

1 **Rapid whole genome sequence typing reveals multiple waves of**
2 **SARS-CoV-2 spread**

3

4 Ahmed M. Moustafa¹, Paul J. Planet^{1,2,3*}

5

6 **1. Division of Pediatric Infectious Diseases, Children's Hospital of Philadelphia,**
7 **Philadelphia, PA 19104, USA.**

8

9 **2. Department of Pediatrics, Perelman College of Medicine, University of**
10 **Pennsylvania, Philadelphia, PA 19104, USA.**

11

12 **3. Sackler Institute for Comparative Genomics, American Museum of Natural**
13 **History, New York, NY 10024, USA.**

14

15 **Emails**

16 **AMM: moustafaam@email.chop.edu**

17 **PJP: planetp@email.chop.edu**

18

19 ***Corresponding Author**

20

21 **Abstract**

22 As the pandemic SARS-CoV-2 virus has spread globally its genome has diversified to
23 an extent that distinct clones can now be recognized, tracked, and traced. Identifying
24 clonal groups allows for assessment of geographic spread, transmission events, and
25 identification of new or emerging strains that may be more virulent or more
26 transmissible. Here we present a rapid, whole genome, allele-based method (GNUVID)
27 for assigning sequence types to sequenced isolates of SARS-CoV-2 sequences. This
28 sequence typing scheme can be updated with new genomic information extremely
29 rapidly, making our technique continually adaptable as databases grow. We show that
30 our method is consistent with phylogeny and recovers waves of expansion and
31 replacement of sequence types/clonal complexes in different geographical locations.
32 GNUVID is available as a command line application
33 (<https://github.com/ahmedmagds/GNUVID>).

34

35 **Keywords**

36 *SARS-CoV-2, COVID-19, nomenclature, lineages, WhatsGNU, cgMLST, wgMLST,*
37 *clonal complex*

38

39 **Introduction**

40 Rapid sequencing of the SARS-CoV-2 pandemic virus has presented an
41 unprecedented opportunity to track the evolution of the virus and to understand the
42 emergence of a new pathogen in near-real time. During its explosive radiation and
43 global spread, the virus has accumulated enough genomic diversity that we are now

44 able to identify distinct lineages and track their spread in distinct geographic locations
45 and over time [1-6]. Phylogenetic analyses in combination with rapidly growing
46 databases [1, 7] have been instrumental in identifying distinct clades and tracing how
47 they have spread across the globe, as well as estimating calendar dates for the
48 emergence of certain clades [1-4]. This information is extremely useful in assessing the
49 impact of early measures to combat spread as well as identifying missed opportunities
50 [3]. Going forward whole genome sequences will be useful for identifying emerging
51 clones or hotspots of reemergence.

52 In all of these efforts, identification of specific clones, clades, or lineages, is a
53 critical first step, and there are few systems available to do this [1]. As of June 1st there
54 are already 35,291 and 4,636 complete genomes (>29,000bp) available at GISAID [7]
55 and GenBank [8], respectively. To address the problem of identifying sequence types in
56 SARS-CoV-2 and leverage these huge datasets, we took inspiration from a an
57 approach used widely in bacterial nomenclature, multilocus sequence typing (MLST) [9].
58 Our panallelome approach to developing a whole genome (wgMLST) scheme for
59 SARS-CoV-2 uses a modified version of our recently developed tool, WhatsGNU [10],
60 to rapidly assign an allele number to each gene nucleotide sequence in the virus's
61 genome creating a sequence type (ST). The ST is codified as the sequence of allele
62 numbers for each of the 10 genes in the viral genome.

63 Here we show that this approach allows us to link STs into clearly defined clonal
64 complexes (CC) that are consistent with phylogeny. We show that assessment of STs
65 and CCs agrees with multiple introductions of the virus in certain geographical locations.
66 In addition, we use temporal assessment of STs/CCs to uncover waves of expansion

67 and decline, and the apparent replacement of certain STs with emerging lineages in
68 specific geographical locations.

69

70 **Results and Discussion**

71 We developed the GNU-based Virus IDentification (GNUVID) system as a tool
72 that automatically assigns a number to each unique allele of the 10 open reading
73 frames (ORFs) of SARS-CoV-2 (**Figure 1A**) by modifying our tool WhatsGNU [10]
74 (**Supplementary Methods**). GNUVID compressed the 104,220 ORFs in 10,422 high
75 quality GISAID genomes (**Supplementary Table 1**) to 6244 unique alleles in less than
76 one minute on a standard desktop, achieving 17-fold compression and losing no
77 information. The majority of these alleles (65%) are for ORF1ab which represents 71%
78 of the genome length (**Figure 1A**). Strikingly, the most abundant alleles of each ORF
79 (except ORF1ab) were present in at least 79% of the 10,422 isolates, and for 8 ORFs
80 (ORF3a-10) the allele that was observed in the earliest genomes was also the most
81 prevalent, suggesting strong nucleotide level conservation over time.

82 Some widespread alleles corresponded to mutations that have been
83 hypothesized to be important to the evolution or pathogenesis of the virus. For instance,
84 for the S gene, the gene for the Spike protein, 64% (526/817) of unique alleles have the
85 A23403G (D614G) mutation (**Figure 1B**) that has been associated with the emergence
86 of increased transmission whether through increased transmissibility [11] or lapses in
87 control around this variant [3]. The first allele isolated and sequenced (allele 17) that
88 carries this mutation was first recorded on January 24th in China. The most common S
89 gene allele that carries the A23403G mutation (allele 26) was present in 55% of the

90 isolates. For ORF3a, which was shown to activate the NLRP3 inflammasome [12], 35%
91 (126/357) of alleles have the G25563T (Q57H) mutation representing 33% of the
92 isolates. The earliest sequenced, and most common, ORF3a allele that carries this
93 mutation (allele 25) was isolated in France on February 21st in a virus that also carries
94 also the A23403G mutation in the spike gene.

95 To create an ST for each isolate GNUVID automatically assigned 5510 unique
96 ST numbers based on their allelic profile (**Supplementary Table 2**). We then used a
97 minimum spanning tree (MST) to group STs into larger taxonomic units, clonal
98 complexes (CCs), which we define here as clusters of >20 STs that are single or double
99 allele variants away from a “founder”. Using the goeBURST algorithm [13, 14] to build
100 the MST and identify founders, we found 24 CCs representing 79% (4352/5510) of all
101 unique STs (**Figure 1B**).

102 When the global region of origin for each genome sequence was mapped to
103 each CC there was a strong association of some CCs with certain geographical
104 locations. For instance, genomes from CCs 255, 300, 301, 317, 348, 355, 369, 399,
105 454, 498, 985, 1063, 1148 are predominantly from Europe while genomes from CCs 26,
106 800 and 927 are mainly from Asia (**Figure 1B**). Interestingly, genomes originating from
107 the US appear to be associated with 2 very divergent CCs, potentially reflecting two
108 major introductions. The first, CC256, is associated with locations on the West Coast,
109 specifically Washington state. The first two isolates belonging to CC256 are from China
110 followed by the first isolate from Washington (01/19/2020). The second predominant US
111 CC, CC258, is closely related to other CCs found predominantly in Europe (**Figure 1B**
112 **and 1C**). Isolates of CC258 were initially found and sequenced in Europe, followed by

113 the US East Coast, and later in other US locations (**Figure 1B**). Interestingly, almost all
114 isolates (99%) from CC258 and its descendants CCs 768, 800, 844 and 1063 (**Figure**
115 **1B**) carry the G25563T mutation in ORF3a, representing 88% of all isolates that carry
116 this mutation; the other 12% are from STs that were not assigned CCs. CC800 is
117 interesting for its geographic predominance in the Middle East (75% from Saudi Arabia
118 and Turkey) and its close relationship to ST338 and ST258, which are mostly found in
119 the US. This may signal a transmission event from the US to the Middle East.

120 To show that CCs are mostly consistent with whole genome phylogenetic trees
121 we produced a maximum likelihood tree and mapped the CC designations onto the tree.
122 Figure 1C shows that members of the same CC usually grouped together in clades
123 (**Supplementary File 4**). One limitation of any ST/CC classification strategy is that
124 paraphyletic groups can occur as a new ST arises from an older ST (e.g. CC301
125 emerged from CC255 making CC255 paraphyletic). While this means not all ST/CC
126 groups will be monophyletic, this property of the nomenclature may be helpful in
127 gauging emergence and replacement of an ancestral form.

128 To further validate our wgMLST classification system we compared it to the
129 recently proposed “dynamic lineages nomenclature” for SARS-CoV-2 using the pangolin
130 application[1]. A high percentage of viruses (90.5%;40-100%) with the same CC were
131 assigned to the same lineage. When sublineages of the dominant lineage designation
132 were included, this average rose to 99% (89-100%), showing strong agreement
133 between these classification schemes (**Supplementary Table 2**).

134 Because we included collection dates for each genomic sequence, we can use
135 STs and CCs to better understand the emergence and replacement of certain lineages

136 in certain geographical regions over time. **Figure 2A** shows temporal plots of the most
137 common 12 CCs around the world. This makes clear the emergence of new CCs over
138 time such as CC255, CC300 and CC258. CC4, the earliest CC, started by representing
139 60% of sequenced genomes in mid-January, but had dropped to only 5% by mid-March.

140 Of course, relative proportions of STs or CCs isolated and sequenced may be a
141 highly biased statistic that is contingent upon where the isolate comes from, the
142 decision to sequence its genome, and the local capacity to sequence a whole genome.
143 Certain regions (US and Europe) clearly sequenced more genomes later in the
144 pandemic compared to other countries.

145 Focusing on specific geographic regions may help to partially ameliorate this
146 bias, and we chose to focus on three different regions (China, Europe and the US). The
147 temporal plot of China shows expansion of local clones (CC4 and CC256) that likely
148 spread to other countries early in the pandemic and then decreased in China over time.
149 In contrast, two new CCs 927 and 454 appear to have emerged more recently with
150 earliest isolation dates of March 18th and April 16th, respectively, though this should be
151 interpreted with caution because few sequences (n=7 and 6) were available/included.
152 Interestingly, CC258 was first isolated in China in mid-March while it already
153 represented 14% of the genomes in Europe by the end of February (**Figure 2B and D**),
154 potentially reflecting transmission of new lineages back to China later in the pandemic.
155 By the end of January, although CC4 represented 39% of the sequenced genomes in
156 China, only one isolate (1/6) of CC4 was isolated in Wuhan, showing different patterns
157 of circulating clones at the same timepoint in different parts of the same country (**Figure**
158 **2B and C**).

159 Interestingly, Europe showed a general CC diversity over time resembling that of
160 the worldwide temporal plot, and then showed expansion of the local CC300 and
161 CC255 after mid-February (**Figure 2D**).

162 The US plot (**Figure 2E**) reflects the two possible introductions on the west and
163 east coasts from Asia and Europe, respectively, with the current dominance (more than
164 45%) of CC258. Focusing on Washington, it is interesting to note the possible
165 replacement of CC256 by CC258 perhaps by introduction from the East Coast or
166 Europe (**Figure 2F**) [2, 4]. In New York, a different pattern is seen with CC258 being
167 persistently dominant (**Figure 2G**). However, a more granular view of STs in New York,
168 not CCs, shows a shifting epidemiology with ST258 declining and the rise of closely
169 related SLVs and DLVs of ST258 (**Figure 2H**).

170 While our wgMLST approach is rapid and robust it has several limitations.
171 Because a change in any allele creates a new ST our method may accumulate and
172 count “unnecessary” STs that have been seen only once or may be due to a
173 sequencing error. This is partially ameliorated by the use of the CC definition that allows
174 some variability amongst the members of a group. A large number of STs also may
175 allow more granular approaches to tracking new lineages. Our method is also limited by
176 the quality and extent of the database. For this implementation we limited the database
177 to genomes that do not have any ambiguity or degenerate bases. However, these
178 genomes could be queried through our tool to be assigned to the closest ST/CC.
179 Another limitation is the stability of the classification system, some virus genomes may
180 be reassigned to new CCs as clones expand epidemiologically, but this may also reflect
181 a dynamic strength as circulating viruses emerge and replace older lineages.

182

183 **Conclusion**

184 The genomic epidemiology of the 10,422 SARS-CoV-2 isolates studied here
185 show six predominant CCs circulated/circulating globally. Our tool (GNUVID) allows for
186 fast sequence typing and clustering of whole genome sequences in a rapidly changing
187 pandemic. As illustrated above, this can be used to temporally track emerging clones or
188 identify the likely origin of viruses. With stored metadata for each sequence on date of
189 isolation, geography, and clinical presentation, new genomes could be matched almost
190 instantaneously to their likely origins and potentially related clinical outcomes.

191

192 **Methods**

193 All SARS-CoV-2 genomes (n=17,504) that are complete and high coverage were
194 downloaded from GISAID [7] on May 17th 2020. We kept 16,866 that were at least
195 29,000 bp in length and had less than 1% "N"s. Our wgMLST scheme was composed of
196 all 10 ORFs in the SARS-CoV-2 genome [15]. The 10 ORFs were identified in the
197 remaining 16,866 genomes using blastn [16] and any genome that had any ambiguity or
198 degenerate bases (any base other than A,T,G and C) in the 10 open reading frames
199 (ORF) was excluded. The remaining 10,422 genomes were fed to the GNUVID tool in a
200 time order queue (first-collected to last-collected), which assigned a ST profile to each
201 genome. The identified STs by GNUVID were fed into the PHYLOViZ tool [17] to identify
202 CCs at the double locus variant (DLV) level using the goeBURST MST [13, 14]. CCs
203 were mapped back to the STs using a custom script. Pie charts were plotted using a

204 custom script. Temporal plots were extracted using a custom script and plotted in
205 GraphPad Prism v7.0a.
206
207 To show the relationship between our typing scheme and phylogeny, we constructed a
208 maximum likelihood tree. Briefly, we masked the 5' and 3' untranslated regions in the
209 10,422 genomes. We aligned these sequences using MAFFT's FFT-NS-2 algorithm
210 (options: --add --keeplength) [18] to the reference MN908947.3 [15]. A maximum
211 likelihood tree using IQ-TREE 2 [19] was estimated using the HKY model of nucleotide
212 substitution [20], default heuristic search options, and ultrafast bootstrapping with 1000
213 replicates [21]. The tree was rooted to MN908947.3. The tree and ST/CC data were
214 visualized in iTOL [22]. We assigned a lineage [1] to each member of the 24 CCs using
215 pangolin (<https://github.com/hCoV-2019/pangolin>) (options: -t 8). The GNUVID
216 database will be updated weekly with new added high-quality genomes from GISAID
217 [7]. Detailed methods are in **Additional file 1**.
218

219 **List of abbreviations**

220 WhatsGNU What is Gene Novelty Unit
221 GNUVID Gene Novelty Unit-based Virus Identification
222 ST Sequence Type
223 CC Clonal Complex
224 SARS-CoV-2 Severe Acute Respiratory Syndrome Corona Virus 2
225 COVID-19 Corona Virus Disease 2019
226 MLST Multilocus Sequence Typing

227 cgMLST core genome MLST

228 wgMLST whole genome MLST

229

230 **Figure Legends**

231 **Figure 1.** Sequence Typing Scheme for SARS-CoV-2. **A.** Map of SARS-CoV-2 virus
232 genome showing the length in base pairs (bp) of the 10 ORFs, numbers of alleles in the
233 current database, and the prevalence of the top two alleles of each ORF in the 10,422
234 database isolates. **B.** Minimum spanning tree from goeBURST of the 5510 Sequence
235 Types (STs) showing the 24 Clonal Complexes (CCs) identified in the dataset. The
236 largest six CCs are red and the other 18 CCs are in black. The pie charts show the
237 percentage distribution of genomes from the different geographic regions in each CC.
238 The letter A and G next to the pie charts represent the Spike ORF nucleotide at position
239 23403 in MN908947.3. The ancestral nucleotide is A and the mutation is G resulting in
240 D614G amino acid change. At least 98% of the genomes of each CC had the reported
241 nucleotide (except for CC26 where it was 93%). **C.** Maximum likelihood phylogeny of
242 the 10,422 global high-quality SARS-CoV-2 sequences downloaded from the GISAID
243 database (<http://gisaid.org>) on May 17th 2020 (**Supplementary Table 1**). The tree is
244 rooted on the reference sequence MN908947.3. The tree was visualized in iTOL. Only
245 the most common seven CCs were shown for easier visualization. Nodes with 200-500
246 leaves were collapsed for better visualization. The raw tree is available as
247 **Supplementary File 4.**

248

249 **Figure 2.** Temporal Plots of circulating STs/CCs at different geographical locations
250 (Global, China, Wuhan, Europe, USA, Washington, NY (CC) and NY (ST)). The
251 visualizations were limited to the most common CCs/STs. The raw data can be obtained
252 from the authors upon request.

253

254 **Additional files**

255 **Additional file 1: Supplementary Methods** (txt, 34 Kb).

256 **Additional file 2: Table S1. Acknowledgment Table** (xls, 2.1 Mb).

257 **Additional file 3: Table S2. GNUVID Database Strains Report Table** (xlsx, 778 Kb).

258 **Additional file 4: Maximum Likelihood Tree of the 10422 strains** (nex, 369 Kb).

259

260 **Availability of data and material**

261 The compressed genomes from our quality controlled dataset are available from the
262 corresponding author and available online for download. The compressed database will
263 be updated weekly on <https://github.com/ahmedmagds/GNUVID>. Source code for
264 GNUVID can be found in its most up-to-date version here,
265 <https://github.com/ahmedmagds/GNUVID>, under the GNU General Public License.

266

267 **Competing interests**

268 The authors declare that they have no competing interests

269

270 **Funding**

271 PJP and AMM are supported by NIH 1R01AI137526-01, PLANET19G0,

272 1R21AI144561-01A1. PJP is further supported by R01NR015639,

273

274 **Authors' contributions**

275 Conceptualization: AMM, PJP; Coding: AMM; Writing – Reviewing and Editing: AMM,

276 PJP.

277

278 **Acknowledgements**

279 We would like to thank Lidiya Denu and Michael Silverman for helpful comments and

280 discussion. We would like to thank the Global Initiative on Sharing All Influenza Data

281 (GISAID) and thousands of contributing laboratories for making the genomes publicly

282 available. A full acknowledgements table is available as supplemental information.

283

284 **References**

285 1. Rambaut A, Holmes EC, Hill V, O'Toole Á, McCrone JT, Ruis C, du Plessis L, Pybus OG: **A**
286 **dynamic nomenclature proposal for SARS-CoV-2 to assist genomic epidemiology.**
287 *bioRxiv* 2020:2020.2004.2017.046086.

288 2. Deng X, Gu W, Federman S, Du Plessis L, Pybus O, Faria N, Wang C, Yu G, Pan C-Y,
289 Guevara H, et al: **A Genomic Survey of SARS-CoV-2 Reveals Multiple Introductions into**
290 **Northern California without a Predominant Lineage.** *medRxiv*
291 2020:2020.2003.2027.20044925.

292 3. Worobey M, Pekar J, Larsen BB, Nelson MI, Hill V, Joy JB, Rambaut A, Suchard MA,
293 Wertheim JO, Lemey P: **The emergence of SARS-CoV-2 in Europe and the US.** *bioRxiv*
294 2020:2020.2005.2021.109322.

295 4. Bedford T, Greninger AL, Roychoudhury P, Starita LM, Famulare M, Huang M-L, Nalla A,
296 Pepper G, Reinhardt A, Xie H, et al: **Cryptic transmission of SARS-CoV-2 in Washington**
297 **State.** *medRxiv* 2020:2020.2004.2002.20051417.

298 5. Shen L, Dien Bard J, Biegel JA, Judkins AR, Gai X: **Comprehensive genome analysis of**
299 **6,000 USA SARS-CoV-2 isolates reveals haplotype signatures and localized**
300 **transmission patterns by state and by country.** *medRxiv*
301 2020:2020.2005.2023.20110452.

302 6. Chen Z-w, Li Z, Li H, Ren H, Hu P: **Global genetic diversity patterns and transmissions of**
303 **SARS-CoV-2.** *medRxiv* 2020:2020.2005.2005.20091413.

304 7. Shu Y, McCauley J: **GISAID: Global initiative on sharing all influenza data - from vision**
305 **to reality.** *Euro Surveill* 2017, **22**.

306 8. Sayers EW, Cavanaugh M, Clark K, Ostell J, Pruitt KD, Karsch-Mizrachi I: **GenBank.**
307 *Nucleic Acids Res* 2019, **47**:D94-D99.

308 9. Maiden MC, Bygraves JA, Feil E, Morelli G, Russell JE, Urwin R, Zhang Q, Zhou J, Zurth K,
309 Caugant DA, et al: **Multilocus sequence typing: A portable approach to the**
310 **identification of clones within populations of pathogenic microorganisms.** *PNAS* 1998,
311 **95**:3140-3145.

312 10. Moustafa AM, Planet PJ: **WhatsGNU: a tool for identifying proteomic novelty.** *Genome*
313 *Biology* 2020, **21**:58.

314 11. Korber B, Fischer WM, Gnanakaran S, Yoon H, Theiler J, Abfalterer W, Foley B, Giorgi EE,
315 Bhattacharya T, Parker MD, et al: **Spike mutation pipeline reveals the emergence of a**
316 **more transmissible form of SARS-CoV-2.** *bioRxiv* 2020:2020.2004.2029.069054.

317 12. Siu K-L, Yuen K-S, Castaño-Rodriguez C, Ye Z-W, Yeung M-L, Fung S-Y, Yuan S, Chan C-P,
318 Yuen K-Y, Enjuanes L, Jin D-Y: **Severe acute respiratory syndrome coronavirus ORF3a**
319 **protein activates the NLRP3 inflammasome by promoting TRAF3-dependent**
320 **ubiquitination of ASC.** *The FASEB Journal* 2019, **33**:8865-8877.

321 13. Francisco AP, Bugalho M, Ramirez M, Carriço JA: **Global optimal eBURST analysis of**
322 **multilocus typing data using a graphic matroid approach.** *BMC Bioinformatics* 2009,
323 **10**:152.

324 14. Feil EJ, Li BC, Aanensen DM, Hanage WP, Spratt BG: **eBURST: Inferring Patterns of**
325 **Evolutionary Descent among Clusters of Related Bacterial Genotypes from Multilocus**
326 **Sequence Typing Data.** *Journal of Bacteriology* 2004, **186**:1518.

327 15. Wu F, Zhao S, Yu B, Chen YM, Wang W, Song ZG, Hu Y, Tao ZW, Tian JH, Pei YY, et al: **A**
328 **new coronavirus associated with human respiratory disease in China.** *Nature* 2020,
329 **579**:265-269.

330 16. Altschul SF, Gish W, Miller W, Myers EW, Lipman DJ: **Basic local alignment search tool.**
331 *Journal of Molecular Biology* 1990, **215**:403-410.

332 17. Nascimento M, Sousa A, Ramirez M, Francisco AP, Carrico JA, Vaz C: **PHYLOViZ 2.0:**
333 **providing scalable data integration and visualization for multiple phylogenetic**
334 **inference methods.** *Bioinformatics* 2017, **33**:128-129.

335 18. Katoh K, Misawa K, Kuma K, Miyata T: **MAFFT: a novel method for rapid multiple**
336 **sequence alignment based on fast Fourier transform.** *Nucleic Acids Res* 2002, **30**:3059-
337 3066.

338 19. Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, von Haeseler A,
339 Lanfear R: **IQ-TREE 2: New Models and Efficient Methods for Phylogenetic Inference in**
340 **the Genomic Era.** *Mol Biol Evol* 2020, **37**:1530-1534.

341 20. Hasegawa M, Kishino H, Yano T: **Dating of the human-ape splitting by a molecular clock**
342 **of mitochondrial DNA.** *J Mol Evol* 1985, **22**:160-174.

343 21. Hoang DT, Chernomor O, von Haeseler A, Minh BQ, Vinh LS: **UFBoot2: Improving the**
344 **Ultrafast Bootstrap Approximation.** *Mol Biol Evol* 2018, **35**:518-522.

345 22. Letunic I, Bork P: **Interactive Tree Of Life (iTOL) v4: recent updates and new**
346 **developments.** *Nucleic Acids Res* 2019, **47**:W256-W259.
347

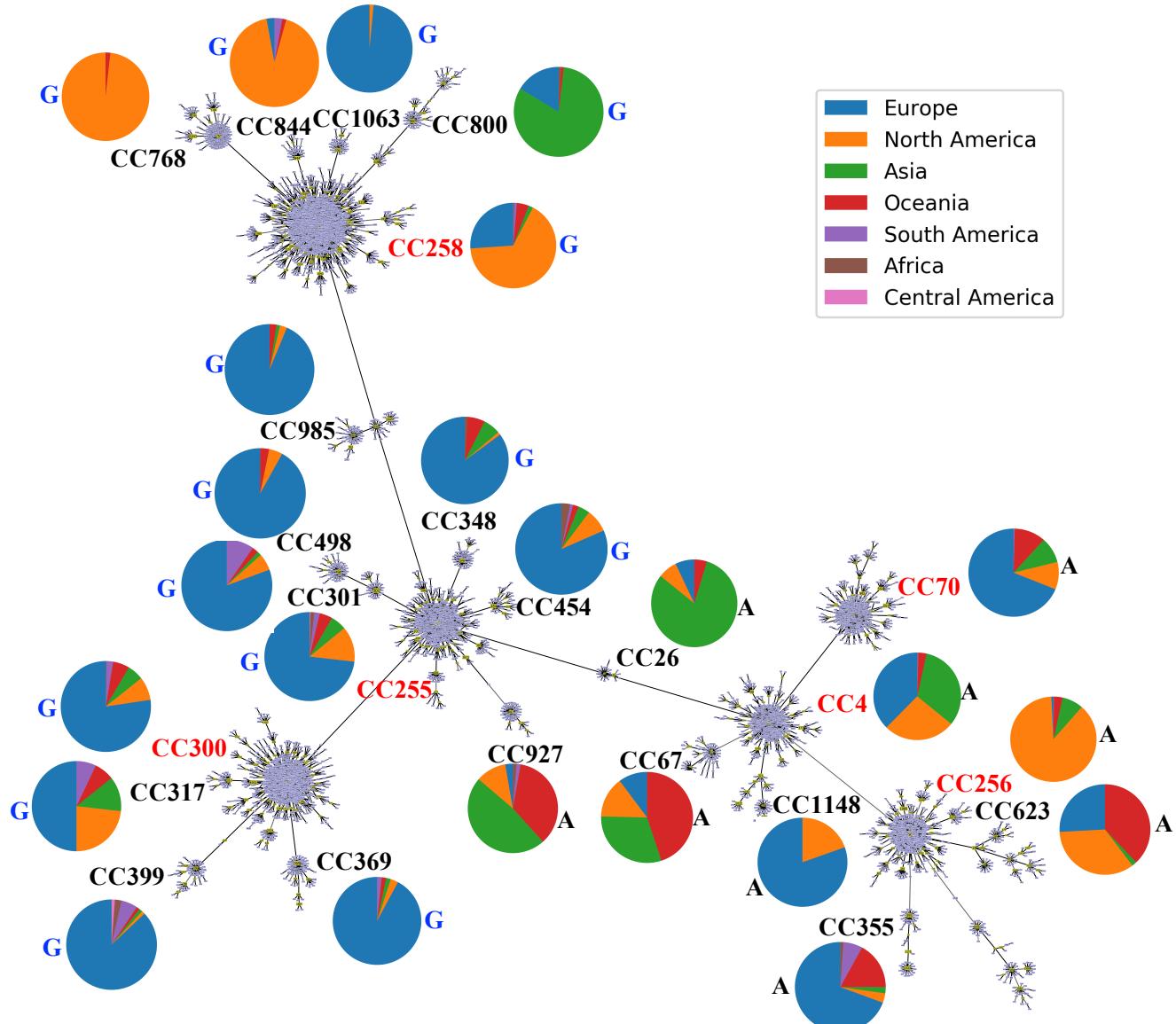
Figure 1 Sequence Typing Scheme for SARS-CoV-2

A

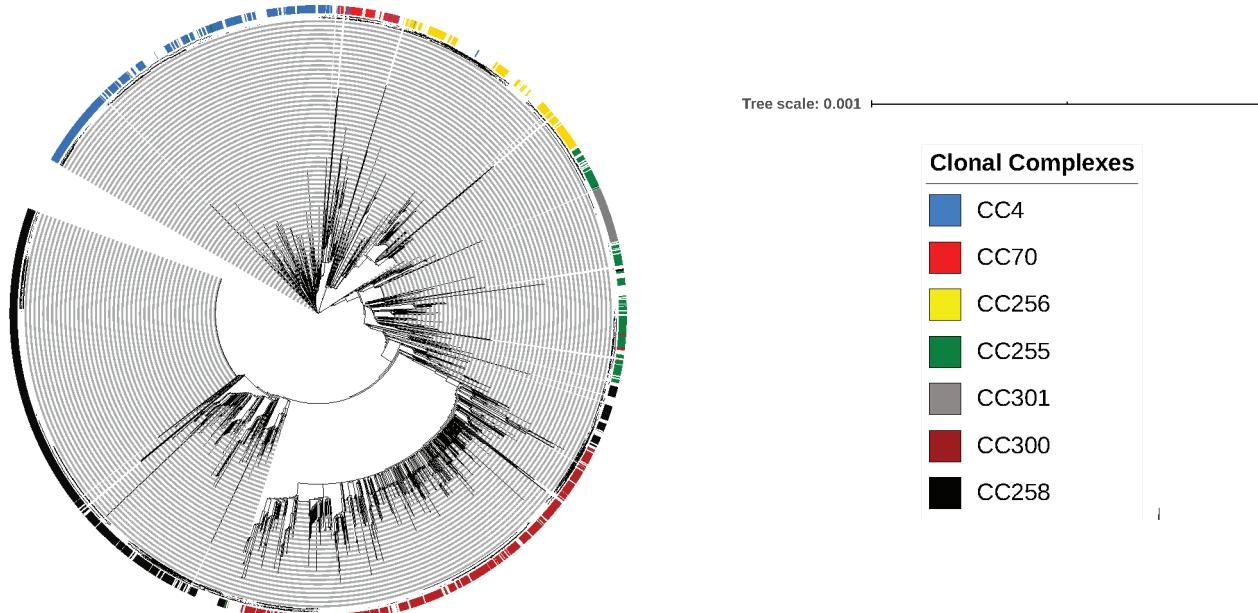
bioRxiv preprint doi: <https://doi.org/10.1101/2020.06.08.139055>; this version posted June 9, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

	1	2	3	4	5	6	7	8	9	10
Length (bp)	21290	3822	828	228	669	186	366	366	1260	117
Number of Alleles	4050	817	357	50	139	50	116	127	495	43
Top Two Alleles Prevalence (%)	19.5	79	83.6	98.9	92.6	98.7	97.6	93.7	82.1	98.9

B



C



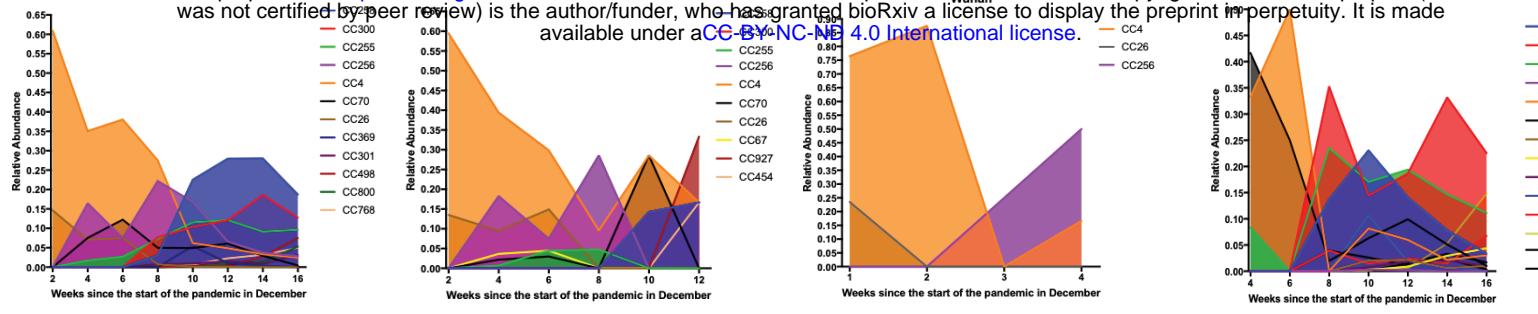
A

B

C

D

bioRxiv preprint doi: <https://doi.org/10.1101/2020.06.08.139055>; this version posted June 9, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.



E

F

G

H

