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Genetic diversity and epidemic histories of rice yellow mottle virus in Ghana

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Abstract

Rice yellow mottle virus (RYMV) has persisted as a major biotic constraint to rice production in Africa. However, no data on RYMV epidemics were available in Ghana, although it is an intensive rice-producing country. Surveys were performed from 2010 to 2020 in eleven rice-growing regions of Ghana. Symptom observations and serological detections confirmed that RYMV is circulating in most of these regions. Coat protein gene and complete genome sequencings revealed that RYMV in Ghana almost exclusively belongs to the strain S2, one of the strains covering the largest area in West Africa. We also detected the presence of the S1ca strain which is being reported for the first time outside its area of origin. These results suggested a complex

30 epidemiological history of RYMV in Ghana and a recent expansion of S1ca to West Africa.
31 Phylogeographic analyses reconstructed at least five independent RYMV introductions in Ghana
32 for the last 40 years, probably due to rice cultivation intensification in West Africa leading to a
33 better circulation of RYMV. In addition to identifying some routes of RYMV dispersion in Ghana,
34 this study contributes to the epidemiological surveillance of RYMV and helps to design disease
35 management strategies, especially through breeding for rice disease resistance.

36

37 **Keywords:** *Solemoviridae*; Phylogeography; Spatio-temporal dynamics; Epidemiological
38 surveillance

39

40 **1. Introduction**

41 Rice yellow mottle virus (RYMV) was first identified in East Africa in 1966 (Bakker, 1974) and
42 subsequently in 1975 in West Africa (Fauquet and Thouvenel, 1977). Since then, this virus has
43 progressively been reported in almost all rice-producing countries of sub-Saharan Africa and
44 Madagascar (Abo et al., 1997; Pinel-Galzi et al., 2015). Endemic to Africa, rice yellow mottle virus
45 (RYMV) has become one of the most important biotic constraints to rice production in Africa
46 (Kouassi et al., 2005; Savary et al., 2019; Séré et al., 2013), where it causes high yield losses in
47 most rice-growing agroecosystems (Agnoun et al., 2019; Suvi et al., 2018).

48 RYMV belongs to the *Sobemovirus* genus of the *Solemoviridae* family. It has icosahedral particles
49 and a single-stranded positive-sense RNA genome (Hébrard et al., 2020). The RYMV has a narrow
50 host range limited predominantly to rice species and a few wild *Poacea* (Allarangaye et al., 2007;
51 Bakker, 1974; Traoré et al., 2009). In infected rice plants, RYMV infection shows symptoms that
52 include mottling and yellowing of the leaves, stunting, reduced tillering, partial panicle exertion,
53 sterility and, in severe cases, death of the plant (Attere, 1983; Bakker, 1974). RYMV is mainly
54 transmitted at short-distance by chrysomelid beetles and by contact between plants during
55 cultural practices (Traoré et al., 2009). No evidence of seed transmission has been found so far
56 in rice species (Allarangaye et al., 2006; Bakker, 1974; Fauquet and Thouvenel, 1977; Konate et
57 al., 2001)

58 Based on RYMV genetic data collected from 24 African countries since the 1970's, the genetic
59 diversity of this virus has been well described (Pinel-Galzi et al., 2015), and its evolutionary history
60 and its global dispersion across Africa and Madagascar has started to be deciphered (Issaka et al.,
61 2021; Rakotomalala et al., 2019; Trovão et al., 2015). All these genetic data revealed a spatially
62 structured genetic diversity, with strains specifically identified in West and East Africa (Fargette
63 et al., 2004; Pinel-Galzi et al., 2015). This structure of the genetic diversity results from an
64 independent dynamic of dispersion of RYMV between these two regions (Trovão et al., 2015). Six
65 strains have been specifically identified in West Africa: S1ca, S1wa, S2, S3, Sa and Sg (Hébrard et
66 al., 2020).

67 Three major resistance genes (named *rymv1*, *rymv2* and *RYMV3*) were identified in rice, mainly
68 in African rice species, *Oryza glaberrima* (Orjuela et al., 2013; Pidon et al., 2020; Pidon et al.,
69 2017; Thiémélé et al., 2010). Note that these resistant genes have not been used for the
70 development of commercial rice varieties, *i.e.* the deployment of resistant varieties in fields has
71 not yet widely been performed. Almost all rice varieties cultivated in Africa currently is of the
72 Asian species, *O. sativa*, which is highly susceptible to RYMV infection.

73 It has been shown in controlled conditions that RYMV is able to adapt and to overcome the
74 resistance. The molecular mechanism underlying the resistance-breaking (RB) process has been
75 identified. It involved the emergence of specific point mutations on different regions of the RYMV
76 genome (Bonnamy et al., 2022; Pinel-Galzi et al., 2016, 2007; Poulicard et al., 2014; Traore et al.,
77 2010). Interestingly, the RYMV strains present contrasted RB abilities depending on the
78 resistance gene. Based on these experimental results and considering the spatial distribution of
79 RYMV strains in Africa, resistance-breaking risk maps were established (Hébrard et al., 2018).
80 However, the validity and the sustainability of these risk maps are strictly dependent on the
81 dispersion of the strains in field conditions and on the evolution of the local RYMV genetic
82 diversity.

83 With more than 323,900 hectares dedicated to rice cultivation, Ghana is an important rice
84 producer country in Africa (FAOSTAT 2021;
85 <https://data.un.org/Data.aspx?d=FAO&f=itemCode%3A27>). Distributed across 6 ecological
86 zones and 16 regions (Fig. 1A), there are mainly three agroecosystems for rice production in

87 Ghana, namely irrigated, rained lowland and upland rice areas. During the last decades, the
88 acreage of cultivated rice is rapidly increasing and rice cultivation intensified to cope with the
89 rising demand due to demographic and societal changes. Such agricultural changes surely make
90 rice cultivation more exposed and vulnerable to pathogen epidemics. However, very little is
91 known about the distribution and the genetic diversity of rice pathogens in Ghana, especially
92 RYMV. Actually, only one coat protein (CP) sequence has been reported so far from a single
93 isolate collected in Ghana in 1995 (Pinel et al., 2000). This CP sequence indicates that the S2 strain
94 is present in Ghana but, as Ghana is surrounded by countries where high RYMV genetic diversity
95 have been reported (with the presence of S1wa, S1ca, and S2 strains in Ivory Coast, Burkina Faso
96 and Togo (Pinel-Galzi et al., 2015), the genetic diversity of RYMV in Ghana could be much higher.

97
98 Thus, the aim of this study was to assess the geographical distribution of RYMV in the most
99 important rice cultivation regions of in Ghana and analyze the genetic diversity using the CP and
100 complete genome sequencing. In addition, this genetic information will allow us to reconstruct
101 the spatio-temporal dynamics of the RYMV in Ghana and to identify the ways of introduction and
102 dispersion of the virus within Ghana and between neighboring countries. Our results will greatly
103 contribute to the epidemiological surveillance of rice in Ghana and will facilitate the development
104 of efficient and sustainable control strategies based on the deployment in fields of resistant
105 varieties against RYMV adapted to this viral diversity to minimize the risk of emergence of RB
106 variants.

107 108 **2. Methods**

109 *2.1 Field survey and sampling*

110 Surveys to collect symptomatic RYMV leaf samples were conducted in 2010, 2012 and 2020
111 during the major rice cropping season (July-September) to cover a total of 11 rice growing regions
112 spread across different agroecological zones of Ghana, notably Ashanti, Ahafo, Bono, Bono East,
113 Central, Eastern, Greater Accra, Northern, Upper East, Western and Volta regions (Fig. 1A). All
114 the samples were collected from rainfed lowland fields. The GPS coordinates were noted for leaf
115 samples collected in each location, and the rice variety plus the age of the plants were recorded

116 during the 2020 survey (Table S1). The symptomatic leaves sampled from each plant were cut
117 using a pair of scissors and stored in a notebook used as herbarium. The scissors were disinfected
118 by dipping in 70% ethanol before sampling from the subsequent plants. The sample locations
119 were reported on a map based on MapChart website (<https://mapchart.net/>).

120

121 *2.2 Serological detection and genome sequencing*

122 The DAS-ELISA tests were performed with polyclonal antibodies targeting the RYMV coat protein
123 (CP) on the leaf samples as described previously (N'Guessan et al., 2001) to confirm the infection
124 status of symptomatic leaves. To obtain the coat protein (CP) gene (ORF4; 720 nt) or the complete
125 genome (ca. 4,45kb) sequences, total RNA from infected leaves were first extracted using
126 GeneJET Plant RNA Purification Kit (ThermoFisher SCIENTIFIC, MA, USA). Then, the CP genes
127 and/or the complete genomes were specifically amplified by RT-PCR as previously described
128 (Pinel et al., 2000). The RT-PCR products were sequenced using the Sanger technique (Genewiz,
129 NJ, USA) and the sequences were deposited in GenBank (Accession Nos. from OQ200610 to
130 OQ200655 for CP, from OQ225940 to OQ225946 for complete genomes; Table S2).

131

132 *2.3 Genetic diversity and phylogenetic analyses*

133 The partial and complete genome sequences obtained from Ghana were compared to those
134 already deposited in NCBI (July 2021; cf. (Issaka et al., 2021), i.e. 261 CP gene sequences and 37
135 complete genome sequences from isolates collected in nearly all-rice growing countries from
136 West Africa. Multiple sequence alignments were performed using MUSCLE (Edgar, 2004)
137 implemented in SEAVIEW v4.7 (Gouy et al., 2010). A search for potential recombination signals
138 in the RYMV sequences was performed with the pairwise homoplasy test (PHI test) using
139 SplitsTree v4.14.6 (Huson and Bryant, 2006) and the seven algorithms implemented in RDP v4.97
140 (Martin et al., 2015). Recombination events detected by at least 4 methods and with *P*-values
141 below 10^{-5} were considered.

142 We reconstructed Maximum-likelihood (ML) phylogenetic trees with SEAVIEW using the best-
143 fitted nucleotide substitution models (Tamura 3-parameter+G+I and GTR+G+I for the CP and the
144 complete genome datasets, respectively) determined with MEGA6 (Tamura et al., 2013) and 100

145 bootstrap replications. Phylogenetic trees were drawn using FigTree v1.3.1
146 (<http://tree.bio.ed.ac.uk/software/figtree/>). The genetic diversity of the ORF4 dataset was
147 estimated using the best-fitted nucleotide substitution model, with standard errors of each
148 measure based on 1000 replicate bootstraps, as implemented in MEGA6.

149

150 *2.4 Tests of temporal signal*

151 In order to examine the degree of temporal signal in the CP dataset, we first used an exploratory
152 linear regression approach (Duchêne et al., 2015; Murray et al., 2016). Based on ML phylogenetic
153 tree reconstructed with the CP dataset, the temporal signal of this sequence dataset was
154 visualized and tested in PhyloStemS (Doizy et al., 2020) to regress phylogenetic root-to-tip
155 distances against sampling date using the root that minimized the residual mean squares.

156 Then, the significance of the temporal signal was evaluated by a date-randomization test. Thus,
157 the mean rate and its 95% highest probability density (HPD) estimated with the observed
158 sampled dates using the Bayesian Evolutionary Analysis Sampling Trees BEAST v1.10.4 package
159 (Suchard et al., 2018), see below) were compared with a null distribution obtained by randomly
160 permutating the tip dates 10 times (Firth et al., 2010). As previously described (Duchêne et al.,
161 2015; Murray et al., 2016), the criterion for a significant temporal signal was that the 95% HPD
162 for the rate estimate obtained with the observed sampled dates should not overlap with the 95%
163 HPD for the estimate obtained with randomized sampling times.

164

165 *2.5 Bayesian evolutionary inferences*

166 We reconstructed time-calibrated epidemic histories of the RYMV in West Africa based on the
167 CP dataset using a Bayesian statistical framework implemented in BEAST version 1.10.4 software
168 (Suchard et al., 2018) and the BEAGLE library (Ayres et al., 2012) to improve computational
169 performance. BEAST program uses Markov chain Monte Carlo (MCMC) integration to average
170 over all plausible evolutionary histories for the data, as reflected by the posterior probability. The
171 nucleotide substitution process was reconstructed using HKY85+G substitution model, the
172 lognormal relaxed clock model and an initial substitution rate of 10^{-3} substitutions/site/year as
173 previously determined for RYMV (Dellicour et al., 2018; Issaka et al., 2021; Trovão et al., 2015).

174 To study the geographic dispersion of RYMV in continuous time and space, we used a Bayesian
175 SkyGrid coalescence model (Gill et al., 2013) and a relaxed random walk model for the continuous
176 location traits (latitude and longitude of each isolate) with a Cauchy probability distribution
177 (according to the best model identified in (Trovão et al., 2015). Bayesian inference using
178 continuous diffusion models yield a posterior distribution of phylogenetic trees, each having
179 ancestral nodes annotated with location estimates.

180 The MCMC analyses were run for 5 billion generations, sampled every 100,000th and discarding
181 10% as the chain burn-in until adequate effective sample sizes were obtained (ESS>200 for all
182 statistics). The parameter estimates were inspected using Tracer 1.7.2
183 (<http://tree.bio.ed.ac.uk/software/tracer>). A maximum clade credibility (MCC) tree was
184 summarized from the posterior tree distribution using TreeAnnotator v1.10.4 (BEAST v1.10.4
185 package) and visualized with FigTree v1.3.1. The dates and the 95% HPD intervals of RYMV
186 movements (introduction or release of RYMV to/from Ghana) were estimated as the interval
187 between the nodes from the same clade with different geographical locations as identified in the
188 MCC tree.

189 The visualization of the continuous phylogeographic reconstruction of the dispersal history of
190 RYMV into West Africa and Ghana were performed with R functions available in the package
191 “SERAPHIM” (Dellicour et al., 2016).

192

193 **3. Results**

194 *3.1 Field samplings and geographic distribution of RYMV in Ghana*

195 A total of 63 samples showing symptoms that could be attributed to a viral infection, were
196 collected in 11 regions (Table S1). Serological detection by DAS-ELISA confirmed that 49 of these
197 samples were positive to RYMV. These positive samples were collected in 9 regions (Ahafo,
198 Ashanti, Bono East, Central, Eastern, Greater Accra, Northern, Volta, Western, Fig. 1B, Table S1).
199 In addition, RYMV infection was reported in 9 rice varieties, both improved (AGRA, Bouake189,
200 CRI-AGRA, Jasmine85, Legon1, Togo Marshall) and local varieties (Aifaifa, Anyifila and Samasa)
201 (Table S1). During that survey, RYMV was not reported in only two regions (Bono and Upper East),

202 although these regions are characterized by rice varieties and ecological zones similar to those
203 where RYMV has been observed (Fig. 1A-B; Table S1).

204

205 *3.2 Genetic diversity of RYMV in Ghana*

206 All positive samples collected in 2010, 2012 and 2020 were used to analyze the genetic diversity
207 of RYMV in Ghana. The coat protein gene was successfully amplified by RT-PCR and sequenced
208 for 46 RYMV isolates (Table S2). These sequences were compared to the 261 CP gene sequences
209 previously published (Issaka et al., 2021) coming from isolates collected in 15 West-African
210 countries between 1975 and 2018, including one CP sequence from an isolate collected in 1995
211 in Ghana. This dataset is thereafter referred to as the WA307 dataset. Based on this CP dataset,
212 phylogenetic analysis showed that almost all RYMV isolates sampled in Ghana clustered within
213 the S2 strain (Fig. S1, Fig. 1C), a strain which was previously reported in Ghana in 1995 (Gh1
214 isolate) and detected in several countries surrounding Ghana (Ivory Coast, Guinea, Mali, Burkina
215 Faso and Benin). The genetic diversity of S2 RYMV isolates from Ghana is similar to that observed
216 for the S2 isolates from Ivory Coast and Guinea, and significantly higher than those from Mali or
217 Benin (Table 1). In addition to the S2 strain, we identified that two isolates (out of 5) from the
218 Northern region and one isolate (out of 5) from the Eastern region belong to the S1ca strain (Fig.
219 1C, isolates 2020Gh113, 2020Gh139 and 2020Gh140 in Fig. S1 and Table S1). The genetic diversity
220 of S1ca RYMV isolates from Ghana is similar to that observed in most of West-African countries
221 (Table 1). The PHI test did not find statistically significant evidence for recombination within the
222 WA307 dataset ($p = 0.93$).

223 Based on this CP phylogenetic tree, seven isolates representing the genetic diversity of RYMV in
224 Ghana were selected to be fully-sequenced (S2 strain: 2010Gh47, 2010Gh55, 2020Gh106,
225 2020Gh109 and 2020Gh112; S1ca strain: 2020Gh113 and 2020Gh140) and then compared to the
226 37 complete genome sequences from West Africa. This dataset is thereafter referred to as the
227 WA44 dataset. The reconstruction of the phylogenetic tree by maximum likelihood confirmed
228 that these isolates from Ghana clustered within the S2 and S1ca strains and demonstrated that
229 these isolates are not directly genetically related between each other (Fig. 2). No statistically

230 significant evidence for recombination was detected in the RYMV genomes from Ghana (data not
231 shown).

232 Altogether, these results showed that the genetic diversity of the S2 and S1ca isolates from
233 Ghana is representative of those circulating in West Africa, which suggests that several
234 introductions of RYMV to Ghana occurred and account for the genetic diversity in this country.

235

236 *3.3 Epidemic histories of RYMV in Ghana*

237 To reconstruct the evolutionary history of RYMV in West Africa and to gain information on the
238 epidemic histories and trajectories of this virus in Ghana, we first examined the strength of the
239 temporal signal of the WA307 sequence dataset. The linear regression exploration of root-to-tip
240 distances as a function of sampling time suggested a weak but consistent temporal signal (Fig.
241 S2), with a low correlation coefficient (adjusted $R^2 < 0.1$; $p < 10^{-6}$). The presence of temporal signal
242 was then confirmed consistently using BEAST and date-permutation tests (tip-date and clustered
243 tip randomizations). Actually, the estimates of the permutations did not overlap those of the real
244 (non-permuted) WA307 dataset (Fig. S3). As no signal for recombination event was detected
245 on the WA307 dataset, we reconstructed the evolutionary and the dispersal histories of the
246 RYMV in West Africa by Bayesian inferences. The generated maximum clade credibility (MCC)
247 tree strengthened the topology of the phylogenetic tree previously obtained by maximum
248 likelihood (Fig. 3A). In addition, this MCC tree and the projection of this MCC tree on sequential-
249 dated maps (Fig. 3B-E; Fig. S4) highlighted that several independent introductions occurred in
250 Ghana.

251 By extracting information from the MCC tree and by mapping the tip locations of the MCC tree
252 in geographic space, we identified at least three independent introductions of isolates belonging
253 to S2 strain (branches labelled 1 to 3 in Fig. 3A) to southern part of Ghana. Interestingly, all the
254 S2 clusters identified in Ghana are directly genetically related to isolates from Ivory Coast (Fig.
255 3A), suggesting that S2 strain introductions to Ghana resulted from RYMV movements from the
256 Ivory Coast. The date intervals between the nodes of branches 1 to 3 provide estimates of the
257 timing of these introductions. Thus, a first S2 introduction occurred during the early 1990's
258 (interval between the node 1 and the date of collection of the 1995Gh1 isolate, *i.e.* 1987.8-1995.6

259 with 95%HPD [1983.3-1995.6]; Fig. 3A-C; Table2). Then, a second S2 introduction occurred during
260 the early 2000's (branch 2, interval between the nodes 2a and 2b, *i.e.* 1999.2-2003.5 [1993.1-
261 2007.3]; Fig. 3A-C; Table2). Finally, a more recent S2 introduction occurred after the 2000's
262 (branch 3, interval between node 3 and the date of collection of the 2020Gh133 isolate, *i.e.*
263 1999.8-2020.6 [1995.0-2020.6]; Fig. 3A-E; Table2). Although S2 isolates circulated in the South
264 since the early 1990's, it is interesting to note that these isolates dispersed to the Northern Ghana
265 only from the 2010's (branch 6, interval between nodes 6a and 6b, *i.e.* 2009.9-2013.8 [2007.3-
266 2016.8]; Fig. 3A-E; Table2). We also identified one S2 dispersion from Ghana to Benin that
267 occurred between 2008 and 2010 (branch 7, interval between nodes 7a and 7b, *i.e.* 2008.8-
268 2009.6 [2007.1-2010.5]; Fig. 3A-D; Table2).

269 In parallel with the dispersion of the S2 strain, the phylogeographic reconstruction showed two
270 independent introductions of RYMV isolates belonging to the S1ca strain in Ghana (branches
271 labelled 4 and 5 in Fig. 3A). Because there are few isolates of S1ca strain in Ghana, the range of
272 dating estimates are more extended than for those of S2, but the phylogeographic
273 reconstructions suggested that these RYMV movements occurred after the 1990's. A first S1ca
274 introduction to Ghana was identified as the 2020Gh113 isolate (branch 4, interval between the
275 node 4 and the date of collection of the 2020Gh113 isolate, *i.e.* 1986.9-2020.6 [1970.7-2020.6];
276 Fig. 3A-E; Table2). This isolate clustered with isolates from Nigeria and Niger, suggesting an RYMV
277 way of transmission from these countries (or other intermediate ones as Benin or Togo) to the
278 South-eastern part of Ghana. In addition, an independent S1ca introduction occurred in the
279 Northern regions of Ghana at the same period (1992.89-2015.02 [1979.46-2019.32]; Fig. 3A-D,
280 Table2), probably from isolates genetically related to the ones reported in South-East of Burkina
281 Faso.

282

283 **4. Discussion**

284 The observation of rice plants with RYMV characteristic symptoms and the confirmation of the
285 infectious status of these plants by DAS-ELISA and coat protein (gene or complete genome
286 sequencing demonstrated that the virus has been widely distributed in Ghana since 1995, the
287 date of collection of the first RYMV isolate in this country. Actually, RYMV has been detected in

288 nine regions covering five ecological zones as Guinea savannah (Northern region), forest
289 savannah transition (Bono East), semi-deciduous rainforest (Ahafo, Ashanti, Central and Eastern
290 regions), high rainforest (Western region) and coastal savannah (Greater Accra and Volta regions)
291 (Fig. 1A-B). In addition, RYMV was detected in all improved and local rice varieties surveyed
292 during this study (Table S1), suggesting that the resistance to RYMV is not yet a “usual selection”
293 criteria for the industrial rice producers or the small farm holders.

294 Field surveys between 1995 and 2012 only collected isolates from S2 strain in Ghana. The survey
295 in 2020 covered a wider geographical scale and larger agro-environmental conditions (from 2 to
296 11 regions) and confirmed that RYMV isolates circulating in this country belong mainly to the S2
297 strain (Fig. 2, Fig. S1). Surprisingly, the genetic diversity detected with the CP gene sequences of
298 the S2 isolates in Ghana is high, which is similar to that reported for the whole S2 strain dataset
299 (96 isolates) from Ivory Coast, Guinea, Mali, Benin and Burkina Faso (Table1). This observation
300 suggests that the RYMV isolates collected in Ghana are representative of the genetic diversity of
301 the S2 strain in West Africa, which reflect the complex epidemiological history of RYMV in Ghana.
302 In addition, the field survey in 2020 identified three isolates (out of 47, i.e. ca. 6%) from the
303 Northern and the Eastern regions clustering within the S1ca strain. This suggests that Ghana has
304 faced dynamic RYMV epidemics in the last decades. Although both RYMV strains circulate within
305 the same agro-environment (Fig. 1A, Table S1), the analysis of complete RYMV genomes of
306 isolates from Ghana did not reveal any recombination event (data not shown).

307
308 Based on 307 CP gene sequences of RYMV isolates collected in 15 West African countries since
309 1975, including 49 isolates from Ghana sampled from 1995 to 2020, the phylogeographic
310 reconstructions showed that RYMV was first introduced in Ghana in the 1990’s (Fig. 3C). This
311 introduction date is remarkably later than that in other countries from West and Central Africa,
312 including neighboring countries of Ghana. Actually, spatio-temporal modeling revealed that
313 RYMV disseminated efficiently from Mali to Burkina Faso and Ivory Coast during the 1950’s, to
314 Nigeria during the 1960’s, to Gambia, Sierra Leone and Cameroon during the 1970’s, and then to
315 Guinea, Niger and Chad during the 1980’s (Fig. S4; Dellicour et al., 2018; Issaka et al., 2021; Trovão
316 et al., 2015). We identified at least five independent introductions of RYMV into Ghana (Fig. 3).

317 An important way of S2 strain transmission was identified between Ivory Coast and the Southern
318 Ghana (probably Ahafo, Ashanti and Western regions). In addition to similar environmental
319 conditions on both sides of this border (high rainforest), these reiterated RYMV introductions
320 could be favored by agronomical interactions between Ivory Coast and Ghana that could
321 drastically increase the probabilities of RYMV dispersion by movement of infected biological
322 material. The most recent introduction in Ghana was apparent through the isolate 2020Gh133
323 only (branch 3, Fig. 3A-E) collected in 2020 in Western region, *i.e.* at the border with Ivory Coast,
324 illustrating the continuous introduction of RYMV isolates from this country since the 1990's.
325 Interestingly, these introductions are paralleled to the regular increase in rice cultivation areas in
326 Ghana from the 1990's and more intensively from 2008 (FAOSTAT 2021;
327 <https://data.un.org/Data.aspx?d=FAO&f=itemCode%3A27>). Note that the number of RYMV
328 introductions in Ghana is certainly underestimated by these epidemiological models as not all
329 introductions lead to an epidemic success that maintains the virus in time and space. For
330 instance, our study shows that no RYMV isolates genetically related to the 1995Gh1 isolate
331 (branch 1, Fig. 3A) were sampled during the 2010, 2012 and 2020 surveys, which suggest that
332 this RYMV lineage went extinct.

333 While RYMV isolates belonging to the S2 strain were present in Ghana since the 1990's, the virus
334 spread very recently to the Northern regions (2010-2017; Table 2, Fig. 3E). The delay of RYMV
335 dispersion to the North could be due to agronomical and topological factors. The discontinuity of
336 the rice cultivation landscape in Ghana, and especially with less rice cultivation area in the Central
337 regions (Fig. 1A), could make a barrier against the RYMV expansion between the Southern and
338 the Northern regions. Actually, the rice connectivity landscape has been suggested (Trovão et al.,
339 2015), although not statistically confirmed (Dellicour et al., 2018), to be the major determinant
340 of RYMV spread. The barrier to RYMV dispersion at the North could also be due to
341 biogeographical factors. As Northern Ghana is characterized by drier conditions, the agricultural
342 and environmental conditions could be less favorable to RYMV epidemics in this region (different
343 cultural practices, less alternative hosts, rice landscape more fragmented; Traore et al., 2009).
344 However, the initial limitation of RYMV to spread from the South to the North certainly lessened
345 in the last decades in parallel to rice intensification and extensification in Ghana (Demont, 2013);

346 FAOSTAT 2021, <https://data.un.org/Data.aspx?d=FAO&f=itemCode%3A27>). Similarly, the late
347 introduction of S1ca could also demonstrate the tendency of RYMV to circulate more easily
348 during the last decades. Actually, while the phylogeographic reconstructions estimate that RYMV
349 is present in South-East of Burkina Faso since the 1950's (Fig. 3B) and later on in Niger and Nigeria,
350 we identified two RYMV movements from these countries to the Northern and the South-eastern
351 regions of Ghana only after the 1990's (branches 4 and 5 in Fig. 3A-E; Table2). Altogether, because
352 of the recent introductions of RYMV to the Northern regions of Ghana (both S2 and S1ca strains)
353 and the agro-environmental factors that could be unfavorable to virus transmission or dispersion,
354 RYMV has probably not reached an epidemic status in the North of Ghana. This could explain why
355 no RYMV infected plant has been detected in the Upper East region (Fig. 1B).

356 Surprisingly, although S1wa strain is also present in Ivory Coast (Pinel-Galzi et al., 2015), our
357 results show that only the S2 strain was introduced several times in Ghana from Ivory Coast. This
358 suggests that S2 strain has advantageous biological or genetic properties to disperse in time and
359 space compared to S1wa strain. Contrary to the lineage genetically related to Gh1 that probably
360 got extinct (branch 2, Fig. 3A), we observed that one RYMV lineage (branch 2, Fig. 3A) has been
361 detected during the 2010, 2012 and 2020 surveys and showed an efficient expansion to several
362 Southern and Northern regions of Ghana, and also to Benin (branches 6 and 7, respectively; Fig.
363 3A-E). These observations suggest that, in addition to agronomical and anthropological factors,
364 some intrinsic genetic factors could favor the epidemic success of specific RYMV lineages or
365 strains in West Africa. Earlier studies showed that isolates from S2 strain dominated over those
366 from S1wa strain in experimental conditions (N'Guessan et al., 2000).

367
368 The phylogeographic reconstructions established only one release of RYMV from Ghana. One
369 route of RYMV dispersion was identified from Ghana to Benin (branch 7 in Fig. 3A-D) with a date
370 estimated between 2008 and 2010 (Table2, interval between nodes 7a and 7b). In West Africa
371 RYMV history, this movement is only the second dispersion event of RYMV to pass across the
372 Ghana/Burkina Faso axis, *i.e.* dispersion from West Africa to Central Africa. Actually, a first
373 expansion of RYMV to Central Africa occurred during the 1950's through Burkina Faso and led to
374 the genetic differentiation and the emergence of the S1ca strain (Dellicour et al., 2018; Issaka et

375 al., 2021; Trovão et al., 2015). Sixty years later, our results show that RYMV dispersed for a second
376 time to Central Africa through Ghana, which resulted in the introduction of the S2 strain in West-
377 Central Africa. Altogether, while the dispersion of RYMV from West Africa to Central Africa across
378 the Burkina Faso/Ghana axis has been very rare during the RYMV history, this study show that
379 Ghana corresponds to a junction area of RYMV populations that have circulated independently
380 in West and Central Africa until the 1990's. Such movements will probably occur more frequently
381 in the next decades because of the drastic intensification and the extensification of rice
382 cultivation and in the increase of commercial and agronomical exchanges in all this region
383 (Demont, 2013).

384

385 **5. Conclusion**

386 The generalization of the RYMV movements in West and Central Africa will definitely favor the
387 coexistence of several strains in fields. As each RYMV strain is characterized by specific biological
388 and pathogenic properties (Bonnamy et al., 2022; Hébrard et al., 2018; Pidon et al., 2020; Pinel-
389 Galzi et al., 2007; Poulicard et al., 2012; Traore et al., 2010), the overlapping of the distribution
390 area of RYMV strains could, in the future, lead to difficulties by controlling RYMV through the
391 local deployment of rice varieties resistant to the virus. Thus, our study underlines the
392 importance of both epidemiological surveillance and sanitary regulation at the local, regional,
393 and international levels to limit the RYMV strain circulation in West Africa to avoid the co-
394 circulation of RYMV genetic diversity that could make more difficult the design of sustainable
395 control strategies against the virus.

396

397 **CRedit authorship contribution statement**

398 **Emmanuel Gilbert Omiat:** Resources, Investigation, Data Curation, Writing - Original Draft.

399 **Maxwell Darko Asante:** Conceptualization, Supervision, Resources, Investigation, Data Curation,
400 Writing - Review & Editing. **Valentin Stanislas Edgar Traoré:** Resources, Investigation, Writing -

401 Review & Editing. **Allen Oppong:** Validation, Investigation, Writing - Review & Editing. **Beatrice**

402 **Elohor Ifie:** Validation, Investigation. **Kirpal Agyemang Ofofu:** Validation, Investigation, Writing

403 - Review & Editing. **Jamel Aribi:** Methodology, Investigation. **Agnès Pinel-Galzi:** Methodology,

404 Investigation. **Aurore Comte:** Software, Data Curation, Visualization. **Denis Fargette:**
405 Conceptualization, Software, Writing - Review & Editing, Supervision. **Eugénie Hébrard:** Writing
406 - Review & Editing, Supervision, Funding acquisition. **Oumar Traoré:** Supervision, Project
407 administration, Funding acquisition. **Samuel Kwame Offei:** Conceptualization, Supervision,
408 Project administration, Funding acquisition. **Eric Yirenkyi Danquah:** Conceptualization,
409 Supervision, Project administration, Funding acquisition. **Nils Poulicard:** Conceptualization,
410 Software, Data Curation, Writing - Original Draft, Visualization, Funding acquisition.

411

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423

424 **Figure captions**

425 **Fig. 1.** Rice cultivation in Ghana and location of the rice samples/RYMV isolates.

426 **(A)** Rice production in Ghana. Regions are colored according to the surface (in hectares, ha)
427 dedicated to rice cultivation. The Upper West (UW), Upper East (UE), North East (NE), Savannah
428 Region (SR), Northern (NO), Bono (BO), Bono East (BE), Oti (OT), Ahafo (AH), Ashanti (AS), Eastern
429 (EA), Volta (VO), Western North (WN), Western (WE), Central (CE) and Greater Accra (GA) regions
430 and the borders of the ecological zones (dotted lines) are indicated. **(B)** Schematic locations of
431 the RYMV isolates sampled in Ghana in 1995 (yellow), 2010 (orange), 2012 (brown) and 2020
432 (black). Samples collected in 2020 and negative to RYMV detection by DAS-ELISA are indicated by

433 white spots. (C) Schematic location of the RYMV isolates belonging to S1ca (red) and S2 (blue)
434 strains.

435

436 **Fig. 2.** Maximum-likelihood trees inferred from the WA44 complete genome sequence dataset.
437 The names of the RYMV isolates from Ghana (Gh) are indicated in black, the fully-sequenced
438 isolates from Ghana are highlighted, and the branches are colored according to the six RYMV
439 strains of West and Central Africa (S1wa, S1ca, S2, S3, Sa, Sg). Number at each node indicates
440 bootstrap percentages based on 100 replicates (only values above 60 are indicated). The country
441 of origin of the isolates is mentioned in these phylogenetic trees: Benin (Be), Burkina Faso (BF),
442 Cameroon (Ca), Central African Republic (Ce), Ivory Coast (CI), Gambia (Ga), Mali (Ma), Niger (Ng),
443 Nigeria (Ni), Senegal (Se), Sierra Leone (SL), Chad (Tc) and Togo (Tg).

444

445 **Fig. 3.** Phylogeographic reconstructions of RYMV epidemics in Ghana.

446 (A) Time-calibrated maximum clade credibility (MCC) tree reconstructed by continuous Bayesian
447 evolutionary inference with the 307 coat protein gene sequence dataset (WA307). Branches are
448 colored according to the six RYMV strains of West Africa (S1wa, S1ca, S2, S3, Sa, Sg). The values
449 on the nodes correspond to their posterior probabilities (only values above 0.60 are indicated).
450 The bottom axis gives the timeframe (by date) of the RYMV diversification. Seven branches of
451 interest are labeled on the MCC tree (from 1 to 7) and their relative nodes (1, 2a, 2b, 3, 4, 5a, 5b,
452 6a, 6b, 7a, 7b) were annotated with their time to the most common ancestor and their 95%
453 highest probability density (HPD) intervals (Table 2). (B to D) Reconstruction of the continuous
454 spatio-temporal dispersion of RYMV in West Africa with snapshots in 1992 (B), 2008 (C) and 2020
455 (D) that capture introductions and release of RYMV in/out Ghana (delimited by the grey area).
456 Black lines show a spatial projection of the MCC tree and colored areas represent statistical
457 uncertainty in the dated estimated locations of RYMV internal nodes (95% HPD; from red to green
458 to cover the time period from 1900 to 2020). The seven branches of interest in Figure 3A are
459 indicated.

460

461 **Supplementary Materials**

462 **Fig. S1:** Maximum-likelihood trees inferred from the WA307 CP sequence dataset.
463 The names of RYMV isolates from Ghana (Gh) are indicated in black, the fully-sequenced isolates
464 from Ghana are highlighted, and the clades of the six RYMV strains of West Africa (S1wa, S1ca,
465 S2, S3, Sa, Sg) are indicated. Number at each node indicates bootstrap percentages based on 100
466 replicates (only values above 60 are indicated). The country of origin of the isolates is mentioned
467 by their names: Benin (Be), Burkina Faso (BF), Cameroon (Ca), Central African Republic (Ce), Ivory
468 Coast (Ci), Gambia (Ga), Mali (Ma), Niger (Ng), Nigeria (Ni), Senegal (Se), Sierra Leone (SL), Chad
469 (Tc) and Togo (Tg).

470
471 **Fig. S2:** Exploration of the temporal signal from the RYMV WA307 dataset by a linear regression
472 approach.

473 Root-to-tip divergence as a function of sampling time for Maximum Likelihood tree clusters
474 obtained with 307 non-recombinant RYMV CP sequences. Plot representations in a 1970-2020
475 **(A)** and a 1800-2020 **(B)** dating range.

476
477 **Fig. S3:** Exploration of the temporal signal from the RYMV WA307 dataset by date-randomization
478 tests.

479 Violin plots representing the intervals of the substitution rate (substitution/site/year; **A** and **C**)
480 and the time to most recent common ancestor (years; **B** and **D**) in the RYMV CP sequence dataset
481 from the sampled dates (WA307) and from the dates after tip (A and B) or cluster (C and D)
482 permutations (from perm1 to perm10). The blue areas represent the range of the 95% HPD
483 estimates.

484
485 **Fig. S4:** Reconstruction of the continuous spatio-temporal dispersion of RYMV in West-Central
486 Africa based on the Time-calibrated maximum clade credibility (MCC) tree reconstructed by
487 continuous Bayesian evolutionary inference with the 307 coat protein gene sequence dataset
488 (WA307).

489 Snapshots of the spatio-temporal dispersion of RYMV in 1992 **(A)**, 2008 **(B)**, 2010 **(C)** and 2020
490 **(D)**. Ghana is delimited by the grey area. Black lines show a spatial projection of the MCC tree

491 and colored areas represent statistical uncertainty in the dated estimated locations of RYMV
492 internal nodes (95% HPD; from red to green to cover the time period from 1900 to 2020).

493

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Strain	Group	d	S.E.
S2	All S2	0.016	0.002
	CI	0.015	0.003
	Gh	0.014	0.002
	Gu	0.014	0.003
	Ma	0.009	0.002
	Be	0.001	0.001
	BF	nd	nd
S1ca	All S1ca	0.042	0.006
	Ni	0.039	0.006
	Ca	0.039	0.008
	Gh	0.031	0.003
	BF	0.029	0.009
	Ce	0.024	0.006
	Ng	0.018	0.003
	Ch	0.017	0.003
	Tg	0.007	0.003
	Be	0.007	0.002

653

654 **Table 1.** Genetic diversity of the S2 and S1ca strains in West- and West-Central Africa.

655 d: genetic diversity estimated in substitution per site; S.E.: standard error; Benin (Be), Burkina
656 Faso (BF), Cameroon (Ca), Central African Republic (Ce), Chad (Ch), Ivory Coast (CI), Ghana (Gh),
657 Guinea (Gu), Mali (Ma), Niger (Ng), Nigeria (Ni), Togo (Tg). S.E.: standard errors; nd: not
658 determined.

659

n° node	<i>Time before present (2020.6)</i>		Date	Date 95%HPD
	Time	Time 95%HPD		
1	32.8	[37,3 - 28,2]	1987.8	[1983,3 - 1992,5]
2a	21.4	[27,5 - 18,1]	1999.2	[1993,1 - 2002,5]
2b	17.1	[21,6 - 13,3]	2003.5	[1999,0 - 2007,3]
3	20.8	[25,6 - 18,2]	1999.8	[1995,0 - 2002,4]
4	33.7	[50,0 - 16,4]	1986.9	[1970,7 - 2004,2]
5a	27.7	[41,1 - 16,0]	1992.9	[1979,5 - 2004,6]
5b	5.6	[9,8 - 1,3]	2015.0	[2010,8 - 2019,3]
6a	10.7	[13,3 - 8,0]	2009.9	[2007,3 - 2012,6]
6b	6.8	[10,7 - 3,8]	2013.8	[2009,9 - 2016,8]
7a	11.8	[13,5 - 10,4]	2008.8	[2007,1 - 2010,2]
7b	11.0	[12,0 - 10,1]	2009.6	[2008,6 - 2010,5]

660

661 **Table 2.** Dating estimates of nodes of the seven branches of interest identified in the maximum
662 clade credibility (MCC) tree (Figure 3A).

663 The estimates of the time to the most common ancestor (in years before July 2020, *i.e.* 2020.6),
664 the dates and the 95% highest probability density (HPD) intervals are mentioned.

665

Samples	Year	Region	Variety	Latitude	Longitude	Rice age	DAS-	RYMV		
						(weeks)	ELISA	CP Seq.	Full Seq.	strain
Gh1	1995	Ashanti	nd	6.7	-1.6	nd	+	1995Gh1	S2	
Gh46	2010	Ashanti	nd	6.7	-1.6	nd	+	2010Gh46	S2	
Gh47	2010	Ashanti	nd	6.7	-1.6	nd	+	2010Gh47	2010Gh47	
Gh48	2010	Ashanti	nd	6.7	-1.6	nd	+	2010Gh48	S2	
Gh49	2010	Ashanti	nd	6.7	-1.6	nd	+	2010Gh49	S2	
Gh50	2010	Ashanti	nd	6.7	-1.6	nd	+	2010Gh50	S2	
Gh51	2010	Ashanti	nd	6.7	-1.6	nd	+	2010Gh51	S2	
Gh52	2010	Greater Accra	nd	5.6	-0.2	nd	+	2010Gh52	S2	
Gh53	2010	Greater Accra	nd	5.6	-0.2	nd	+	2010Gh53	S2	
Gh54	2010	Greater Accra	nd	5.6	-0.2	nd	+	2010Gh54	S2	
Gh55	2010	Greater Accra	nd	5.6	-0.2	nd	+	2010Gh55	2010Gh55	
Gh3227	2012	Ashanti	nd	6.6	-1.3	nd	+	2012Gh3227	S2	
Gh3229	2012	Ashanti	nd	6.6	-1.3	nd	+	2012Gh3229	S2	
Gh3244	2012	Central	nd	5.6	-1.2	nd	+	2012Gh3244	S2	
Gh3245	2012	Central	nd	5.6	-1.2	nd	+	2012Gh3245	S2	
Gh3387	2012	Ashanti	nd	6.7	-1.6	nd	+	2012Gh3387	S2	
Gh3397	2012	Ashanti	nd	6.7	-1.6	nd	+	2012Gh3397	S2	
Gh3399	2012	Ashanti	nd	6.7	-1.6	nd	+	2012Gh3399	S2	
Gh3416	2012	Ashanti	nd	6.7	-1.6	nd	+	2012Gh3416	S2	
Gh101	2020	Ashanti	CRI-AGRA	6.8	-1.8	7	+	2020Gh101	S2	
Gh102	2020	Ashanti	CRI-AGRA	6.8	-1.8	7	+	2020Gh102	S2	
TOGO										
Gh103	2020	Ashanti	MARSHALL	6.7	-1.5	7	+	2020Gh103	S2	
Gh104	2020	Ashanti	BOUAKE 189	nd	nd	7	-			
Gh105	2020	Ashanti	CRI-AGRA	6.6	-1.3	7	+	2020Gh105	S2	
Gh106	2020	Ashanti	CRI-AGRA	6.6	-1.3	8	+	2020Gh106	S2	
Gh107	2020	Ashanti	JASMINE 85	6.7	-1.4	8	-			
Gh108	2020	Ashanti	JASMINE 85	nd	nd	12	-			
Gh109	2020	Ashanti	CRI-AGRA	6.7	-1.5	7	+	2020Gh109	S2	
Gh110	2020	Ashanti	CRI-AGRA	6.7	-1.5	8	-			
Gh111	2020	Volta	CRI-AGRA	6.1	0.9	8	+	2020Gh111	S2	
Gh112	2020	Volta	CRI-AGRA	6.1	0.9	8	+	2020Gh112	S2	

Gh113	2020	Eastern	LEGON1	6.1	0.1	12	+	2020Gh113	2020Gh113	S1ca
Gh114	2020	Eastern	LEGON1	6.1	0.1	7	-			
Gh115	2020	Eastern	JASMINE 85	6.0	-1.0	8	+	2020Gh115		S2
Gh116	2020	Eastern	JASMINE 85	6.0	-1.0	7	+	2020Gh116		S2
Gh117	2020	Eastern	CRI-AGRA	6.0	-1.1	12	+	2020Gh117		S2
Gh118	2020	Eastern	JASMINE 85	6.5	-0.7	12	+	2020Gh118		S2
Gh119	2020	Bono East	JASMINE 85	7.5	-1.6	11	+	partial CP		S2
Gh120	2020	Bono East	CRI-AGRA	7.5	-1.6	10	+	2020Gh120		S2
Gh121	2020	Bono East	JASMINE 85	7.5	-1.6	8	+	2020Gh121		S2
Gh122	2020	Ahafo	CRI-AGRA	7.4	-2.2	12	+	2020Gh122		S2
Gh123	2020	Bono	CRI-AGRA	7.3	-2.9	8	-			
Gh124	2020	Ahafo	JASMINE 85	7.1	-2.7	12	+	2020Gh124	2020Gh124	S2
Gh125	2020	Ahafo	JASMINE 85	6.8	-2.5	12	+	2020Gh125		S2
Gh126	2020	Ahafo	JASMINE 85	6.8	-2.5	11	+	2020Gh126		S2
Gh127	2020	Central	JASMINE 85	5.9	-1.3	12	+	2020Gh127		S2
Gh128	2020	Central	CRI-AGRA	5.9	-1.3	14	+	2020Gh128		S2
Gh129	2020	Central	nd	5.9	-1.3	12	+	2020Gh129		S2
Gh130	2020	Western	Local var.	5.7	-2.0	12	-			
Gh131	2020	Western	Local var.	5.8	-2.0	8	-			
Gh132	2020	Western	CRI-AGRA	5.8	-2.0	13	-			
Gh133	2020	Western	CRI-AGRA	5.8	-2.0	12	+	2020Gh133	2020Gh133	S2
Gh134	2020	Greater Accra	CRI-AGRA	5.7	0.0	8	-			
Gh135	2020	Greater Accra	CRI-AGRA	5.7	-0.1	7	-			
Gh136	2020	Greater Accra	CRI-AGRA	5.8	0.1	12	-			
Gh137	2020	Greater Accra	JET3	5.8	0.1	12	-			
Gh138	2020	Northern	nd	9.3	-1.0	6	+	2020Gh138		S2
Gh139	2020	Northern	CRI-AGRA	9.4	-1.0	4	+	2020Gh139		S1ca
Gh140	2020	Northern	CRI-AGRA	9.3	-1.0	6	+	2020Gh140	2020Gh140	S1ca
Gh141	2020	Northern	Salmasaa Local var. TOGO	9.6	-1.0	5	+	2020Gh141		S2
Gh142	2020	Northern	MARSHALL	9.6	-1.0	6	+	2020Gh142	2020Gh142	S2
Gh143	2020	Upper East	CRI-AGRA	10.8	-1.1	10	-			
Gh144	2020	Upper East	CRI-AGRA	10.8	-1.1	10	-			

668

669 **Table S1:** Location, metadata and experimental treatments on rice samples collected in 2020 in
670 Ghana.

671 Only a portion of the CP gene was amplified and sequenced for the 2020Gh 119 isolates, but the
672 genetic information was sufficient to confirm that this isolate belongs to the S2 strain. (local var.):

673 local rice variety. nd: not determined.

674

Isolate	Year	Region	CP	Complete genome
Gh1	1995	Ashanti	AJ279919	
Gh46	2010	Ashanti	OQ200610	
Gh47	2010	Ashanti	OQ200611	OQ225940
Gh48	2010	Ashanti	OQ200612	
Gh49	2010	Ashanti	OQ200613	
Gh50	2010	Ashanti	OQ200614	
Gh51	2010	Ashanti	OQ200615	
Gh52	2010	Greater Accra	OQ200616	
Gh53	2010	Greater Accra	OQ200617	
Gh54	2010	Greater Accra	OQ200618	
Gh55	2010	Greater Accra	OQ200619	OQ225941
Gh3227	2012	Ashanti	OQ200620	
Gh3229	2012	Ashanti	OQ200621	
Gh3244	2012	Central	OQ200622	
Gh3245	2012	Central	OQ200623	
Gh3387	2012	Ashanti	OQ200624	
Gh3397	2012	Ashanti	OQ200625	
Gh3399	2012	Ashanti	OQ200626	
Gh3416	2012	Ashanti	OQ200627	
Gh101	2020	Ashanti	OQ200628	
Gh102	2020	Ashanti	OQ200629	
Gh103	2020	Ashanti	OQ200630	
Gh105	2020	Ashanti	OQ200631	
Gh106	2020	Ashanti	OQ200632	
Gh109	2020	Ashanti	OQ200633	
Gh111	2020	Volta	OQ200634	
Gh112	2020	Volta	OQ200635	
Gh113	2020	Eastern	OQ200636	OQ225942
Gh115	2020	Eastern	OQ200637	
Gh116	2020	Eastern	OQ200638	
Gh117	2020	Eastern	OQ200639	

Gh118	2020	Eastern	OQ200640	
Gh120	2020	Bono East	OQ200641	
Gh121	2020	Bono East	OQ200642	
Gh122	2020	Ahafo	OQ200643	
Gh124	2020	Ahafo	OQ200644	OQ225943
Gh125	2020	Ahafo	OQ200645	
Gh126	2020	Ahafo	OQ200646	
Gh127	2020	Central	OQ200647	
Gh128	2020	Central	OQ200648	
Gh129	2020	Central	OQ200649	
Gh133	2020	Western	OQ200650	OQ225944
Gh138	2020	Northern	OQ200651	
Gh139	2020	Northern	OQ200652	
Gh140	2020	Northern	OQ200653	OQ225945
Gh141	2020	Northern	OQ200654	
Gh142	2020	Northern	OQ200655	OQ225946

675

676 **Table S2:** Sequence dataset from Ghana and accession numbers.

677