; hospitalized vs. reported infection: *rg* [95%CI] = 0.85 [0.68, 1.02], $P = 1.1 \times 10^{-22}$). To better understand which traits are genetically correlated and/or potentially causally associated with COVID-19 hospitalization, critical illness and SARS-CoV-2 reported infection, we chose a set of 38 disease, health and neuropsychiatric phenotypes as potential COVID-19 risk factors based on their clinical correlation with disease susceptibility, severity, or mortality (**Supplementary Table 10**).

We found evidence (FDR<0.05) of significant genetic correlations between 9 traits and hospitalized COVID-19 and SARS-CoV-2 reported infection (**Fig. 3; Extended Data Figure 9; Supplementary Table 11**). Interesting findings include that genetic liability to ischemic stroke was only significantly positively

correlated with critical illness or hospitalization due to COVID-19, but not with a higher likelihood of reported SARS-CoV-2 infection (infection $r_g = 0.019$ vs. hospitalization $r_g = 0.41$, $z = 2.7$, $P = 0.006$; infection $r_g = 0.019$ vs. critical illness $r_g = 0.40$, $z = 2.49$, $P = 0.013$).

We next used two-sample Mendelian randomization (MR) to infer potentially causal relationships between these traits. After correcting for multiple testing ($FDR < 0.05$), 8 exposure — COVID-19 trait-pairs showed suggestive evidence of a causal association (**Fig. 3; Supplementary Table 12; Extended Data Figure 10; Supplementary Figure 3**). Five of these associations were robust to potential violations of the underlying assumptions of MR. Corroborating our genetic correlation results and evidence from epidemiological studies, genetically predicted higher BMI (OR [95%CI] 1.4 [1.3, 1.6], $P = 8.5 \times 10^{-11}$) and smoking (OR [95%CI] = 1.9 [1.3, 2.8], $P = 0.0012$) were associated with increased risk of COVID-19 hospitalization, with BMI also being associated with increased risk of SARS-CoV-2 infection (OR [95%CI] = 1.1 [1.1, 1.2], $P = 4.8 \times 10^{-7}$). Genetically predicted increased height (OR [95%CI] = 1.1 [1, 1.1]), $P = 8.9 \times 10^{-4}$) was associated with an increased risk of reported infection, and genetically predicted higher red blood cell count (OR [95%CI] = 0.93 [0.89, 0.96], $P = 5.7 \times 10^{-5}$) with a reduced risk of reported infection. Despite the evidence of genetic correlation between type II diabetes and COVID-19 outcomes, there was no evidence of a causal association in the MR analyses, suggesting that the observed genetic correlations are due to pleiotropic effects between BMI and type II diabetes. Further sensitivity analyses relating to sample overlap are discussed in **Supplementary Information**.

DISCUSSION

The COVID-19 Host Genetics Initiative has brought together investigators from across the world to advance genetic discovery for SARS-CoV-2 infection and severe COVID-19 disease. We report 13 genome-wide significant loci associated with some aspect of SARS-CoV-2 infection or COVID-19. Many of these loci overlap with previously reported associations with lung-related phenotypes or autoimmune/inflammatory diseases, but some loci have no obvious candidate gene.

Four out of the 13 genome-wide significant loci showed similar effects in the reported infection analysis (a proxy for disease susceptibility) and all-hospitalized COVID-19 (a proxy for disease severity). Of these, one locus was in close proximity, but yet independent, to the major genetic signal for COVID-19 severity at 3p21.31. Surprisingly, this locus was associated with COVID-19 susceptibility rather than severity. The locus overlaps SLC6A20, which encodes an amino acid transporter that interacts with ACE2. Nonetheless,

we caution that more data is needed to resolve the nature of the relationship between genetic variation and COVID-19 at this locus, particularly as the physical proximity, linkage disequilibrium structure and patterns of association suggest that untagged genetic variation might be drive the association signal in the region. Our findings support the notion that some genetic variants, most notably at *ABO* and *PPP1R15A* loci, in addition to the aforementioned *SLC6A20*, might indeed impact susceptibility to infection rather than progression to severe COVID-19 once infected.

Several of the loci reported here, as noted in previous publications^{13,15}, intersect with well-known genetic variants that have established genetic associations. Examples of these include variants at *DPP9* and *FOXP4* which show prior evidence of increasing risk for interstitial lung disease⁵, and missense variants within *TYK2* that show a protective effect on several autoimmune-related diseases³³⁻³⁶. Together with the heritability enrichment observed in genes expressed in lung tissues, these results highlight the involvement of lung-related biological pathways in developing severe COVID-19. Several other loci show no prior documented genome-wide significant associations, even despite the high significance and attractive candidate genes for COVID-19 (e.g., *CXCR6*, *LZTFL1*, *IFNAR2* and *OAS1/2/3* loci). The previously reported associations for the strongest association for COVID-19 severity at 3p21.31 and monocytes count are likely to be due to proximity and not a true co-localization.

Increasing the global representation in genetic studies enhances the ability to detect novel associations. Two of the loci affecting disease severity were only discovered by including the four studies of individuals with East Asian ancestry. One of these loci, close to *FOXP4*, is common particularly in East Asian (32%) as well as Admixed American in the Americas (20%) and Middle Eastern samples (7%), but has a low frequency in most European ancestries (2-3%) in our data. Although we cannot be certain of the mechanism of action of *FOXP4* association is an attractive biological target, as it is expressed in the proximal and distal airway epithelium³⁷, and has been shown to play a role in controlling epithelial cell fate during lung development³⁸. The COVID-19 Host genetics Initiative continues to pursue expansion of the datasets included in the consortium's analyses to populations from underrepresented populations in upcoming data releases. We plan to release ancestry-specific results in full once the sample sizes allow for a well-powered meta-analysis.

Care should be taken when interpreting the results from a meta-analysis because of challenges with cases and controls ascertainment and collider bias (see **Supplementary Note** for a more detailed discussion on study limitations). Drawing a comprehensive and reproducible map of the host genetics factors associated with COVID-19 severity and SARS-CoV-2 requires a sustained international effort to include diverse ancestries and study designs. To accelerate downstream research and therapeutic discovery, the COVID-19 Host Genetic Initiative regularly publishes meta-analysis results from periodic data freezes on the website www.covid19hg.org and provides an interactive explorer where researchers can browse the results and the genomic loci in more detail. Future work will be required to better understand the biological and clinical value of these findings. Continued efforts to collect more samples and detailed phenotypic data should be endorsed globally, allowing for more thorough investigation of variable, heritable symptoms^{39,40}, particularly in the light of newly emerging strains of SARS-CoV-2 virus, which may provoke different host responses leading to disease.

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FIGURE LEGENDS

Figure 1. Geographical overview of the contributing studies to the COVID-19 HGI and composition by major ancestry groups. Populations are defined as Middle Eastern (MID), South Asian (SAS), East Asian (EAS), African (AFR), Admixed American (AMR), European (EUR).

Figure 2. Genome-wide association results for COVID-19. a. Top panel shows results of genome-wide association study of hospitalized COVID-19 ($n=13,641$ cases and $n=2,070,709$ controls), and bottom panel the results of reported SARS-CoV-2 infection ($n=49,562$ cases and $n=1,770,206$ controls). Loci highlighted in yellow (top panel) represent regions associated with severity of COVID-19 manifestation i.e. increasing

odds for more severe COVID-19 phenotypes. Loci highlighted in green (bottom panel) are regions associated with susceptibility to SARS-CoV-2 infection, i.e. the effect is the same across mild and severe COVID-19 phenotypes. We highlight in red genome-wide significant variants that had high heterogeneity across contributing studies, and were therefore excluded from the list of loci found. **b.** Results of gene prioritization using different evidence measures of gene annotation. Genes in linkage disequilibrium (LD) region, genes with coding variants and eGenes (fine-mapped cis-eQTL variant PIP > 0.1 in GTEx Lung) are annotated if in LD with a COVID-19 lead variant ($r^2 > 0.6$). V2G: Highest gene prioritized by OpenTargetGenetics' V2G score.

Figure 3. Genetic correlations and Mendelian randomization causal estimates between 38 traits and COVID-19 critical illness, hospitalization and SARS-CoV-2 reported infection. Larger squares correspond to more significant P-values, with genetic correlations or MR causal estimates significantly different from zero at a $P < 0.05$ shown as a full-sized square. Genetic correlations or causal estimates that are significantly different from zero at a false discovery rate (FDR) of 5% are marked with an asterisk. Two-sided P-values were calculated using LDSC for genetic correlations and Inverse variance weighted analysis for MR.

METHODS

Contributing studies

All subjects were recruited following protocols approved by local Institutional Review Boards (IRBs); this information is collected in **Supplementary Table 1** for all 46 studies. All protocols followed local ethics recommendations and informed consent was obtained when required. Information about sample numbers, sex and age from for each contributing study is given in **Supplementary Table 1**. In total, 16 studies contributed data to analysis of critical illness due to COVID-19, 29 studies contributed data to hospitalized COVID-19 analysis, and 44 studies contributed to the analysis of all COVID-19 cases. Each individual study that contributed data to a particular analysis met a minimum threshold of 50 cases, as defined by the aforementioned phenotypic criteria, for statistical robustness. The effective sample sizes for each ancestry group shown in Figure 1 were calculated for display using the formula: $(4 \times N_{\text{cases}} \times N_{\text{controls}}) / (N_{\text{cases}} + N_{\text{controls}})$. Details of contributing research groups are described in **Supplementary Table 1**.

Phenotype Definitions

COVID-19 disease status (critical illness, hospitalization status) was assessed following the Diagnosis and Treatment Protocol for Novel Coronavirus Pneumonia ⁴¹. The critically ill COVID-19 group included patients who were hospitalized due to symptoms associated with laboratory-confirmed SARS-CoV-2 infection and who required respiratory support or whose cause of death was associated with COVID-19. The hospitalized COVID-19 group included patients who were hospitalized due to symptoms associated with laboratory-confirmed SARS-CoV-2 infection.

The reported infection cases group included individuals with laboratory-confirmed SARS-CoV-2 infection or electronic health record, ICD coding or clinically confirmed COVID-19, or self-reported COVID-19 (e.g. by questionnaire), with or without symptoms of any severity. Genetic ancestry-matched controls for the three case definitions were sourced from population-based cohorts, including individuals whose exposure status to SARS-CoV-2 was either unknown or infection- negative for questionnaire/electronic health record based cohorts. Additional information regarding individual studies contributing to the consortium are described in **Supplementary Table 1**.

GWAS and meta-analysis

Each contributing study genotyped the samples and performed quality controls, data imputation and analysis independently, but following consortium recommendations (information available at www.covid19hg.org). We recommended to run GWAS analysis using Scalable and Accurate Implementation of GEneralized mixed model (SAIGE) ⁴² on chromosomes 1-22 and X. The recommended analysis tool was SAIGE, but studies also used other software such as PLINK ⁴³. The suggested covariates

were age, age2, sex, age*sex, and 20 first principal components. Any other study-specific covariates to account for known technical artefacts could be added. SAIGE automatically accounts for sample relatedness and case-control imbalances. Individual study quality control and analysis approaches are reported in **Supplementary Table 1**.

Study-specific summary statistics were then processed for meta-analysis. Potential false positives, inflation, and deflation were examined for each submitted GWAS. Standard error values as a function of effective sample size was used to find studies which deviated from the expected trend. Summary statistics passing this manual quality control were included in the meta-analysis. Variants with allele frequency of >0.1% and imputation INFO>0.6 were carried forward from each study. Variants and alleles were lifted over to genome build GRCh38, if needed, and harmonized to gnomAD 3.0 genomes⁴⁴ by finding matching variants by strand flipping or switching ordering of alleles. If multiple matching variants, the best match was chosen by minimum absolute allele frequency fold change. Meta-analysis was performed using the inverse-variance weighted method on variants that were present in at least 2/3 of studies contributing to the phenotype analysis. The method summarizes effect sizes across the multiple studies by computing the mean of the effect sizes weighted by the inverse variance in each individual study.

We report 13 meta-analysis variants that pass genome-wide significance threshold after adjusting the threshold for multiple traits tested ($P < 5 \times 10^{-8} / 3$). We report the unadjusted P -values for each variant. We tested for heterogeneity between estimates from contributing studies using Cochran's Q test^{45,46}. This is calculated for each variant as the weighted sum of squared differences between the effects sizes and their meta-analysis effect, the weights being the inverse variance of the effect size. Q is distributed as a chi-square statistic with k (number of studies) minus 1 degrees of freedom. Two loci reached genome-wide significance but were excluded from **Supplementary Table 2** significant results due to heterogeneity between estimates from contributing studies and missingness between studies at chr6:31057940-31380334 and chr7:54671568-54759789; however these regions are not excluded from the corresponding summary statistics in data release 5. For each of the lead variants reported in **Supplementary Table 2**, we aimed to find loci specific to susceptibility or severity by testing whether there was heterogeneity between the effect sizes associated with hospitalized COVID-19 (progression to severe disease) and reported SARS-CoV-2 infection. We used Cochran's Q measure^{45,46}, calculated for each variant as the weighted sum of squared differences between the two analysis effects sizes and their meta-analysis effect, the weights being the inverse variance of the effect size. A significant P -value <0.004 (0.05/13 loci) for multiple tests) indicates that the effect sizes for a particular variant are significantly different in the two analyses (**Supplementary Table 2**). For the 9 loci, where the lead variant effect size was significantly higher for hospitalized COVID-19, we carried out the same test again but comparing effect sizes from hospitalized COVID-19 with critically ill COVID-19 (**Supplementary Table 4**). Further, we carried out the same test comparing meta-analyzed hospitalized COVID-19 (population as controls) and hospitalized COVID-19 (SARS-CoV-2 positive but non-hospitalized as controls) (**Supplementary Table 4**). For these pairs of phenotype comparisons, we generated new meta-analysis summary statistics to use; including only those studies that could contribute data to both phenotypes that were under comparison.

PC projection

To project every GWAS participant into the same PC space, we used pre-computed PC loadings and reference allele frequencies. For reference, we used unrelated samples from the 1000 Genomes Project and the Human Genome Diversity Project (HGDP) and computed PC loadings and allele frequencies for the 117,221 SNPs that are i) available in every cohort, ii) MAF > 0.1% in the reference, and iii) LD pruned ($r^2 < 0.8$; 500kb window). We then asked each cohort to project their samples using our automated script provided at <https://github.com/covid19-hg/>. It internally uses PLINK2 ⁴⁷ --score function with variance-standardize option and reference allele frequencies (--read-freq); so that each cohort-specific genotype/dosage matrix is mean-centered and variance-standardized with regards to reference allele frequencies, not cohort-specific allele frequencies. We further normalized the projected PC scores by dividing by a square root of the number of variants used for projection to account for a subtle difference due to missing variants.

Gene prioritization

To prioritize candidate causal genes reported in full in **Supplementary Table 2**, we employed various gene prioritization approaches using both locus-based and similarity-based methods. Because we only referred *in-silico* gene prioritization results without characterizing actual functional activity *in-vitro/vivo*, we aimed to provide a systematic approach to nominate potential causal genes in a locus using the following criteria:

1. Closest gene: a gene that is closest to a lead variant by distance to the gene body
2. Genes in LD region: genes that overlap with a genomic range containing any variants in LD ($r^2 > 0.6$) with a lead variant. For LD computation, we retrieved LD matrices provided by the gnomAD v2.1.1 ⁴⁴ for each population analyzed in this study (except for Admixed American, Middle Eastern, and South Asian that are not available). We then constructed a weighted-average LD matrix by per-population sample sizes in each meta-analysis, which we used as a LD reference.
3. Genes with coding variants: genes with at least one loss of function or missense variant (annotated by VEP ⁴⁸ v95 with GENCODE v29) that is in LD with a lead variant ($r^2 > 0.6$).
4. eGenes: genes with at least one fine-mapped *cis*-eQTL variant (PIP > 0.1) that is in LD with a lead variant ($r^2 > 0.6$) (**Supplementary Table 5**). We retrieved fine-mapped variants from the GTEx v8²¹ (<https://www.finucanelab.org/>) and eQTL catalogue⁴⁹. In addition, we looked up significant associations in the Lung eQTL Consortium ²² ($n = 1,103$) to further support findings in lung with a larger sample size (**Supplementary Table 7**). We note that, unlike the GTEx or eQTL catalogue, we only looked at associations and didn't finemap in the Lung eQTL Consortium data.
5. V2G: a gene with the highest overall Variant-to-Gene (V2G) score based on the Open Targets Genetics (OTG) ²⁷. For each variant, the overall V2G score aggregates differentially weighted evidence of variant-gene association from several data sources, including molecular *cis*-QTL data (e.g., *cis*-pQTLs from ⁵⁰., *cis*-eQTLs from GTEx v7 etc.), interaction-based datasets (e.g., Promoter Capture Hi-C), genomic distance, and variant effect predictions (VEP) from Ensembl. A detailed description of the evidence sources and weights used is provided in the OTG documentation (<https://genetics-docs.opentargets.org/our-approach/data-pipeline>) ^{27,51}.

Phenome-wide association study

To investigate the evidence of shared effects of 15 index variants for COVID-19 and previously reported phenotypes, we performed a phenome-wide association study. We considered phenotypes in (Open Target) OTG obtained from the GWAS catalog (this included studies with and without full summary statistics, $n = 300$ and $14,013$, respectively)⁵², and from UK Biobank. Summary statistics for UK Biobank traits were extracted from SAIGE⁴² for binary outcomes ($n = 1,283$ traits), and Neale v2 ($n = 2,139$ traits) for both binary and quantitative traits (<http://www.nealelab.is/uk-biobank/>) and FinnGen Freeze 4 cohort (https://www.finnngen.fi/en/access_results). We report PheWas results for phenotypes for which the lead variants were in high LD ($r^2 > 0.8$) with the 13 genome-wide significant lead variants from our main COVID-19 meta-analysis (**Supplementary Table 6**). This conservative approach allowed spurious signals primarily driven by proximity rather than actual colocalization to be removed (see **Methods**).

To remove plausible spurious associations, we retrieved phenotypes for GWAS lead variants that were in LD ($r^2 > 0.8$) with COVID-19 index variants.

Heritability

LD score regression v 1.0.1⁵³ was used to estimate SNP heritability of the phenotypes from the meta-analysis summary statistic files. As this method depends on matching the linkage disequilibrium (LD) structure of the analysis sample to a reference panel, the European-only summary statistics were used. Sample sizes were $n = 5,101$ critically ill COVID-19 cases and $n = 1,383,241$ controls, $n = 9,986$ hospitalized COVID-19 cases and $n = 1,877,672$ controls, and $n = 38,984$ cases and $n = 1,644,784$ controls for all cases analysis, all including the 23andMe cohort. Pre-calculated LD scores from the 1000 Genomes European reference population were obtained online (<https://data.broadinstitute.org/alkesgroup/LDSCORE/>). Analyses were conducted using the standard program settings for variant filtering (removal of non-HapMap3 SNPs, the HLA region on chromosome 6, non-autosomal, chi-square > 30 , MAF $< 1\%$, or allele mismatch with reference). We additionally report SNP heritability estimates for the all-ancestries meta-analyses, calculated using European panel LD scores, in **Supplementary Table 8**.

Partitioned heritability

We used partitioned LD score regression⁵⁴ to partition COVID-19 SNP heritability in cell types in our European ancestries only summary statistics. We ran the analysis using the baseline model LD scores calculated for European populations and regression weights that are available online. We used the COVID-19 European only summary statistics for the analysis.

Genome-wide association summary statistics

We obtained genome-wide association summary statistics for 43 complex disease, neuropsychiatric, behavioural, or biomarker phenotypes (**Supplementary Table 10**). These phenotypes were selected based on their putative relevance to COVID-19 susceptibility, severity, or mortality, with 19 selected based on

the Centers for Disease Control list of underlying medical conditions associated with COVID-19 severity⁵⁵ or traits reported to be associated with increased risk of COVID-19 mortality by OpenSafely⁵⁶. Summary statistics generated from GWAS using individuals of European ancestry were preferentially selected if available. These summary statistics were used in subsequent genetic correlation and Mendelian randomization analyses.

Genetic Correlation

LD score regression⁵⁴ was also used to estimate genetic correlations between our COVID-19 meta-analysis phenotypes reported using European ancestries only samples, and between these and the curated set of 38 summary statistics. Genetic correlations were estimated using the same LD score regression settings as for heritability calculations. Differences between the observed genetic correlations of SARS-CoV-2 infection and COVID-19 severity were compared using a z score method⁵⁷.

Mendelian Randomization

Two-sample Mendelian randomization was employed to evaluate the potential for causal association of the 38 traits on COVID-19 hospitalization, on COVID-19 severity and SARS-CoV-2 reported infection using European-only samples. Independent genome-wide significant SNPs robustly associated with the exposures of interest ($P < 5 \times 10^{-8}$) were selected as genetic instruments by performing LD clumping using PLINK⁴³. We used a strict r^2 threshold of 0.001, a 10MB clumping window, and the European reference panel from the 1000 Genomes project⁵⁸ to discard SNPs in linkage disequilibrium with another variant with smaller p-value association. For genetic variants that were not present in the hospitalized COVID analysis, PLINK was used to identify proxy variants that were in LD ($r^2 > 0.8$). Next, the exposure and outcome datasets were harmonized using the R-package TwoSampleMR⁵⁹. Namely, we ensured that the effect of a variant on the exposure and outcome corresponded to the same allele, we inferred positive strand alleles and dropped palindromes with ambiguous allele frequencies, as well as incompatible alleles. **Supplementary Table 10** includes the harmonized datasets used in the analyses.

Mendelian Randomization Pleiotropy residual sum and outlier (MR-PRESSO) Global test⁶⁰ was used to investigate overall horizontal pleiotropy. In short, the standard IVW meta-analytic framework was employed to calculate the average causal effect by excluding each genetic variant used to instrument the analysis. A global statistic was calculated by summing the observed residual sum of squares, i.e., the difference between the effect predicted by the IVW slope excluding the SNP, and the observed SNP-effect on the outcome. Overall horizontally pleiotropy was subsequently probed by comparing the observed residual sum of squares, with the residual sum of squares expected under the null hypothesis of no pleiotropy. The MR-PRESSO Global test was shown to perform well when the outcome and exposure GWASs are not disjoint (although the power to detect horizontal pleiotropy is slightly reduced by complete sample overlap). We also used the MR-Egger regression intercept⁶¹ to evaluate potential bias due to directional pleiotropic effects. This additional check was employed in MR analyses with an I^2_{MR} index surpassing the recommended threshold ($I^2_{MR} > 90\%$;⁶²). Contingent on the MR-PRESSO Global test results we probed the causal effect of each exposure on COVID-19 hospitalization by using a fixed effect inverse-weighted (IVW) meta-analysis as the primary analysis, or, if pleiotropy was present, the MR-PRESSO outlier corrected test. The IVW approach estimates the causal effect by aggregating the single-

SNP causal effects (obtained using the ratio of coefficients method, i.e., the ratio of the effect of the SNP on the outcome on the effect of the SNP on the exposure) in a fixed effects meta-analysis. The SNPs were assigned weights based on their inverse variance. The IVW method confers the greatest statistical power for estimating causal associations⁶³, but assumes that all variants are valid instruments and can produce biased estimates if the average pleiotropic effect differs from zero. Alternatively, when horizontal pleiotropy was present, we used MR-PRESSO Outlier corrected method to correct the IVW test by removing outlier SNPs. We conducted further sensitivity analyses using alternative MR methods that provide consistent estimates of the causal effect even when some instrumental variables are invalid, at the cost of reduced statistical power including: 1) Weighted Median Estimator (WME); 2) Weighted Mode Based Estimator (WMBE); 3) MR-Egger regression. Robust causal estimates were defined as those that were significant at an FDR of 5% and either 1) showed no evidence of heterogeneity (MR-PRESSO Global test $P > 0.05$) or horizontal pleiotropy (Egger Intercept $P > 0.05$), or 2) in the presence of heterogeneity or horizontal pleiotropy, either the WME, WMBE, MR-Egger or MR-PRESSO corrected estimates were significant ($P < 0.05$). All statistical analyses were conducted using R version 4.0.3. MR analysis was performed using the “TwoSampleMR” version 0.5.5 package⁵⁹.

Website and data distribution

In anticipation of the need to coordinate many international partners around a single meta-analysis effort, we created the COVID-19 HGI website (<https://covid19hg.org>). We were able to centralize information, recruit partner studies, rapidly distribute summary statistics, and present preliminary interpretations of the results to the public. Open meetings are held on a monthly basis to discuss future plans and new results; video recordings and supporting documents are shared (<https://covid19hg.org/meeting-archive>). This centralized resource provides a conceptual and technological framework for organizing global academic and industry groups around a shared goal. The website source code and additional technical details are available at <https://github.com/covid19-hg/covid19hg>.

To recruit new international partner studies, we developed a workflow whereby new studies are registered and verified by a curation team (<https://covid19hg.org/register>). Users can explore the registered studies using a customized interface to find and contact studies with similar goals or approaches (<https://covid19hg.org/partners>). This helps to promote organic assembly around focused projects that are adjacent to the centralized effort (<https://covid19hg.org/projects>). Visitors can query study information, including study design and research questions. Registered studies are visualized on a world map and are searchable by institutional affiliation, city, and country.

To encourage data sharing and other forms of participation, we created a rolling acknowledgements page (<https://covid19hg.org/acknowledgements>) and directions on how to contribute data to the central meta-analysis effort (<https://covid19hg.org/data-sharing>). Upon the completion of each data freeze, we post summary statistics, plots, and sample size breakdowns for each phenotype and contributing cohort (<https://covid19hg.org/results>). The results can be explored using an interactive web browser (<https://app.covid19hg.org>). Several computational research groups carry out follow-up analyses, which are made available for download (<https://covid19hg.org/in-silico>). To enhance scientific communication to the public, preliminary results are described in blog posts by the scientific communications team and shared on

Twitter. The first post was translated to 30 languages with the help of 85 volunteering translators. We compile publications and preprints submitted by participating groups and summarize genome-wide significant findings from these publications (<https://covid19hg.org/publications>).

Data availability

Summary statistics generated by COVID-19 HGI are available at <https://www.covid19hg.org/results/r5/> and are available on GWAS Catalog (study code GCST011074). The analyses described here utilize the freeze 5 data. COVID-19 HGI continues to regularly release new data freezes. Summary statistics for non-European ancestry samples are not currently available due to the small individual sample sizes of these groups, but results for 13 loci lead variants are reported in **Supplementary Table 3**. Individual level data can be requested directly from contributing studies, listed in **Supplementary Table 1**. We used publicly available data from GTEx (<https://gtexportal.org/home/>), the Neale lab (<http://www.nealelab.is/uk-biobank/>), Finucane lab (<https://www.finucanelab.org>), FinnGen Freeze 4 cohort (https://www.finnngen.fi/en/access_results), and eQTL catalogue release 3 (<http://www.ebi.ac.uk/eql/>).

Code availability

The code for summary statistics liftover, projection PCA pipeline including precomputed loadings and meta-analysis are available at <https://github.com/covid19-hg/> and the code for Mendelian randomization and genetic correlation pipeline at <https://github.com/marcoralab/MRcovid>.

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EXTENDED DATA FIGURE LEGENDS

Extended Data Figure 1. Analytical summary of the COVID-19 HGI meta-analysis.

Using the analytical plan set by the COVID-19 HGI, each individual study runs their analyses and uploads the results to the Initiative, who then runs the meta-analysis. There are three main analyses that each study can contribute summary statistics to; critically ill COVID-19, hospitalized COVID-19 and reported SARS-CoV-2 infection. The phenotypic criteria used to define cases are listed in the dark grey boxes, along with the numbers of cases (N) included in the final all ancestries meta-analysis. Controls were defined in the same way across all three analyses; as everybody that is not a case e.g. population controls (light grey box). Sensitivity analyses, not reported in this Figure, also used mild/asymptomatic COVID-19 cases as controls. Sample number (N) of controls differed between the analyses due to the difference in number of studies contributing data to these.

Extended Data Figure 2. Projection of contributing studies samples into the same PC space.

We asked participating studies to perform PC projection using the 1000 Genomes Project and Human Genome Diversity Project as a reference, with a common set of variants. For each panel (except for the reference), colored points correspond to contributed samples from each cohort, whereas gray points correspond to 1000 Genomes reference samples. Color represents a genetic population that each cohort specified. Since 23andme, genomicsengland100kpg, and MVP only submitted PCA images, we overlaid their submitted transparent images using the same coordinates, instead of directly plotting them.

Extended Data Figure 3. Locuszoom plots of the 3p21.31 region for reported infection.

a. A standard plot without exclusion. Here, the severity lead variant rs10490770 (chr3:45823240:T:C) is shown as a lead variant. b. Additional independent susceptibility signal(s) after excluding variants with $r^2 > 0.05$ with rs10490770. The susceptibility lead variant rs2271616 (chr3:45796521:G:T) is highlighted.

Extended Data Figure 4. Genome-wide meta-analysis association results for critical illness due to COVID-19.

The locus on chromosome 6 is the HLA locus, which was removed from the list of reported loci in Table 1 due to the high heterogeneity in effect size estimated between studies included in the analysis. The locus on chromosome 7 was also not reported in Table 1 due to missingness across studies, i.e. the high number of studies in the meta-analysis that did not report summary statistics for this region. There are two association peaks on chromosome 19.

Extended Data Figure 5. Sensitivity analyses for overlapping controls in genomICC and UK Biobank.

Comparison of the beta effect sizes (top panel) and unadjusted *P*-values (bottom panel) of the 13 lead variants, using data from the COVID-19 critical illness meta-analysis in all the cohorts (y-axis) to leaving out genomICC (case = 4,354; control = 1,474,655; total n = 1,479,009), leaving out UK Biobank (UKBB, case = 5,870; control = 1,155,203; total n = 1,161,073) and leaving out genomICC + UKBB (case = 4,045; control = 1,146,078; total n = 1,150,123), respectively (x-axis). Top panel dots and grey bars represent the beta effect size estimates \pm standard error from the corresponding GWAS meta-analysis, bottom panel dots represent two-sided *P*-values from the corresponding GWAS meta-analysis. Filled dots indicate variants that were genome-wide significant in the full meta-analysis of critical illness due to COVID-19, and empty dots represent variants that were not significant for critical illness but were significant for either hospitalization due to COVID-19 or SARS-CoV-2 reported infection. Red dots represent variants that were genome-wide significant in leave-one-out analysis for genomICC, UKBB or genomICC + UKBB.

Extended Data Figure 6. Comparison of chi-squared statistics vs r^2 values to the lead variant in the 3p21.31 region.

For **a.** critical illness **b.** hospitalization, and **c.** reported infection. The left blue peak in panel **c**, which is uncorrelated with the lead variants in the region, indicates that there are independent signals.

Extended Data Figure 7. Comparison of lead variant effect sizes between pairs of COVID-19 meta-analyses.

Comparison of effect sizes for the nine variants associated with severity of COVID-19 disease. A. Comparing hospitalized COVID-19 cases vs population controls (x-axis, n=10,428 cases and n=1,483,270 controls) and critically ill COVID-19 cases vs population controls (y-axis, n=6,179 cases and n=1,483,780 controls). B. hospitalized COVID-19 cases vs population controls (x-axis, n=5,806 cases and n=1,144,263 controls) and hospitalized COVID-19 cases vs non-hospitalized COVID-19 cases (y-axis, n=5,773 and n=15,497 controls). Sample sizes for hospitalized COVID-19 cases vs population controls differ between panels A and B due to differences in the sampling of studies selected for the analysis. This selection included all studies that were able to contribute data to the respective analysis that the data were compared to (on the y-axis) in each panel. Dots represent the effect size beta estimates, bars represent the 95% confidence interval of the estimates. Effect size estimates and *P*-values for heterogeneity test (Cochran's *Q*, two-tailed test) are reported in **Supplementary Table 3**.

Extended Data Figure 8. PheWas for genome-wide significant lead variants. Selected phenotypes associated with genome-wide significant COVID-19 variants (see **Supplementary Table 6** for a complete list). We report those associations for which a lead variant from a prior GWAS results was in high LD ($r^2 > 0.8$) with the index COVID-19 variants. The colour represents the Z-scores of correlated risk increasing alleles for the trait. The total number of associations for each COVID-19 variant is highlighted in the grey box.

Extended Data Figure 9. Genetic correlation with COVID-19 phenotypes.

Each column shows genetic correlation results for the three COVID-19 phenotypes (European ancestry analyses only): critical illness, hospitalization and reported infection. The traits the genetic correlation is run against are listed on the left. Significant correlations (FDR<0.05) are shown with their 95% confidence intervals in red, nominally significant ($P<0.05$) in black and non-significant in grey. Two-sided P -values were calculated using LDSC for genetic correlations and exact estimates, unadjusted standard errors and two-sided P -values are available in **Supplementary Table 11**.

Extended Data Figure 10. Mendelian Randomization sensitivity analyses. Genetic correlations and Forest plots displaying the causal estimates for each of the sensitivity analyses used in the MR analysis for trait pairs that were significant at an FDR of 5% . Two-sided P -values were estimated using Inverse variance weighted analysis (IVW), Weighted median estimator (WME), weighted mode based estimator (WMBE), and Mendelian Randomization Pleiotropy RESidual Sum and Outlier (MR-PRESSO). RBC: Red blood cell count.

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COMPETING INTEREST STATEMENT

A full list of competing interests is supplied as **Supplementary Table 13**.

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537. John Radcliffe Hospital, Oxford University Hospitals NHS Foundation Trust, Oxford, UK
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543. St Thomas Hospital, Guys and St Thomas Foundation Trust, London, UK
544. University Hospitals Coventry and Warwickshire, Coventry, UK
545. St Michaels Hospital (Bristol), University Hospitals Bristol and Weston NHS Foundation Trust, Bristol, UK
546. Stepping Hill Hospital, Stockport NHS Foundation Trust, Manchester, UK
547. Royal Liverpool Hospital, Liverpool University Hospitals NHS Foundation Trust, Liverpool, UK
548. Bristol Royal Hospital (Children's), University Hospitals Bristol and Weston NHS Foundation Trust, Bristol, UK
549. Scarborough Hospital, York teaching Hospitals NHS Foundation Trust, York, UK
550. Liverpool Heart & Chest Hospital, Liverpool Heart & Chest NHS Foundation Trust, Liverpool, UK
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607. The Walton Centre, The Walton Centre, Liverpool, UK
608. Hull Royal Infirmary, Hull University Teaching Hospital Trust, Hull, UK
609. Darlington Memorial Hospital, County Durham and Darlington Foundation Trust, Darlington, UK
610. Queen Elizabeth Hospital (Gateshead), Gateshead NHS Foundation Trust, Newcastle, UK
611. Warrington Hospital, Warrington & Halton Hospitals NHS Foundation Trust, Warrington, UK
612. University Hospitals Bristol and Weston NHS Foundation Trust, Bristol, UK
613. St Mary's Hospital (Isle of Wight), Isle of Wight NHS Trust, Isle of Wight, UK
614. The Maidstone Hospital, Maidstone & Tunbridge Wells NHS Trust, Maidstone, UK
615. Huddersfield Royal, Calderdale and Huddersfield NHS Foundation Trust, Huddersfield, UK
616. Royal Surrey County Hospital, Surrey, UK
617. Countess of Chester Hospital, Countess of Chester Hospital NHS Foundation Trust, Chester, UK
618. Frimley Park Hospital, Frimley Health Foundation Trust, Surrey, UK
619. Royal Hallamshire Hospital, Sheffield Teaching Hospitals NHS FoundationTrust, Sheffield, UK

620. Leeds General Infirmary, Leeds Teaching Hospitals, Leeds, UK
621. North Middlesex Hospital, North Middlesex University Hospital NHS Trust, London, UK
622. Arrowe Park Hospital, Wirral University Teaching Hospital NHS Foundation Trust, Wirral, UK
623. Great Ormond Street Hospital, Great Ormond Street Hospital for Children NHS Foundation Trust, London, UK
624. Royal Shrewsbury Hospital, Shrewsbury and Telford Hospital NHS Trust, Shropshire, UK
625. East Surrey Hospital (Redhill), Surrey & Sussex Healthcare, Surrey, UK
626. Burton Hospital, University Hospitals of Derby & Burton NHS Foundation Trust, Burtom, UK
627. Kent and Canterbury Hospital, East Kent Hospitals NHS Foundation Trust, Kent, UK
628. Weston Area General Trust, University Hospitals Bristol and Weston NHS Foundation Trust, Bristol, UK
629. Luton and Dunstable University Hospital, Bedford, UK
630. Glasgow Royal Infirmary, Greater Glasgow and Clyde, Glasgow, UK
631. Derbyshire Healthcare, Derbyshire Healthcare, Derby, UK
632. Macclesfield General Hospital, East Cheshire NHS Foundation Trust, Cheshire, UK
633. Chelsea and Westminster Hospital, Chelsea and Westminster NHS Trust, London, UK
634. Institute of Microbiology and Infection, University of Birmingham, Birmingham, UK
635. Prince Philip Hospital, Hwyl Dda University Health Board, Llanelli, Wales
636. George Eliot Hospital - Acute Services, George Eliot Hospital, Nuneaton, UK
637. Kettering General Hospital, Kettering General Hospital NHS Foundation Trust, Kettering, UK
638. Heartlands Hospital, Birmingham, Birmingham, UK
639. Russells Hall Hospital, The Dudley Group NHS Foundation Trust, Dudley, UK
640. Harefield Hospital , Royal Brompton & Harefield Trust, London, UK
641. Lister Hospital, East and North Hertfordshire NHS Trust, Stevenage, UK
642. Musgrove Park Hospital (Taunton & Somerset), Somerset NHS Foundation Trust, Somerset, UK
643. Queen's Hospital, Havering (Romford), Barking, Havering and Redbridge University Hospitals NHS Trust, London, UK
644. Southport & Formby District General Hospital, Southport and Ormskirk Hospital NHS Trust, Southport, UK
645. New Cross Hospital, The Royal Wolverhampton NHS Trust, Wolverhampton, UK
646. Kings College Hospital (Denmark Hill), London, UK
647. The Royal Victoria Infirmary, Newcastle Hospitals NHS Trust, Newcastle, UK
648. The Great Western Hospital, Great Western Hospitals NHS Foundation Trust, Swindon, UK
649. Ninewells Hospital, Tayside, Dundee, UK
650. Poole Hospital NHS Trust, Dorset, UK
651. Burton Hospital, University Hospitals of Derby & Burton NHS Foundation Trust, Derby, UK
652. William Harvey Hospital, Ashford, East Kent Hospitals NHS Foundation Trust, Kent, UK
653. Kings Mill Hospital, Sherwood Forest Hospitals NHS Foundation Trust, Nottinghamshire, UK
654. Liverpool Women's NHS Foundation Trust, Liverpool, UK
655. Dewsbury Hospital, Mid Yorkshire Hospitals NHS Trust, Dewsbury, UK
656. Northern Devon District Hospital, Northern Devon Healthcare NHS Trust, Devon, UK
657. Tameside General Hospital, Tameside and Glossop Integrated Care NHS Foundation Trust, Manchester, UK
658. Sandwell General Hospital, Sandwell And West Birmingham Hospitals NHS Trust, Birmingham, UK
659. Broomfield Hospital, Mid and South Essex University Hospitals Group, Essex, UK
660. Wycombe Hospital, Buckingham Healthcare NHS Trust, Buckinghamshire, UK
661. University Hospital of North Tees, North Tees and Hartlepool NHS Trust, Stockton-on-Tees, UK
662. Royal Manchester Children's Hospital, Manchester University Hospitals NHS Foundation Trust, Manchester, UK

663. Bedford Hospital, Bedford, UK
664. Colchester General Hospital, East Suffolk and North Essex Foundation Trust, Essex, UK
665. Queen Elizabeth Hospital (Birmingham) and Heartlands, University Hospital Birmingham NHS Foundation Trust, Birmingham, UK
666. Chesterfield Royal Hospital, Chesterfield Royal Hospital NHS Foundation Trust, Chesterfield, UK
667. Princess Alexandra Hospital, The Princess Alexandra Hospital NHS Trust, Essex, UK
668. Watford General Hospital, West Hertfordshire Hospitals NHS Trust, Watford, UK
669. Milton Keynes Hospital, Milton Keynes University Hospital NHS Foundation Trust, Milton Keynes, UK
670. Royal Bolton General Hospital, Bolton Foundation Trust, Bolton, UK
671. Royal Gwent (Newport), Aneurin Bevan University Health Board, Newport, UK
672. The Royal Marsden Hospital (London), The Royal Marsden NHS Foundation Trust, London, UK
673. Queen Victoria Hospital (East Grinstead), Queen Victoria Hospital NHS Foundation Trust, Sussex, UK
674. County Hospital (Stafford), University Hospitals Of North Midlands NHS Trust, Stafford, UK
675. Whiston Hospital, St Helen's & Knowlsey Hospitals NHS Trust, Prescot, UK
676. Croydon University Hospital, Croydon University Hospital, London, UK
677. Gloucester Royal, Gloucestershire Hospitals NHS Foundation Trust, Gloucester, UK
678. Medway Maritime Hospital, Medway Maritime NHS Trust, Kent, UK
679. Royal Papworth Hospital Everard, Royal Papworth Hospital NHS Foundation Trust, Cambridge, UK
680. Derriford (Plymouth), University Hospital Plymouth NHS Trust, Plymouth, UK
681. St Helier Hospital, Epsom and St Helier University Hospital NHS Trust, London, UK
682. Royal Berkshire Hospital, Royal Berkshire Foundation Trust, London, UK
683. Bradford Royal Infirmary, Bradford Teaching Hospitals NHS Foundation Trust, Bradford, UK
684. Northwick Park, London North West University Hospital Trust, London, UK
685. Ealing Hospital, London North West University Hospital Trust, London, UK
686. Royal Cornwall Hospital (Tresliske), Royal Cornwall NHS Trust, Cornwall, UK
687. Ashford Hospital, Ashford & St. Peter's Hospital, Surrey, UK
688. Leicester Royal Infirmary (Includes Glenfield Site), University Hospitals of Leicester, Leicester, UK
689. Grantham and District Hospital, United Lincolnshire Hospitals NHS Trust, Grantham, UK
690. University Hospital Aintree, Liverpool University Hospitals NHS Foundation Trust, Liverpool, UK
691. North Tyneside General Hospital, Northumbria Healthcare NHS Trust, Northumbria, UK
692. Queen Elizabeth Hospital (King's Lynn), Queen Elizabeth Hospital, King's Lynn, NHS Foundation Trust, Norfolk, UK
693. The Crick Institute, London, UK
694. Genomics England, London, UK
695. William Harvey Research Institute, Barts and the London School of Medicine and Dentistry, Queen Mary University of London, London EC1M 6BQ, UK.
696. Centre for Genomic and Experimental Medicine, Institute of Genetics and Molecular Medicine, University of Edinburgh, Western General Hospital, Crewe Road, Edinburgh, EH4 2XU, UK
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698. Intensive Care Unit, Royal Infirmary of Edinburgh, 54 Little France Drive, Edinburgh, EH16 5SA, UK.
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700. Wellcome Centre for Human Genetics, University of Oxford, Oxford, UK.
701. Genomics England, London, UK.
702. Roslin Institute, University of Edinburgh, Easter Bush, Edinburgh, EH25 9RG, UK.
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704. Intensive Care National Audit & Research Centre, London, UK.

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706. Great Ormond Street Hospital for Children NHS Foundation Trust, London, UK.

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713. Biostatistics Group, School of Life Sciences, Sun Yat-sen University, Guangzhou, China.

714. Centre for Medical Informatics, The Usher Institute, University of Edinburgh, Edinburgh, UK

715. Liverpool Clinical Trials Centre, University of Liverpool, Liverpool, UK

716. Centre for Health Informatics, Division of Informatics, Imaging and Data Science, School of Health Sciences, Faculty of Biology, Medicine and Health, University of Manchester, Manchester Academic Health Science Centre, Manchester, UK

717. MRC Human Genetics Unit, MRC Institute of Genetics and Molecular Medicine, University of Edinburgh, Edinburgh, UK

718. School of Informatics, University of Edinburgh, Edinburgh, UK

719. Royal Hospital for Children, Glasgow, UK

720. William Harvey Research Institute, Barts and the London School of Medicine and Dentistry, Queen Mary University of London, London EC1M 6BQ, UK

721. MRC-University of Glasgow Centre for Virus Research, Institute of Infection, Immunity and Inflammation, College of Medical, Veterinary and Life Sciences, University of Glasgow, Glasgow, UK

722. Centre for Tropical Medicine and Global Health, Nuffield Department of Medicine, University of Oxford, Old Road Campus, Roosevelt Drive, Oxford, OX3 7FZ, UK

723. Wellcome Centre for Human Genetics, University of Oxford, Oxford, UK

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725. Department of Critical Care Medicine, Queen's University and Kingston Health Sciences Centre, Kingston, ON, Canada

726. Wellcome-Wolfson Institute for Experimental Medicine, Queen's University Belfast, Belfast, Northern Ireland, UK

727. Department of Intensive Care Medicine, Royal Victoria Hospital, Belfast, Northern Ireland, UK

728. UCL Centre for Human Health and Performance, London, W1T 7HA, UK

729. Clinical Research Centre at St Vincent's University Hospital, University College Dublin, Dublin, Ireland

730. National Heart and Lung Institute, Imperial College London, London, UK

731. Imperial College Healthcare NHS Trust:London,London,UK

732. NIHR Health Protection Research Unit for Emerging and Zoonotic Infections, Institute of Infection, Veterinary and Ecological Sciences University of Liverpool, Liverpool, L69 7BE, UK

733. Respiratory Medicine, Alder Hey Children's Hospital, Institute in The Park, University of Liverpool, Alder Hey Children's Hospital, Liverpool, UK

734. Department of Intensive Care Medicine, Guy's and St. Thomas NHS Foundation Trust, London, UK

735. Department of Medicine, University of Cambridge, Cambridge, UK

736. Airedale General Hospital, Keighley, UK

737. Barts Health NHS Trust, London, UK

738. Basildon Hospital, Basildon, UK

739. BHRUT (Barking Havering) - Queens Hospital and King George Hospital, Essex, UK

740. Bradford Royal Infirmary, Bradford, UK

741. Bronglais General Hospital, Aberystwyth, UK
742. Broomfield Hospital, Chelmsford, UK
743. Calderdale Royal Hospital, Halifax, UK
744. Charing Cross Hospital, St Mary's Hospital and Hammersmith Hospital, London, UK
745. Barnet Hospital, London, UK
746. Birmingham Children's Hospital, Birmingham, UK
747. St John's Hospital Livingston, Livingston, UK
748. Aberdeen Royal Infirmary, Aberdeen, UK
749. Addenbrooke's Hospital, Cambridge, UK
750. Aintree University Hospital, Liverpool, UK
751. aintree University Hospital, Liverpool, UK
752. Arrowe Park Hospital, Wirral, UK
753. Ashford and St Peter's Hospital, Surrey, UK
754. Basingstoke and North Hampshire Hospital, Basingstoke, UK
755. Borders General Hospital, Melrose, UK
756. Chesterfield Royal Hospital Foundation Trust, Chesterfield, UK
757. Eastbourne District General Hospital, East Sussex, UK and Conquest Hospital, East Sussex, UK
758. Barnsley Hospital, Barnsley, UK
759. Blackpool Victoria Hospital, Blackpool, UK
760. East Surrey Hospital, Redhill, UK
761. Good Hope Hospital, Birmingham, UK
762. Hereford County Hospital, Hereford, UK
763. Hull Royal Infirmary, Hull, UK
764. Hull Royal Infirmary, Hull, UK
765. Kent & Canterbury Hospital, Canterbury, UK
766. Manchester Royal Infirmary, Manchester, UK
767. Nottingham University Hospital, Nottingham, UK
768. Pilgrim Hospital, Lincoln, UK
769. Queen Elizabeth Hospital, Birmingham, UK
770. Salford Royal Hospital, Manchester, UK
771. Tameside General Hospital, Ashton Under Lyne, UK
772. The Tunbridge Wells Hospital and Maidstone Hospital, Kent, UK
773. The Royal Oldham Hospital, Manchester, UK
774. The Royal Papworth Hospital, Cambridge, UK
775. University College Hospital, London, UK
776. Withybush General Hospital, Pembrokeshire, Wales
777. Wythenshawe Hospital, Manchester, UK
778. Yeovil Hospital, Yeovil, UK
779. Cumberland Infirmary, Carlisle, UK
780. Darent Valley Hospital, Dartford, UK
781. Dumfries and Galloway Royal Infirmary, Dumfries, UK
782. Ealing Hospital, Southall, UK
783. Fairfield General Hospital, Bury, UK
784. George Eliot Hospital NHS Trust, Nuneaton, UK
785. Glan Clwyd Hospital, Bodelwyddan, UK
786. Glangwili General Hospital, Camarthen, UK
787. The Great Western Hospital, Swindon, UK
788. Guys and St Thomas' Hospital, London, UK
789. Harefield Hospital, London, UK

790. Harrogate and District NHS Foundation Trust, Harrogate, UK
791. Heartlands Hospital, Birmingham, UK
792. James Paget University Hospital NHS Trust, Great Yarmouth, UK
793. King's College Hospital, London, UK
794. King's Mill Hospital, Nottingham, UK
795. Kingston Hospital, Surrey, UK
796. Lincoln County Hospital, Lincoln, UK
797. Liverpool Heart and Chest Hospital, Liverpool, UK
798. Macclesfield District General Hospital, Macclesfield, UK
799. Medway Maritime Hospital, Gillingham, UK
800. Milton Keynes University Hospital, Milton Keynes, UK
801. Morrision Hospital, Swansea, UK
802. National Hospital for Neurology and Neurosurgery, London, UK
803. Norfolk and Norwich University hospital (NNUH), Norwich, UK
804. North Middlesex University Hospital NHS trust, London, UK
805. north Middlesex University Hospital NHS trust, London, UK
806. Northumbria Healthcare NHS Foundation Trust, North Shields, UK
807. Peterborough City Hospital, Peterborough, UK
808. Prince Charles Hospital, Merthyr Tydfil, UK
809. Royal Sussex County Hospital, Brighton, UK
810. Princess Royal Hospital, Haywards Heath, UK
811. Princess of Wales Hospital, Llantrisant, UK
812. Queen Alexandra Hospital, Portsmouth, UK
813. Queen Elizabeth Hospital, Woolwich, London, UK
814. Queen Elizabeth the Queen Mother Hospital, Margate, UK
815. Queen Victoria Hospital, West Sussex, UK
816. Queens Hospital Burton, Burton-On-Trent, UK
817. Raigmore Hospital, Inverness, UK
818. Rotherham General Hospital, Rotherham, UK
819. Royal Blackburn Teaching Hospital, Blackburn, UK
820. Royal Preston Hospital, Preston, UK
821. Royal Surrey County Hospital, Guildford, UK
822. Royal Albert Edward Infirmary, Wigan, UK
823. The Royal Alexandra Children's Hospital, Brighton, UK
824. Royal Alexandra Hospital, Paisley, UK
825. Royal Bolton Hospital, Bolton, UK
826. University Hospitals Dorset NHS Foundation Trust
827. Royal Brompton Hospital, London, UK
828. Imperial College London, London, UK
829. Royal Cornwall Hospital, Truro, UK
830. Royal Free Hospital, London, UK
831. Royal Glamorgan Hospital, Pontyclun, UK
832. Royal Gwent Hospital, Newport, UK
833. Royal Hallamshire Hospital and Northern General Hospital, Sheffield, UK
834. Royal Hampshire County Hospital, Hampshire, UK
835. Royal Manchester Children's Hospital, Manchester, UK
836. Royal Stoke University Hospital, Staffordshire, UK
837. Salisbury District Hospital, Salisbury, UK
838. Sandwell General Hospital, Birmingham, UK

839. Scarborough General Hospital, Scarborough, UK
840. Scunthorpe General Hospital, Scunthorpe, UK
841. Southmead Hospital, Bristol, UK
842. St George's Hospital, London, UK
843. St Mary's Hospital, Newport, UK
844. Stoke Mandeville Hospital, Buckinghamshire, UK
845. Sunderland Royal Hospital, Sunderland, UK
846. Alexandra Hospital, Redditch and Worcester Royal Hospital, Worcester, UK
847. The Christie NHS Foundation Trust, Manchester, UK
848. The Queen Elizabeth Hospital, King's Lynn, UK
849. The Royal Liverpool University Hospital, Liverpool, UK
850. The Royal Marsden NHS Foundation Trust, London, UK
851. Torbay Hospital, Torquay, UK
852. University Hospital Monklands, Airdrie, UK
853. University Hospital Lewisham, London, UK
854. University Hospital North Durham, Darlington, UK
855. University Hospital of North Tees, Stockton on Tees, UK
856. University Hospital of Wales, Cardiff, UK
857. University Hospital Wishaw, Wishaw, UK
858. Victoria Hospital, Kirkcaldy, UK
859. Warrington General Hospital, Warrington, UK
860. West Cumberland Hospital, Whitehaven, UK
861. Western Sussex Hospitals, West Sussex, UK
862. Whiston Hospital, Prescot, UK
863. York Hospital, York, UK
864. Ysbyty Gwynedd, Bangor, UK
865. Countess of Chester Hospital, Chester, UK
866. Croydon University Hospital, Croydon, UK
867. Diana Princess of Wales Hospital, Grimsby, UK
868. Dorset County Hospital, Dorchester, UK
869. Forth Valley Royal Hospital, Falkirk, UK
870. Furness General Hospital, Barrow-in-Furness, UK
871. Alder Hey Children's Hospital, Liverpool, UK
872. Derriford Hospital, Plymouth, UK
873. Glasgow Royal Infirmary, Glasgow, UK
874. Glenfield Hospital, Leicester, UK
875. Gloucestershire Royal Hospital, Gloucester, UK
876. Golden Jubilee National Hospital, Clydebank, UK
877. Great Ormond St Hospital and UCL Great Ormond St Institute of Child Health NIHR Biomedical Research Centre, London, UK
878. Homerton University Hospital Foundation NHS Trust, London UK
879. James Cook University Hospital, Middlesbrough, UK
880. John Radcliffe Hospital, Oxford, UK
881. Leicester Royal Infirmary, Leicester, UK
882. Lister Hospital, Stevenage, UK
883. New Cross Hospital, Wolverhampton, UK
884. Royal Victoria Infirmary, Newcastle Upon Tyne, UK
885. Ninewells Hospital, Dundee, UK
886. North Devon District Hospital, Barnstaple, UK

887. North Manchester General Hospital, Manchester, UK
888. Northwick Park Hospital, London, UK
889. Prince Philip Hospital, Lianelli, UK
890. Pinderfields General Hospital, Wakefield, UK
891. Poole Hospital, Poole, UK
892. Royal Shrewsbury Hospital, Shrewsbury, UK
893. Princess Royal Hospital , Telford , UK
894. Princess Royal Hospital, Telford, UK
895. Princess Royal Hospital Telford, UK
896. Princess Royal Hospital Shrewsbury and Royal Shrewsbury Hospital, Shrewsbury, UK
897. Princess Royal Hospital , Telford, UK
898. Princess Royal Hospital, Telford, UK
899. Queen Elizabeth Hospital Gateshead, Gateshead, UK
900. Queen Elizabeth University Hospital, Glasgow, UK
901. Royal Berkshire NHS Foundation Trust, Berkshire, UK
902. Royal Derby Hospital, Derby, UK
903. Royal Devon and Exeter Hospital, Exeter, UK
904. Royal Infirmary of Edinburgh, Edinburgh, UK
905. Royal Lancaster Infirmary, Lancaster, UK
906. Royal United Hospital, Bath, UK
907. Russell's Hall Hospital, Dudley, UK
908. Sheffield Children's Hospital, Sheffield, UK
909. Southampton General Hospital, Southampton, UK
910. Southend University Hospital, Westcliff-on-Sea, UK
911. Southport and Formby District General Hospital, Ormskirk, UK
912. St James's University Hospital and Leeds General Infirmary, Leeds, UK
913. Bristol Royal Infirmary, Bristol, UK
914. Stepping Hill Hospital, Stockport, UK
915. The Princess Alexandra Hospital, Harlow, UK
916. University Hospital Crosshouse, Kilmarnock, UK
917. University Hospital Hairmyres, East Kilbride, UK
918. Craigavon Area Hospital
919. Warwick Hospital, Warwick, UK
920. West Middlesex Hospital, Isleworth, UK
921. Western General Hospital, Edinburgh, UK
922. Whittington Hospital, London, UK
923. William Harvey Hospital, Ashford, UK
924. MRC-University of Glasgow Centre for Virus Research, Institute of Infection, Immunity and Inflammation, College of Medical, Veterinary and Life Sciences, University of Glasgow, Glasgow, UK.
925. Centre for Tropical Medicine and Global Health, Nuffield Department of Medicine, University of Oxford, Old Road Campus, Roosevelt Drive, Oxford, OX3 7FZ, UK.
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929. Clinical Research Centre at St Vincent's University Hospital, University College Dublin, Dublin, Ireland.
930. Department of Intensive Care Medicine, Guy's and St. Thomas NHS Foundation Trust, London, UK.
931. Department of Medicine, University of Cambridge, Cambridge, UK.

932. Section of Molecular Virology, Imperial College London, London, UK
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934. Department of Infectious Disease, Imperial College London, London, UK
935. National Infection Service, Public Health England, London, UK
936. MRC-University of Glasgow Centre for Virus Research, 464 Bearsden Road, Glasgow, UK
937. Liverpool School of Tropical Medicine, Liverpool, UK
938. Institute of Infection and Global Health, University of Liverpool, Liverpool, UK
939. Centre for Tropical Medicine and Global Health, Nuffield Department of Medicine, University of Oxford, Old Road Campus, Roosevelt Drive, Oxford, UK
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941. Department of Pharmacology, University of Liverpool, Liverpool, UK
942. Nuffield Department of Medicine, Peter Medawar Building for Pathogen Research, University of Oxford, UK
943. The Roslin Institute, University of Edinburgh, Edinburgh, UK
944. Nottingham University Hospitals NHS Trust, Nottingham, UK
945. Nuffield Department of Medicine, John Radcliffe Hospital, Oxford, UK
946. ISARIC Global Support Centre, Centre for Tropical Medicine and Global Health, Nuffield Department of Medicine, University of Oxford, Oxford, UK
947. Division of Infection and Immunity, University College London, UK
948. Institute of Infection, Veterinary and Ecological Sciences, University of Liverpool, Liverpool, UK
949. Centre for Clinical Infection and Diagnostics Research, Department of Infectious Diseases, School of Immunology and Microbial Sciences, King's College London, London, UK
950. Institute of Evolutionary Biology, University of Edinburgh, Edinburgh, UK
951. Department of Pediatrics and Virology, St Mary's Medical School Bldg, Imperial College London, London, UK
952. The Florey Institute for Host-Pathogen Interactions, Department of Infection, Immunity and Cardiovascular Disease, University of Sheffield, Sheffield, UK
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982. Laboratory of Statistical Immunology, Immunology Frontier Research Center (WPI-IFReC), Osaka University, Suita 565-0871, Japan
983. Integrated Frontier Research for Medical Science Division, Institute for Open and Transdisciplinary Research Initiatives, Osaka University, Suita 565-0871, Japan
984. Division of Health Medical Intelligence, Human Genome Center, the Institute of Medical Science, the University of Tokyo, Tokyo, Japan
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986. Department of Surgery, Keio University School of Medicine, Tokyo, Japan.
987. Department of Organoid Medicine, Keio University School of Medicine, Tokyo, Japan.
988. Department of Infectious Diseases, Keio University School of Medicine, Tokyo, Japan.
989. Department of Respiratory Medicine and Clinical Immunology, Osaka University Graduate School of Medicine, Suita 565-0871, Japan
990. Department of Immunopathology, Immunology Frontier Research Center (WPI-IFReC), Osaka University, Suita 565-0871, Japan
991. Institute of Research, Tokyo Medical and Dental University, Tokyo, Japan
992. Department of Insured Medical Care Management, Tokyo Medical and Dental University Hospital of Medicine, Tokyo, Japan
993. Genome Medical Science Project (Toyama), National Center for Global Health and Medicine, Chiba, Japan
994. Division of Gastroenterology and Hepatology, Department of Medicine, Keio University School of Medicine, Tokyo, Japan.
995. M&D Data Science Center, Tokyo Medical and Dental University, Tokyo, Japan
996. Kyoto University, Department of Pathology and Tumor Biology Institute for the Advanced Study of Human Biology (WPI-ASHBi), Kyoto University, Kyoto, Japan

997. Department of Medicine, Center for Hematology and Regenerative Medicine, Karolinska Institute, Stockholm, Sweden
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1000. Department of Anesthesiology, Keio University School of Medicine, 35 Shinanomachi, Shinjuku-ku, Tokyo, Japan.
1001. Department of Laboratory Medicine, Keio University School of Medicine, Tokyo, Japan
1002. Division of Infection Control and Prevention, Osaka University Hospital, Suita 565-0871, Japan
1003. Department of Biomedical Ethics and Public Policy, Osaka University Graduate School of Medicine, Suita 565-0871, Japan
1004. Center for Genomic Medicine, Kyoto University Graduate School of Medicine, Kyoto 606-8507, Japan
1005. Department of Pulmonary Medicine, Faculty of Medicine, University of Tsukuba, Tsukuba 305-8575, Japan
1006. Department of Neurosurgery, Faculty of Medicine, the University of Tokyo, Tokyo 113-8655, Japan
1007. Laboratory of Immune Regulation, Department of Microbiology and Immunology, Osaka University Graduate School of Medicine, Suita 565-0871, Japan
1008. Department of Respiratory Medicine and Clinical Immunology, Osaka University Graduate School of Medicine, Suita 565-0871, Japan Laboratory of Immune Regulation, Department of Microbiology and Immunology, Osaka University Graduate School of Medicine, Suita 565-0871, Japan
1009. Medical Innovation Promotion Center, Tokyo Medical and Dental University, Tokyo, Japan
1010. Clinical Research Center, Tokyo Medical and Dental University Hospital of Medicine, Tokyo, Japan
1011. Department of Medical Informatics, Tokyo Medical and Dental University Hospital of Medicine, Tokyo, Japan
1012. Respiratory Medicine, Tokyo Medical and Dental University, Tokyo, Japan
1013. Clinical Laboratory, Tokyo Medical and Dental University Hospital of Medicine, Tokyo, Japan
1014. Kyoto University, Department of Pathology and Tumor Biology, Kyoto, Japan
1015. Department of Respiratory Medicine, Juntendo University Faculty of Medicine and Graduate School of Medicine, Tokyo, Japan
1016. Department of Emergency and Disaster Medicine, Juntendo University Faculty of Medicine and Graduate School of Medicine, Tokyo, Japan
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