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Occurrence of a substitution or deletion of SARS-CoV-2 spike amino acid 677 in various lineages in Marseille, France

Short title (for the running head): SARS-CoV-2 spike Q677 substitution or deletion

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Supplementary Table: 1

ABSTRACT

Great concerns have been raised about SARS-CoV-2 variants over the past six months. At the end of 2020, an increasing incidence of spike substitutions Q677H/P was described in the United States, which involved six independent lineages. We searched for changes to this amino acid in the sequence database of SARS-CoV-2 genomes obtained at the IHU Méditerranée Infection (Marseille, France) from 3,634 patients sampled between February 2020 and April 2021. In seven genomes (0.2%), we found a deletion of five amino acids at spike positions 675-679 (QTQTN) including Q677, and in 76 genomes (2.3%) we found a Q677H substitution. The 83 genomes were classified in ten different Pangolin lineages. Genomes with a spike Q677 deletion were obtained from respiratory samples collected in six cases between 28 March 2020 and 12 October 2020 and in one case on 1 February 2021. The Q677H substitution was found in genomes all obtained from respiratory samples collected from 19 January 2021 and were classified in seven different lineages. Most of these genomes (41 cases) were UK variants. Two others were classified in the Marseille-4 lineage which was first detected in July 2020 in our institute but was devoid of this substitution until 19 January 2021. Also, eight genomes were classified in the Marseille-501 lineage which was first detected in our institute in January 2021 and which either harboured or did not harbour the Q677H substitution. Thus, the spike Q677H substitution should be considered as another example of convergent evolution, as is is the case of spike substitutions L18F, E484K, L452R, and N501Y which also independently appeared in various lineages.

TEXT

INTRODUCTION

One year after SARS-CoV-2 was declared a pandemic by the WHO, some of its variants with various combinations of amino acid substitutions or deletions in the spike protein have taken centre stage [1]. This protein leads to virus entry into human respir-atory cells [2,3]. It is also the major target of neutralising antibodies which are elicited post-infection or vaccine immunisation, and is the target of most vaccine strategies im-plemented to date [4]. As a result of our surveillance of genomic epidemiology, our in-stitute has observed and described the emergence of a dozen SARS-CoV-2 variants since summer 2020, after the rate of diagnoses fell to almost zero for several weeks between May and June 2020. These included the Marseille-1, Marseille-4, and Marseille-501 variants [5-8]. The variants recently considered to be of greatest concern are those carrying amino acid substitutions N501Y and/or E484K within the spike protein [9,10], as they have increased affinity for the ACE2 cellular receptor, decreased sensitivity to neutralising antibodies, and may escape the immune responses elicited by the vaccines currently used in Western countries [2,3,11]. Nevertheless, various other SARS-CoV-2 variants have been reported as emerging worldwide.

At the end of 2020, the incidence of variants carrying the Q677H, or Q677P substitu-tions in the spike increased, mainly in the United States, where the first sequence origi-nated from Louisiana [12]. Interestingly, these strains were reported as belonging to six independent sub-lineages, including one, two and three in Nextstrain clades 20A, 20B and 20G, respectively. Amino acid 677 of the SARS-CoV-2 spike protein is only three codons upstream of the polybasic/furin cleavage site of S1/S2 spike domains, which is critical for SARS-CoV-2 pathogenesis, as this cleavage induces a spike conformational change that favors the binding

to the Angiotensin-Converting Enzyme 2 (ACE2) cellular SARS-CoV-2 receptor and may enhance viral infection [12-16]. It has been indeed hypothesised that histidine protonation in Q677H could induce a conformational switch that may affect the accessibility to protease of this site, which may enhance the cleavage at the S1/S2 junction and viral entry efficiency [15,16].

RESULTS AND DISCUSSION

We looked in our SARS-CoV-2 genome sequence database that which we have been contributing to since February 2020, in order to analyse the prevalence and genotypic pattern of strains mutated at codon 677 of the spike. A codon change or deletion was detected in 83 (2.4%) of 3,364 SARS-CoV-2 genomes obtained from respiratory samples collected from different patients between February 2020 and April 2021. These 83 genomes were classified in various SARS-CoV-2 lineages, including the locally-defined variants Marseille-1 [6], Marseille-4 [7], Marseille-9 [5], Marseille-501 [8], and Marseille-484K.v3 in three, eight and 21 cases, respectively (Figure 1; Supplementary Table S1). Overall, these 83 sequences belong to Nextstrain clades 19B, 20A, 20B, 20C, and 20I in nine, 26, four, three and 41 cases, respectively (as determined with the Nextclade online tool at URL: https://clades.nextstrain.org/) and were concurrently classified in ten different Pangolin lineages, namely A, A.27, B.1, B.1.1, B.1.1.10, B.1.1.241, B.1.1.7, B.1.160, B.1.416, B.1.525 in three, six, four, three, three, one, 39, three, one, and 21 cases, respectively (as determined using the Pangolin online tool at URL: https://cov-lineages.org/pangolin.html [19]).

In seven of the 3,634 patients (0.2%), a deletion of five amino acids was observed at spike protein positions 675-679 (QTQTN) which includes amino acid 677 (Supplementary Table S1). These sequences were obtained from respiratory samples collected in six cases between 28 March 2020 and 12 October 2020 and in one case on 1 February 2021. They

involved three, one and three viral strains classified in Nextstrain clades 20A, 20B and 20C, respectively. Pangolin lineages were B.1 (n=4 cases), B.1.416 (1), B.1.1.241 (1), and B.1.160 (1). The genome obtained in 2021 was a Marseille-4 variant [7], corresponding to Nextstrain clade 20A.EU2 and Pangolin lineage B.1.160. This deletion of spike amino acids 675-679 (QTQTN) was reported to decrease viral entry and infection in Vero E6 cells [20]. It was also reported to be present at a greater frequency from culture supernatant, in 12 (50%) out of 24 in vitro-isolated viruses, than from respiratory samples, in three (6%) of 68 cases [21].

In 76 patients (2.3%), a spike Q677H substitution was observed in the 3,634 SARS-CoV-2 genomes obtained in our institute. These changes involved viral genomes that were all obtained from respiratory samples collected from 19 January 2021, and were classified as belonging to eight different lineages (Supplementary Table S1). A majority of these genomes were UK variants (Nextclade 20I/N501Y.v1; Pangolin lineage B.1.1.7), in 41 cases (54% of the 76 genomes and 7.2% of all UK variant genomes in our database of 3,364 SARS-CoV-2 genomes). In addition, two were classified in the Marseille-4 lineage which was first detected in our institute in July 2020 [7] and accounted for 573 (17%) genomes in our database, although its members did not harbour this spike Q677H substitution before 19 January 2021. Eight genomes were also classified in the Marseille-501 lineage which was first detected in our institute in January 2021, accounted for 18 genomes in our database and which may or may not harbour Q677H substitution [8]. Overall, these 76 SARS-CoV-2 genomes were classified in five different Nextstrain clades and seven different Pangolin lineages. Codon changes from CAG to CAT or CAC leading to this Q677H substitution deoptimise the viral codon usage relative to that of the human genome. Indeed, in the human genome, CAG, CAT, and CAC usage frequencies are 34.2, 10.9, and 15.1, respectively (https://www.kazusa.or.jp/codon/cgi-bin/showcodon.cgi?species=9606), which represent 3.1-fold and 2.3-fold decreases. Worldwide, 13,659 SARS-CoV-2 genomes were found to encode

this amino acid substitution Q677H according to the Cov-Glue online tool (http://cov-glue.cvr.gla.ac.uk/) [22] (Figure 2). They were classified in 229 different Pangolin lineages, the majority (77%) being classified in lineages B.1.2 (n= 5,537), B.1.1.7 (1,434), B.1.525 (952), B.1.170 (818), B.1.234 (714), B.1.1.316 (560), and B.1.1.284 (512). These genomes were obtained from clinical samples collected in 84 countries, mostly in the USA (89%; n= 7,801), England (1,866), Japan (610), Denmark (497), Canada (379), Switzerland (314), Germany (309), India (194), and Egypt (122).

Therefore, the spike Q677H substitution should be considered as another example of convergent evolution, in addition to spike amino acid substitutions N501Y [23], L452R [24], and L18F [25] which also independently appeared in various lineages. Q677H is notably part of the substitutions that emerged in strains of the UK variant (20I/501Y.V1) [26] and the South African variant (20H/501Y.V2) [27]. Such convergent evolution is deemed to be the result of positive selection, and suggests that these amino acid susbti-tutions confer an evolutionary advantage to the virus [23]. Combined with previous findings, this highlights the great genetic variability of SARS-CoV-2 and warrants broader genomic surveillance of SARS-CoV-2 in order to gain a better insight of the epidemiology and evolution of this virus at the global, national and local scales.

Author Contributions: Conceptualization, D.R. and P.C.; methodology, P.C., and A.L.; investiga-tion, P.C., J.D., E.B., M.B., P.E.F., A.L., and J.C.L.; writing, P.C. and D.R.. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: Data are available from the GISAID database (https://www.gisaid.org/), from the "Our world in data" website (https://ourworldindata.org/), or from the corresponding author upon reasonable request.

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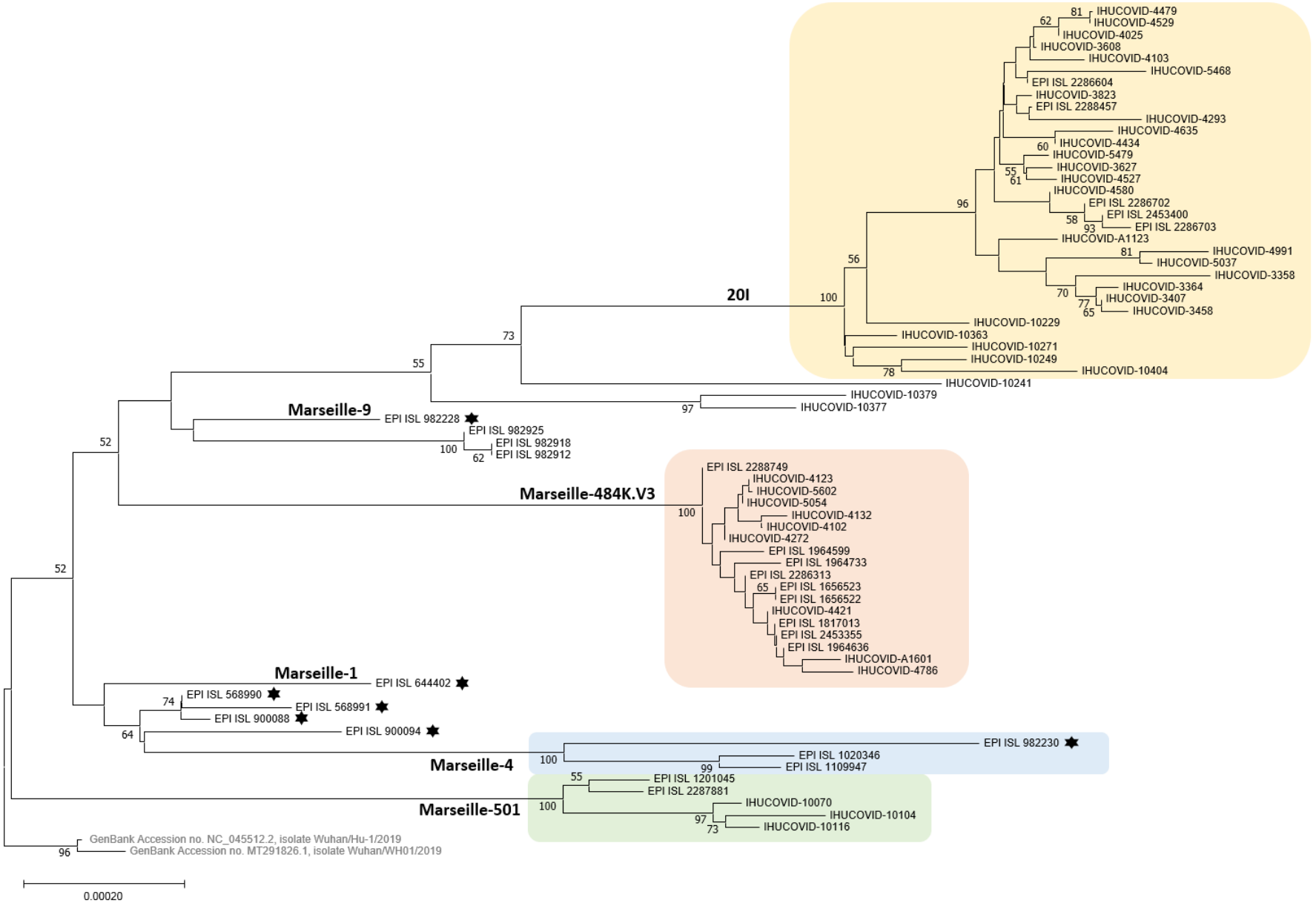
FIGURE LEGENDS

Figure 1. Phylogenetic tree of SARS-CoV-2 genomes harbouring a deletion or substitution from Q to H of spike amino acid 677 and obtained from patients diagnosed with SARS-CoV-2 in our institute.

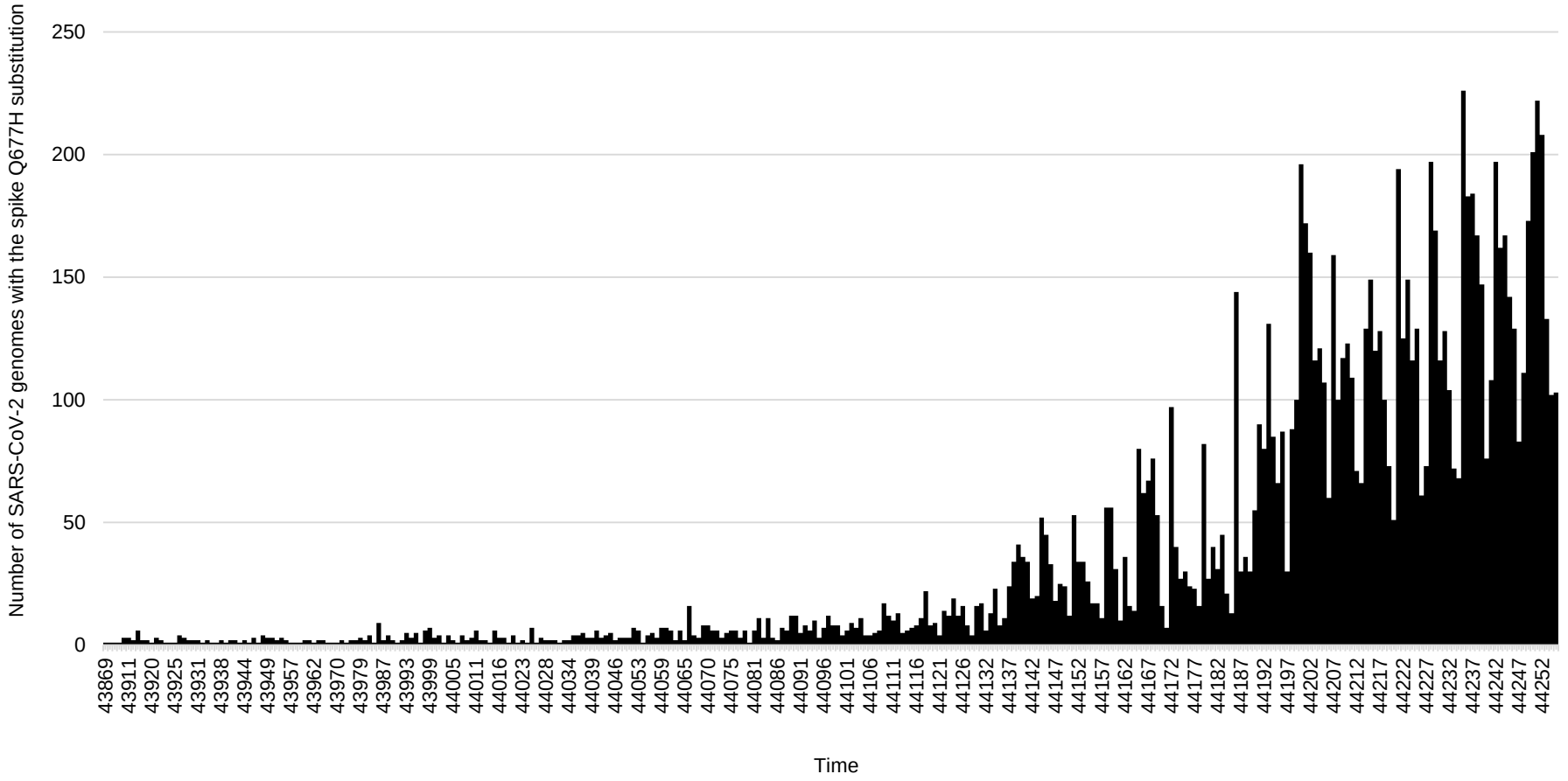
Phylogenetic trees were reconstructed based on 69 of the SARS-CoV-2 genomes described here and visualized using the MEGA-X software v.10.0.5 (https://www.megasoftware.net/) [17] after alignment of genomes using MAFFT v.7 [18]. The evolutionary history was inferred using the Neighbor-Joining method and the evolutionary distances were computed using the Kimura 2-parameter method. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) are shown next to the branches. SARS-CoV-2 genomes harbouring a Q677 deletion are indicated by a black star.


20I
IHUCOVID-4479
IHUCOVID-4529
IHUCOVID-4025
IHUCOVID-3608
IHUCOVID-4103
IHUCOVID-5468
EPI ISL 2286604
IHUCOVID-3823
EPI ISL 2288457
IHUCOVID-4293
IHUCOVID-4635
IHUCOVID-4434
IHUCOVID-5479
IHUCOVID-3627
IHUCOVID-4527
IHUCOVID-4580
EPI ISL 2286702
EPI ISL 2453400
EPI ISL 2286703
IHUCOVID-A1123
IHUCOVID-4991
IHUCOVID-5037
IHUCOVID-3358
IHUCOVID-3364
IHUCOVID-3407
IHUCOVID-3458
IHUCOVID-10229
IHUCOVID-10363
IHUCOVID-10271
IHUCOVID-10249
IHUCOVID-10404
IHUCOVID-10241
IHUCOVID-10379
IHUCOVID-10377
Marseille-9
EPI ISL 982228
EPI ISL 982925
EPI ISL 982918
EPI ISL 982912
Marseille-484K.V3
EPI ISL 2288749
IHUCOVID-4123
IHUCOVID-5602
IHUCOVID-5054
IHUCOVID-4132
IHUCOVID-4102
IHUCOVID-4272
EPI ISL 1964599
EPI ISL 1964733
EPI ISL 2286313
EPI ISL 1656523
EPI ISL 1656522
IHUCOVID-4421
EPI ISL 1817013
EPI ISL 2453355
EPI ISL 1964636
IHUCOVID-A1601
IHUCOVID-4786
Marseille-1
EPI ISL 644402
EPI ISL 568990
EPI ISL 568991
EPI ISL 900088
EPI ISL 900094
Marseille-4
EPI ISL 982230
EPI ISL 1020346
EPI ISL 1109947
Marseille-501
EPI ISL 1201045
EPI ISL 2287881
IHUCOVID-10070
IHUCOVID-10104
IHUCOVID-10116
GenBank Accession no. NC_045512.2, isolate Wuhan/Hu-1/2019
GenBank Accession no. MT291826.1, isolate Wuhan/WH01/2019
0.00020

259

Figure 2. Numbers of SARS-CoV-2 genomes harbouring the spike Q677H mutation worldwide according to timeline.

Data were collected from the Cov-Glue online tool (http://cov-glue.cvr.gla.ac.uk/) (Singer et al., 2020).



SUPPLEMENTARY FIGURES

Supplementary Figure S1. Description of genome sequences obtained at IHU Méditerranée Infection and harbouring a change at codon 677 of the spike-encoding gene.

Supplementary Table S1. Description of genome sequences obtained at IHU Méditerranée Infection and harbouring a change at codon 677 of the spike

Sequence laboratory identifier	GISAID accession no.	Sampling date	Age	Gender	Nextstrain clade	Pangolin lineage	Marseille variants	Spike Q677 substitution or deletion
IHUCOVID-0914	EPI_ISL_568990	28/03/2020	Unk.	Unk.	20C	B.1	-	Q677-
IHUCOVID-0920	EPI_ISL_900094	03/04/2020	Unk.	Unk.	20A	B.1	-	Q677-
IHUCOVID-0921	EPI_ISL_568991	03/04/2020	Unk.	Unk.	20C	B.1	-	Q677-
IHUCOVID-0924	EPI_ISL_900088	03/04/2020	Unk.	Unk.	20C	B.1	-	Q677-
IHUCOVID-1208	EPI_ISL_644402	17/08/2020	24	F	20A	B.1.416	Marseille-1	Q677-
IHUCOVID-2456	EPI_ISL_982228	12/10/2020	63	F	20B	B.1.1.241	Marseille-9	Q677-
IHUCOVID-3132	EPI_ISL_982925	19/01/2021	41	M	20B	B.1.1.10	-	Q677H
IHUCOVID-3116	EPI_ISL_982918	01/02/2021	37	M	20B	B.1.1.10	-	Q677H
IHUCOVID-3126	EPI_ISL_982230	01/02/2021	46	M	20A.EU2	B.1.160	Marseille-4	Q677-
IHUCOVID-3175	EPI_ISL_982912	02/02/2021	25	F	20B	B.1.1.10	-	Q677H
IHUCOVID-3205	EPI_ISL_1020346	06/02/2021	22	F	20A.EU2	B.1.160	Marseille-4	Q677H
IHUCOVID-3312	EPI_ISL_1109947	12/02/2021	50	F	20A.EU2	B.1.160	Marseille-4	Q677H
IHUCOVID-3358	-	17/02/2021	54	M	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-3364	-	17/02/2021	44	F	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-3377	EPI_ISL_1201045	18/02/2021	19	M	19B	A.27	Marseille-501	Q677H
IHUCOVID-3407	-	19/02/2021	15	M	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-3458	-	24/02/2021	61	F	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-3471	EPI_ISL_2288782	25/02/2021	22	F	19B	A.27	Marseille-501	Q677H
IHUCOVID-A1673	EPI_ISL_2287881	04/03/2021	47	M	19B	A.27	Marseille-501	Q677H
IHUCOVID-A1527	EPI_ISL_2288457	12/03/2021	40	F	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-3608	-	16/03/2021	52	M	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-3627	-	17/03/2021	76	F	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-3823	-	24/03/2021	10	F	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-10127	-	25/03/2021	16	M	19B	A	Marseille-501	Q677H
IHUCOVID-10116	-	25/03/2021	20	M	19B	A	Marseille-501	Q677H
IHUCOVID-10104	-	25/03/2021	51	F	19B	A	-	Q677H
IHUCOVID-10070	-	25/03/2021	43	F	19B	A.27	Marseille-501	Q677H
IHUCOVID-10059	-	25/03/2021	39	M	19B	A.27	Marseille-501	Q677H
IHUCOVID-4580	-	25/03/2021	67	F	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-10083	-	29/03/2021	48	F	19B	A.27	Marseille-501	Q677H
IHUCOVID-A1123	-	29/03/2021	52	M	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-4025	-	30/03/2021	23	M	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-10229	-	30/03/2021	24	M	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-4024	-	30/03/2021	33	M	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-A1601	-	30/03/2021	29	F	20A	B.1.525	Marseille-484K.v3	Q677H
IHUCOVID-10241	-	31/03/2021	62	M	20I/501Y.V1	B.1.1	-	Q677H
IHUCOVID-10379	-	01/04/2021	34	M	20I/501Y.V1	B.1.1	-	Q677H
IHUCOVID-10377	-	01/04/2021	36	M	20I/501Y.V1	B.1.1	-	Q677H
IHUCOVID-10271	-	01/04/2021	45	F	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-10249	-	01/04/2021	76	F	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-10363	-	01/04/2021	74	M	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-4256	-	02/04/2021	36	F	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-10404	-	02/04/2021	56	M	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-4272	-	03/04/2021	70	M	20A	B.1.525	Marseille-484K.v3	Q677H
IHUCOVID-4293	-	05/04/2021	70	F	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-4434	-	06/04/2021	31	F	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-4421	-	06/04/2021	38	M	20A	B.1.525	Marseille-484K.v3	Q677H
IHUCOVID-A1053	EPI_ISL_1656523	07/04/2021	28	M	20A	B.1.525	Marseille-484K.v3	Q677H
IHUCOVID-A375	EPI_ISL_1656522	07/04/2021	30	M	20A	B.1.525	Marseille-484K.v3	Q677H
IHUCOVID-A1656	EPI_ISL_2453355	08/04/2021	27	F	20A	B.1.525	Marseille-484K.v3	Q677H
IHUCOVID-A911	EPI_ISL_2453378	09/04/2021	59	F	20A	B.1.525	Marseille-484K.v3	Q677H
IHUCOVID-A1249	EPI_ISL_2453400	11/04/2021	48	M	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-4479	-	12/04/2021	30	F	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-4529	-	12/04/2021	56	F	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-4527	-	12/04/2021	57	M	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-A496	EPI_ISL_1817013	12/04/2021	69	M	20A	B.1.525	Marseille-484K.v3	Q677H
IHUCOVID-A151	EPI_ISL_1964733	13/04/2021	52	M	20A	B.1.525	Marseille-484K.v3	Q677H
IHUCOVID-4103	-	14/04/2021	52	F	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-4132	-	14/04/2021	55	F	20A	B.1.525	Marseille-484K.v3	Q677H
IHUCOVID-4102	-	14/04/2021	53	M	20A	B.1.525	Marseille-484K.v3	Q677H
IHUCOVID-4123	-	14/04/2021	73	M	20A	B.1.525	Marseille-484K.v3	Q677H
IHUCOVID-4635	-	15/04/2021	Unk.	M	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-4991	-	15/04/2021	48	F	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-5033	-	16/04/2021	52	F	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-5037	-	16/04/2021	63	F	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-A330	EPI_ISL_2286702	16/04/2021	73	M	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-5054	-	16/04/2021	17	M	20A	B.1.525	Marseille-484K.v3	Q677H
IHUCOVID-5602	-	17/04/2021	56	M	20A	B.1.525	Marseille-484K.v3	Q677H
IHUCOVID-5479	-	20/04/2021	35	F	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-4746	-	20/04/2021	19	M	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-5468	-	20/04/2021	41	M	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-A723	EPI_ISL_2288749	20/04/2021	47	F	20A	B.1.525	Marseille-484K.v3	Q677H
IHUCOVID-A1290	EPI_ISL_2286313	20/04/2021	48	M	20A	B.1.525	Marseille-484K.v3	Q677H
IHUCOVID-A733	EPI_ISL_2286704	21/04/2021	28	F	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-A1413	EPI_ISL_2286268	21/04/2021	62	F	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-A942	EPI_ISL_2286703	21/04/2021	32	M	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-A1752	EPI_ISL_2286239	21/04/2021	40	M	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-A1540	EPI_ISL_2286604	21/04/2021	46	M	20I/501Y.V1	B.1.1.7	-	Q677H
IHUCOVID-A142	EPI_ISL_1964636	21/04/2021	9	F	20A	B.1.525	Marseille-484K.v3	Q677H
IHUCOVID-A1404	EPI_ISL_1964600	21/04/2021	63	F	20A	B.1.525	Marseille-484K.v3	Q677H
IHUCOVID-4786	-	21/04/2021	18	M	20A	B.1.525	Marseille-484K.v3	Q677H
IHUCOVID-4771	-	21/04/2021	32	M	20A	B.1.525	Marseille-484K.v3	Q677H
IHUCOVID-A1403	EPI_ISL_1964599	21/04/2021	68	M	20A	B.1.525	Marseille-484K.v3	Q677H