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1 LETTER TO THE EDITOR

A comment on the paper: Extended Y chromosome haplotypes resolve multiple and unique lineages of the Jewish Priesthood by M.F. Hammer, D.M. Behar, T.M. Karafet, F.L. Mendez, B. Hallmark, T. Erez, L.A. Zhivotovsky, S. Rosset, K. Skorecki, *Hum Genet*, published online 8 August 2009

7 **Anatole Alex Klyosov**

10 The cited paper is remarkable with respect to haplogroups
11 and haplotypes typing and the large number of individuals
12 tested, including Cohanim, which is the prime target of the
13 study. However, it is open to critique regarding calcula-
14 tions of time spans to common ancestors of presented
15 series of haplotypes.

16   First, the authors have employed an inadequate meth-
17 odology for the calculations, namely the infamous "pop-
18 ulation mutation rates" of 0.00069 mutation/marker/
19 generation. It should not have been used in the first place.
20 More adequate procedures have been developed lately.
21 Second, the authors have not defined criteria when the
22 "population" and when the "pedigree", or the "genea-
23 logical" mutation rates, should be used. As a result, they
24 have applied the "population" mutation rate to "genea-
25 logical" haplotype series, which increased their
26 "TMRCA", i.e., a time span to common ancestors, by
27 about 300%. Third, they have not analyzed genealogical
28 lineages with recent common ancestors (such as 500–
29 800 years bp); therefore, they missed valuable information
30 regarding history of Cohanim in this millennium.

31   Allow me to explain.

Cohanim J1e*-P58*

33 Here is the haplotypes' tree (it is explained in the last
34 section of this comment) for Cohanim, haplogroup J1e*,
35 composed from the Hammer et al. (2009) data, 22-marker
36 haplotypes, Table S3.

A1   A. A. Klyosov (✉)
A2   Newton, MA, USA
A3   e-mail: aklyosov@comcast.net
A4   URL: http://aklyosov.home.comcast.net

37 The tree contains 16 base (ancestral) haplotypes (see the
38 last section for definitions) on the top (in the entire order
39 DYS 393, 390, 19, 391, 385a, 385b, 426, 388, 439, 389-1,
40 393, 389-2, 458, 459a, 459b, 455, 454, 447, 437, 448, 449
41 and 438):

43 12 23 14 10 13 15 11 16 12 13 11 30 – 17 8 9 11 11 26 14 21 26 10

44 All 98 haplotypes contain 191 mutations from the above
45 base haplotype, which gives—employing the linear method
46 (see the last section of this paper)—191/98/0.047 = 41
47 generations (without corrections for back mutations;
48 Klyosov 2009a, b) or 43 generations with the correction, to
49 a common ancestor, i.e., 1,075 ± 130 ybp, the tenth cen-
50 tury AD plus or minus a century.

51 The authors of the cited paper have obtained
52 3,200 ± 1,100 years to a common ancestor for the Coha-
53 nim, using the same haplotypes, albeit with a set of 17-
54 marker haplotypes, and 3,000 ± 1,500 years to a common
55 ancestor using a set of 9-marker haplotypes, and claimed
56 that is it nicely fit to the Biblical description for the origin
57 of the Jewish higher priest. It is not. See below for more
58 details.

59 Since all 98 haplotypes contain 16 base (identical to
60 each other) 22-marker haplotypes (see above), it gives—
61 employing the logarithmic method (see the last section of
62 this paper)—ln(98/16)/0.047 = 39 generations (without a
63 correction) or 41 generations (with the correction), i.e.,
64 1,025 ybp to a common ancestor for Cohanim J1e*
65 haplotypes.

66 Since the logarithmic and the "linear" methods give the
67 same dating to the common ancestor, it means that there
68 was indeed just one common ancestor for the whole series
69 of 98- of 22-marker haplotypes (see the last section), who
70 lived about 1,075 ± 130 ybp.

71 The authors of the cited paper have removed some
72 markers for their analysis, namely five markers, DYS 385a,
73 385b, 459a, 459b and 458, reducing the series from 22- to
74 17-marker haplotypes. Let us consider if there would be any
75 noticeable change. 98- of 17-marker haplotypes contain 140
76 mutations from the above base haplotype (less of the five
77 markers), which gives $1,175 \pm 160$ ybp for the common
78 ancestor. It is practically the same time span within the
79 margin of error.

80 As it was noticed above, the authors of the cited paper
81 have obtained $3,200 \pm 1,100$ years to a common ancestor
82 for the Cohanim, using the same set of 17-marker haplo-
83 types, and claimed that is it nicely fit to the Biblical
84 description for the origin of the Jewish higher priest. It is
85 not, with $1,075 \pm 130$ and $1,175 \pm 160$ ybp.

86 Why such a large difference? The answer is rather
87 obvious. The ratio of 3,200 and 1,075 years is 3.0. The
88 ratio of the "population" mutation rate (0.00069) to the
89 actual "genealogical" one (0.00214) is 3.1. The authors
90 of the cited paper have applied the "population" mutation
91 rate to the "genealogical" series of haplotypes. Actually,
92 that "population" mutation rate should have never been
93 applied in the first place. It is ill defined, it is not gov-
94 erned by any criteria when it should be applied and when
95 it should not.

96 In Table S4 of the cited paper, the authors listed 99- of
97 12-marker Cohanim J1e* (J-P58*) haplotypes. All of them
98 contain 98 mutations from the above base haplotype (in the
99 first 12 markers), which gives $1,175 \pm 170$ years to a
100 common ancestor. It is the same figure obtained above,
101 within the margin of error.

102 Finally, the authors reduced the 22-marker haplotypes to
103 9-marker one (the 12-marker haplotype in the FTDNA for-
104 mat less of DYS 385a, 385b and 426), and, using the same
105 "population" mutation rate, have obtained $3,000 \pm$
106 $1,500$ years to a common ancestor of Cohanim J1e*. In fact,
107 this whole series contain 67 mutations, which gives 67/98/
108 $0.018 = 38$ generations (40 generations with a correction for
109 back mutations), i.e., $1,000 \pm 160$ years to a common
110 ancestor. This is again practically the same figure as given
111 above for 22-marker $(1,075 \pm 130$ ybp), 17-marker
112 $(1,175 \pm 160$ ybp), and 12-marker $(1,175 \pm 170$ ybp)
113 haplotypes, and is far away from the authors' $3,000 \pm$
114 $1,500$ ybp for Cohanim J1e*.

115 In fact, the ancestral haplotype of Cohanim J1e* (in the
116 format previously described)

117 12 23 14 10 13 15 11 16 12 13 11 30 – 17 8 9 11 11 26 14 21 26 10

118

119 was identified in Klyosov (2008a, 2009b) in the form of a
120 67-marker haplotype (the respective 22 markers are shown
121 below for a comparison)

123 12 23 14 10 13 15 11 16 12 13 11 30 -- 17 8 9 11 11 26 14 21 27 10

124 (so-called "the recent extended CMH") of a common
125 ancestor who lived $1,050 \pm 190$ ybp, around the tenth
126 century. One can see, it is practically the same ancestral
127 haplotype and the same time span to a common ancestor.

Recent DNA genealogical branches of Cohanim J1e* 128

129 The tree (Fig. 1) reveals three principal branches (on top
130 and the left-hand side; on the right-hand side; and at the
131 bottom), with their ancestral haplotypes, respectively:

12 23 14 10 13 15 11 16 12 13 11 30 – 17 8 9 11 11 26 14 21 **26** 10

12 23 14 10 13 15 11 16 12 13 11 30 – 17 8 9 11 11 26 14 21 **27** 10

12 23 14 10 13 15 11 16 **11** 13 11 30 – 17 8 9 11 11 26 14 21 26 10

133

134 each having only one mutation (in bold) from the upper
135 base haplotype, common for the whole tree and for the top-
136 left-hand side. Common ancestors for these all branches
137 lived approximately in the range of 625–875 ybp. Just one
138 example—the 27-haplotype branch on the right-hand side
139 has 8 base haplotypes as shown above, with the whole
140 branch having 32 mutations from it. Therefore, a common
141 ancestor of the branch lived $\ln(27/8)/0.047 = 26$ genera-
142 tions bp, i.e., 650 ybp. The linear method gives 32/27/
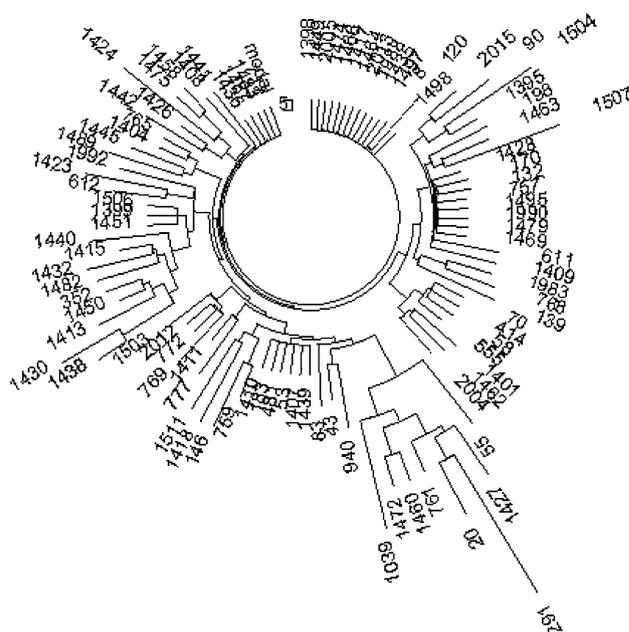

Fig. 1 22-marker haplotype tree for Cohanim, haplogroup J1e*-
P58*, for 98 haplotypes (Hammer et al. 2009). Haplotypes numbering
corresponds to the numbering in the paper, Table S3

143 $0.047 = 25$ generations bp, i.e., 625 ± 130 ybp. The fit
144 shows that the branch has one common ancestor indeed,
145 and that he lived around the fourteenth century AD. Just
146 one mutation per 22-marker haplotypes indicates that all
147 the common ancestors lived within the current millennium,
148 with THEIR common ancestor at the bottom of this time
149 period.
150   That the "young" branches are really young ones can be
151 seen from Fig. 2, which shows a haplotype tree for 12-
152 marker haplotypes of the Cohanim of haplogroup J1e*,
153 listed in the cited paper.
154   Since these haplotypes are lacking 10 markers after their
155 first 12 ones, compared to those in Fig. 1, the tree is
156 slightly rearranged in Fig. 2, following the computer pro-
157 gram. However, it shows the main tree branches in the
158 haplotype series. Since the branches lost many mutations
159 (in markers 13 through 22), "ages" of their common
160 ancestors are reduced for some branches. For example, the
161 right-hand side branch now contains 48 haplotypes, 43 of
162 which are identical to each other (base haplotypes), and the
163 other contains only 7 mutations. This gives $\ln(48/43)/$
164 $0.022 = 5.0$ generations, i.e., 125 ± 50 years to a com-
165 mon ancestor, and $7/48/0.022 = 6.6$ generations, i.e.,
166 165 ± 65 years to a common ancestor. Since the loga-
167 rithmic and linear methods again give practically identical
168 results, it points to a single (in terms of DNA genealogy)
169 common ancestor for the whole branch. It also shows that
170 12-marker haplotypes contain much poorer information
171 regarding a time span to a common ancestor compared to

172 that of 22-marker haplotypes. Hence, it is surprising why
173 the authors were reluctant to consider the 22-marker hap-
174 lotypes of Cohanim, persistently reducing a number of
175 markers in the haplotypes to 17, 12, and even 9.

Cohanim J2a-M410*

177 The 22-marker haplotype tree is shown in Fig. 3
178   One can see that the tree consists of two quite different
179 branches; the older one in turn contains two sub-branches.
180 It is clear that to treat the tree as a whole, without subdi-
181 vision into branches, as it is done in the cited paper, would
182 be incorrect and lead to a phantom common ancestor
183 (though the authors in the paper actually indicated this may
184 be a problem as not all SNPs downstream from M410 were
185 considered). However, the authors did exactly that, they
186 took the whole series of 31 haplotypes, applied the "pop-
187 ulation" mutation rate and obtained $5,900 \pm 2,000$ years
188 to a common ancestor using 17-marker haplotypes, and
189 $4,900 \pm 1,900$ years to a common ancestor using 9-marker
190 ones. Again, they have eliminated markers DYS385a,b and
191 DYS459a,b, as well as DYS449, and reduced the 22-mar-
192 ker haplotypes to 17-marker ones. It is obvious that the
193 younger series of haplotypes and the respective recent

Fig. 2 12-marker haplotype tree for Cohanim, haplogroup J1e*-P58*, for 99 haplotypes (Hammer et al. 2009). Haplotypes numbering follows the order of haplotypes in the paper, Table S4

Fig. 3 22-marker haplotype tree for Cohanim, haplogroup J2a-M410, for 31 haplotypes (Hammer et al. 2009). Haplotypes numbering corresponds to the numbering in the paper, Table S3

common ancestor were lost from considerations in the cited paper.

Let us consider the younger branch, containing 20- of 22-marker haplotypes, having 14 mutations from the base haplotype (in the format described above):

12 23 15 10 14 17 11 16 12 14 11 30 – 15 8 9 11 11 25 15 21 31 9

It contains 11 base haplotypes, hence ln(20/11)/0.047 = 13 generations to a common ancestor. The linear method gives 14/20/0.047 = 15 ± 4 generations to a common ancestor, which is practically the same value obtained by the logarithmic method, within margin of error. Therefore, a common ancestor for the "recent" Cohanim branch lived 375 ± 110 ybp, around the seventeenth century AD.

The older branch is split into two sub-branches. The first one contains five haplotypes of descendants of Cohanim of the former Russian Empire, namely Russia, Ukraine, Belarus, Lithuania and Poland, with only 3 mutations per 110 markers from the base haplotype:

12 23 15 10 14 17 11 **15** 12 **13** 11 29 – 15 8 9 11 11 **24** 15 21 **32** 9

which gives 325 ± 190 years to their common ancestor, who lived around the seventeenth century. The alleles in bold are different from ones of the above base haplotype with a common ancestor of 375 ± 110 ybp. This places their common ancestor to about 1,500 ybp, around the sixth century AD.

It is exactly the ancestral haplotype of Jewish J2 population identified in a 37-marker format (Klyosov 2008a) (the respected alleles are shown here for a comparison):

12 23 15 10 14 17 11 15 12 13 11 29 – 15 8 9 11 11 24 15 21 32 9

with a common ancestor who lived 850 ± 260 ybp (12 mutations in 148 markers).

The older sub-branch is also split into two sub-branches, one includes descendants from Iran, Iraq, Argentina and North Africa, with a common ancestor of 3,650 ± 830 ybp (24 mutations in four 22-marker haplotypes). The last two branches (Cohanim from the Russian Empire, on the one hand, and Iraq, Iran, Argentina and Africa, on the other) differ by 12 mutations per 22 markers that place their common ancestor to about 6,200 ybp.

If, following the authors of the cited paper, to reduce the amount of markers from 22 to 17, then the "young" branch should contain 9 mutations, and a common ancestor lived 9/20/17/0.00184 = 14 generations ago, i.e., 350 ± 120 ybp. This is practically the same as 375 ± 110 ybp, determined using 22-marker haplotypes. The Russian Empire Cohanim (see above), whose common ancestor lived 325 ± 190 ybp (22-marker haplotypes), now fits the value of 325 ± 230 ybp (17-marker haplotypes, two mutations in 110 markers), i.e., just the same value. It is not clear why the authors of the cited paper reduced the haplotypes from 22-marker to 17-marker, 12-marker and 9-marker haplotypes. 22-marker ones worked perfectly.

The same was for the ancient branch. 24 mutations in four 22-marker haplotypes (3,650 ± 830 ybp) reduced to 16 mutations in four 17-marker haplotypes (3,575 ± 960 ybp), which is just the same, albeit with a larger margin of error.

For 9-marker haplotypes, the "younger" branch of 20 haplotypes contains 9 mutations (625 ± 220 ybp) which for the 22-marker haplotypes it contains 14 mutations (375 ± 110 ybp). These values are similar and fit within margin of error, and at any rate point at a recent common ancestor of Cohanim J2a.

Finally, for ancient Cohanim J2a branches, 22- and 9-marker haplotypes give similar time spans to a common ancestor: in the first case, 24 mutations in four haplotypes result in 3,650 ± 830 years to a common ancestor; in the second case, the number of mutations reduced to 7, and gave 2,425 ± 1,200 years to a common ancestor. One can see that the two values are within the margin of error; however, 9-marker haplotypes give much larger error margin.

Cohanim J2e-M12

Fifteen of 22-marker haplotypes of Cohanim J2e-M12 are listed in Table S3 in the cited paper (the authors have reported in Table 1 that they have considered 16 haplotypes). According to the cited paper, a common ancestor of the haplotype lived 12,100 ± 4,400 ybp as determined with 22-marker haplotypes. The haplotype tree is shown in Fig. 4.

The tree reveals two branches. The 8-haplotype branch on the right-hand side contains 15 mutations from the following base haplotype (in the format, explained above)

13 24 15 10 15 17 11 15 12 12 11 29 – 19 8 9 8 11 27 16 19 29 9

It gives 15/8/0.047 = 40 generations (not corrected for back mutations) or 42 generations (corrected), i.e., 1,050 ± 290 years to a common ancestor.

The 7-haplotype branch on the left-hand side contains 37 mutations from the base haplotype

12 24 15 10 15 17 11 15 12 12 11 **28** – **18** 8 9 8 11 27 16 19 29 9

It gives 3,150 ± 600 years from a common ancestor of the branch. The two base haplotypes are separated by three
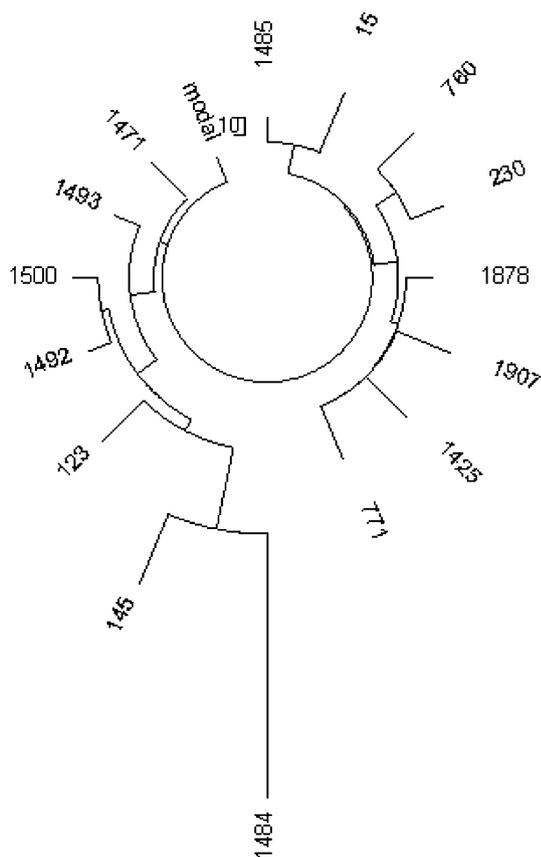
Fig. 4 22-marker haplotype tree for Cohanim, haplogroup J2b-M12, for 15 haplotypes (Hammer et al. 2009). Haplotypes numbering corresponds to the numbering in the paper, Table S3

290 mutations, which places *their* common ancestor to about
291 2,950 ybp, which is the common ancestor of the left-hand
292 branch itself. In other words, the right-hand side branch is a
293 daughter branch of the left-hand side one, and a common
294 ancestor of the whole tree of haplotypes of Cohanim J2b-
295 M12 lived 3,150 ± 600 ybp.
296   The authors of the cited paper, in which the time to a
297 common ancestor was determined as 12,100 ± 4,400 ybp,
298 were in error. They have treated the "father" and the
299 "daughter" branches of the haplotype series as a just a set
300 of haplotypes with a common ancestor outside of the
301 branches, and, besides of it, employed an erroneous
302 "population" mutation rate, as described above. Then, they
303 have considered 17-marker haplotypes, omitting DYS
304 385a,b, DYS459a,b, and DYS449. These 15- of 17-marker
305 haplotypes in fact contained 9 and 29 mutations in the
306 right-hand side and the left-hand side branches, respec-
307 tively, which result in 900 ± 310 and 3,725 ± 800 years
308 to their common ancestors, respectively. These figures are
309 essentially the same with those obtained with the 22-mar-
310 ker haplotypes, within the margins of error.
311   Finally, if to reduce haplotypes to 9-marker ones, which
312 would greatly sacrifice accuracy of calculations, the

313 respective time spans to their common ancestors would be
314 1,100 ± 460 and 1,500 ± 600 years to a common ances-
315 tor, respectively, for the right-hand and left-hand side
316 branches. It just could not possibly be 5,500 ± 1,900 ybp,
317 obtained in the cited paper with the 9-marker haplotypes.
318 The main reason of the errors, again, is wrong methodol-
319 ogy employed in the cited paper for calculations of time
320 spans to common ancestors.

Conclusions

Cohanim J1e*-P58*

323 A common ancestor of all 99 Cohanim lived
324 1,075 ± 130 ybp, and this timing is reproducible for 9-,
325 12-, 17-, 22- and 67-marker haplotypes. A much higher
326 values of 3,190 ± 1,090 and 3,000 ± 1,500 ybp were
327 obtained in the cited paper (Hammer et al. 2009) using
328 incorrect methods and incorrect mutation rates. A common
329 ancestor of all the 99 J1e* Cohanim lived around the tenth
330 century AD. There are three main lineages derived from
331 the common ancestor, with their common ancestors who
332 lived approximately between 625 and 875 ybp.
333   An emphasis of the cited paper on the conclusion that
334 "an extended CMH on the J1e*-P58* background that … is
335 remarkably absent in non-Jews" and having "the estimated
336 divergence time of this lineage… 3,190 ± 1,090 years" is
337 incorrect regarding the divergence time. It is more
338 understandable why the lineage originated only
339 1,075 ± 130 years ago is "remarkably absent in non-
340 Jews".

Cohanim J2a-M410*

342 Common ancestors of 31 Cohanim lived 325 ± 190 and
343 375 ± 110 ybp (recent different DNA lineages), and their
344 common ancestor lived around 1,500 ybp. A common
345 ancestor of another branch of Cohanim of this haplogroup
346 lived 3,560 ± 830 ybp, and yet another common ancestor
347 lived about 6,200 ybp.

Cohanim J2b-M12

349 Common ancestors of 15 Cohanim lived 3,150 ± 600 and
350 1,050 ± 290 ybp, with the second lineage being descen-
351 dant from the first common ancestor.

Analysis of mutations and their rates

353 Haplotype trees were constructed using PHYLIP, the
354 Phylogeny Inference Package program (Felsenstein 2005),

355 as it was explained in detail in Klyosov (2008b, 2009a). A
356 "comb" around the wheel, a "trunk", in haplotype trees
357 identifies "base" haplotypes, identical to each other and
358 carrying no mutations compared to their ancestral haplo-
359 types. The farther the haplotypes lies from the wheel, the
360 more mutations they carry compared to the base haplotype
361 and the older the respective branch.

362 The "base" haplotypes are the ancestral haplotypes in
363 an ideal case. However, since those haplotypes often are
364 deduced ones, it would be inaccurate to call them
365 "ancestral", hence "base" haplotypes.

366 The time span to a common ancestor was calculated
367 using both "logarithmic" and "linear" approaches. The
368 logarithmic method is based on the assumption (which
369 largely or practically always holds) that a transition of the
370 base haplotypes into mutated ones is described by the first-
371 order kinetics:

$$B = A\,e^{kt},$$

373 i.e.,

$$\ln(B/A) = kt$$

375 where

376 B = a total number of haplotypes in a set,
377 A = a number of unchanged (identical, not mutated)
378 base haplotypes in the set,
379 k = an average mutation rate,
380 t = a number of generations to a common ancestor.

381 One can see that the logarithmic method does not con-
382 sider mutations in haplotypes; only mutated and non-
383 mutated (base) haplotypes are considered.

384 Mutation-counting methods are all based on accumula-
385 tion of mutations in haplotypes over time. They include the
386 "linear", "quadratic" (ASD) and "permutational" methods
387 (Klyosov 2009a). In this paper, only "linear" method is
388 employed. In this method, a total number of mutations in a
389 set of haplotypes is counted, an average number of muta-
390 tions per marker is calculated, a correction for back
391 mutations is introduced, either numerically or using a
392 handy table (Klyosov 2008c, 2009a), and a time span to a
393 common ancestor is calculated, either using the table
394 (Klyosov 2008c, 2009a) or applying the respective muta-
395 tion rates. In other words, it is described by the following
396 equation:

$$n/N/\mu = t$$

398 where n is a number of mutations in all N haplotypes in the
399 given series of haplotype, μ is an average mutation rate per
400 haplotype per generation, and t is a number of generations
401 to a common ancestor, corrected for back mutations.

402 Average mutation rates employed in this paper are as
403 follows:

404 For 22-marker haplotypes: 0.047 mutations per haplo-
405 type, 0.00214 mutations per marker; this value was
406 obtained by summing up all 22 mutations rates for each
407 marker, according to Chandler (2006).
408 For 17-marker haplotypes: 0.032 mutations per haplo-
409 type, 0.00188 mutations per marker; this value was
410 obtained by summing up all 17 mutation rates for each
411 marker, according to Chandler (2006).
412 For 12-marker haplotypes: 0.022 mutations per haplo-
413 type, 0.00183 mutations per marker; this value was
414 obtained by summing up all 12 mutation rates for each
415 marker, according to Chandler (2006).
416 For 9-marker haplotypes: 0.018 mutations per haplotype,
417 0.00200 mutations per marker; this value was obtained
418 by summing up all 9 mutation rates for each marker,
419 according to Chandler (2006).

420 Error margin for time spans to common ancestors is
421 calculated as described in Klyosov (2009a) and corre-
422 sponds to the 95% confidence interval.
423 Corrections for back (reverse) mutations can be done
424 either numerically (Klyosov 2009a) or using the conversion
425 table (Klyosov 2008c, 2009a).
426

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