



Testing for Divergent Transmission Histories among Cultural Characters: a Study Using Bayesian Phylogenetic Methods and Iranian Tribal Textile Data

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1 Title:

2 Testing for divergent transmission histories among cultural characters: a study using

3 Bayesian phylogenetic methods and Iranian tribal textile data

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Abstract

31 **Background:** Archaeologists and anthropologists have long recognized that different
32 cultural complexes may have distinct descent histories, but they have lacked analytical
33 techniques capable of easily identifying such incongruence. Here, we show how Bayesian
34 phylogenetic analysis can be used to identify incongruent cultural histories. We employ
35 the approach to investigate Iranian tribal textile traditions.

36

37 **Methods:** We used Bayes factor comparisons in a phylogenetic framework to test two
38 models of cultural evolution: the hierarchically integrated system hypothesis and the
39 multiple coherent units hypothesis. In the hierarchically integrated system hypothesis, a
40 core tradition of characters evolves through descent with modification and characters
41 peripheral to the core are exchanged among contemporaneous populations. In the
42 multiple coherent units hypothesis, a core tradition does not exist. Rather, there are
43 several cultural units consisting of sets of characters that have different histories of
44 descent.

45

46 **Results:** For the Iranian textiles, the Bayesian phylogenetic analyses supported the
47 multiple coherent units hypothesis over the hierarchically integrated system hypothesis.
48 Our analyses suggest that pile-weave designs represent a distinct cultural unit that has a
49 different phylogenetic history compared to other textile characters.

50

51 **Conclusions:** The results from the Iranian textiles are consistent with the available
52 ethnographic evidence, which suggests that the commercial rug market has influenced
53 pile-rug designs but not the techniques or designs incorporated in the other textiles
54 produced by the tribes. We anticipate that Bayesian phylogenetic tests for inferring
55 cultural units will be of great value for researchers interested in studying the evolution of
56 cultural traits including language, behavior, and material culture.

57

58 **Keywords:** Cultural transmission, phylogeny, MrBayes, Bayesian phylogenetics, textiles,
59 Iran

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69 **Introduction**

70

71 Understanding how cultural phenomena change through time to produce the variation in
72 artifacts, behaviors and institutions seen in the ethnographic and archaeological records is
73 a major challenge. Evolutionary theory and methods have reinvigorated the study of
74 cultural variation by allowing anthropologists and archaeologists to infer the nature of
75 past cultural processes with greater rigor. To this end, the phylogenetic analysis of culture
76 has emerged as a major research approach [1-5]. Recent studies have used phylogenetic
77 methods to investigate, for example, the transmission of basketry traditions among
78 Californian Native Americans [6,7], the spread of prehistoric peoples and technologies
79 [8-11], patterns of descent in cultural behaviors among East African societies [12], and
80 the borrowing of linguistic elements in Oceanic [13] and Indo-European languages [14].
81 Additionally, by modeling historical relationships, phylogenies provide the scaffolding
82 on which to investigate cross-cultural questions involving ancestral states [15,16], rates
83 of evolution [17], correlated evolution [18], and the occurrence of horizontal transmission
84 [19].

85 Cultural phenomena can, in principle, diversify through several processes, but to
86 date researchers have focused on two main macro level processes: ‘phylogenesis’ and
87 ‘ethnogenesis’. In phylogenesis, diversification takes place through descent with
88 modification from an ancestral social group, whereas in ethnogenesis it occurs by
89 borrowing and blending of traits among contemporaneous groups [4,20,21]. To assess the
90 relative importance of phylogenesis versus ethnogenesis, researchers have employed
91 measures of ‘tree-likeness,’ which quantify the degree to which a set of traits are

92 consistent with a branching-tree model [4]. These measures include the permutation tail
93 probability test (PTP [22-24]), the phylogenetic bootstrap [25], the consistency and
94 retention indices [26-29], and the network-derived delta index [30,31]. Simulation studies
95 have shown that standard support measures can be used to infer phylogenesis when these
96 measures are high [32-34]. However, these studies have also revealed that such measures
97 are unable to distinguish between ethnogenesis and multiple independent inventions of
98 similar characteristics. Thus, low measures of phylogenetic support are largely
99 uninformative, because they can be due to groups borrowing from each other, or
100 convergent evolutionary change, or a combination of the two [33].

101 More generally, it has become desirable to explore methods that can explicitly
102 investigate the processes that produce non-tree-like patterns in cultural data. Contrary to
103 what many archaeologists and anthropologists have assumed [35-38], horizontal
104 transmission is not a uniquely cultural phenomenon: it is known to occur in many genetic
105 systems [39-42]. An example of how components of an evolving system may become
106 unlinked through time is described in Figure 1. In this case, horizontal transmission
107 produces incongruent gene histories when the males of one species breed with the
108 females of a closely related species (i.e., asymmetric hybridization) [43]. Indeed, descent
109 is strictly tree-like only for a minority of life on Earth, mainly involving sexually
110 reproducing organisms that are separated by substantial amounts of evolutionary time.
111 Biologists have developed approaches to infer horizontal gene transfer, including
112 network techniques, tests for the appropriateness of a tree model, and methods to detect
113 gene-tree incongruence [5, 42,44]. Thus, the horizontal transfer of cultural ideas and
114 practices is not necessarily an intractable problem for cultural phylogenetics [45].

115 In this paper, we use Bayesian methods of phylogenetic reconstruction to address
116 two models of cultural evolution that have been widely discussed in the literature [5, 46-
117 48]. These models – the ‘hierarchically integrated system’ model and the ‘many coherent
118 units’ model [46] – draw from the concepts of ethnogenesis and phylogenesis in
119 populations. Rather than considering the histories of individual traits, however, the
120 models are concerned with understanding the transmission dynamics of sets of traits.
121 Compared to studies that treat traits as independent, these models have received less
122 empirical scrutiny.

123 The hierarchically integrated system model proposes that cultural assemblages are
124 composed of two types of characters: those belonging to a core tradition that evolves
125 through phylogenesis, and peripheral characters that are commonly exchanged among
126 groups and can be gained or lost with relative ease. Bayesian phylogenetic analysis is a
127 useful way to investigate this model because it allows researchers to classify characters
128 into separate partitions (e.g. ‘core traits’ and ‘peripheral traits’) and then to test if
129 allowing rates of change to vary between partitions provides a better model for the
130 evolution of the data than assuming equal rates of change. Because peripheral characters
131 change through horizontal transfers between extant groups as well as through cultural
132 innovation, they are expected to exhibit different rates of change from core characters
133 that evolve by innovation alone.

134 The many coherent units model proposes that cultural assemblages consist of
135 multiple groups of characters that have different transmission histories. These groups are
136 analogous to sections of a chromosome that are sufficiently close that they tend to
137 transfer together during sexual reproduction, rather than being broken up by genetic

138 recombination. In the cultural case, correlated transmission may arise because the traits
139 are functionally or symbolically interrelated (e.g. the rituals, texts and institutions of a
140 religion), or because they are repeatedly borrowed from the same source (e.g. French
141 words in the English language). This model is testable in a Bayesian framework because,
142 unlike in a parsimony analysis, different trees can be incorporated into the analysis as
143 independent parameters [49,50].

144 We tested predictions from these two models using data derived from Iranian
145 tribal textiles that were collected by Tehrani and Collard [21] (Figure 2). Tehrani and
146 Collard’s [21] ethnographic research showed that the majority of techniques and designs
147 used by weavers were acquired ‘vertically’ in two contexts: on an individual level from
148 their mothers, and at a community level from ancestral populations. Weavers have few
149 opportunities to learn traits from members of other tribes due to endogamous marriage
150 practices and social norms that restrict the ability of women to travel far from their camp
151 or village. However, Tehrani and Collard [21] noted that one class of traits was more
152 likely to circulate among groups. These traits comprise the designs that are woven into
153 pile carpets (‘pile-weave designs’), which are often copied from cartoons provided by
154 urban rug merchants and/or learned through temporary employment in commercial
155 workshops.

156 We used the textile data to test the two hypotheses described above. In terms of
157 the hierarchically integrated system hypothesis, weaving techniques and ‘flat-weave
158 designs’ represent a plausible core tradition, since they are relatively isolated from
159 outside influences. Pile-weave designs, on the other hand, might be expected to comprise
160 peripheral elements that are adopted and discarded according to market demands. We

161 therefore predicted different rates of evolution for pile-weave design characters, as they
162 would be more affected by horizontal transfer. Empirical [4] and simulation [33] studies
163 have shown that independent ethnogenetic transfers can increase estimated evolutionary
164 rates if they produce patterns consistent with homoplasy (character state similarity not
165 due to vertical descent). However, horizontal transfers can also decrease the evolutionary
166 rates inferred from comparative data, for example when the ancestral state transfers to a
167 lineage with a derived character state (i.e., homoplasy is potentially obscured). This effect
168 has been demonstrated in some simulation studies, where systematic transfer among
169 historically related societies has tended to erase independent changes that would have
170 been reconstructed in the absence of horizontal transmission, thereby biasing estimates of
171 evolutionary rates downward for traits with greater horizontal transfer [32].

172 To explore the effects of horizontal transfer on inferred evolutionary rates in the
173 present context, we simulated character evolution and transfer on the most parsimonious
174 tree obtained by Tehrani and Collard [21]. We compared the inferred evolutionary rates
175 of the simulated characters with and without horizontal transfers to assess whether the
176 transfers increased or decreased the rates. We then used the simulation results to develop
177 a directional prediction regarding the effect of horizontal transfers on evolutionary rates
178 within the hierarchically integrated system hypothesis.

179 Alternatively, the textile data might fit the many coherent units hypothesis.
180 Market trade could have caused the pile-weave design characters to become a coherent
181 cultural component with a transmission history that differs from the other textile
182 characters. Unlike the hierarchically integrated system model, the many coherent units
183 hypothesis does not predict that pile-weave design characters have different rates of

184 evolution than other kinds of characters. Rather, the many coherent units hypothesis
185 predicts that the pile-weave design characters produce a tree topology that differs from
186 the tree topology yielded by the other textile characters.

187

188 **Materials and methods**

189

190 *2.1 Data*

191 The data for this study are textile design and construction characteristics recorded by JJT
192 from museum collections and during 6 months of ethnographic fieldwork in Iran between
193 May 2001 and June 2003 (see [21] for a breakdown of sources). A total of 122 characters
194 were derived from the textile sample (Supporting Table 1 online). They included 42
195 techniques of preparation and fabrication (e.g. spinning and knotting techniques), 56 flat-
196 weave designs and 24 pile-weave designs (for examples see Figure 2). The characters
197 were coded as presence/absence in a binary matrix that reflects the presence of characters
198 used by a particular tribe in any of their textiles. That is, for a character to be coded as
199 present for a tribe, the tribe was observed to use the character in at least some of its
200 textiles. Characters coded as absent for a tribe were not observed in any of the tribe's
201 textiles.

202 Following Tehrani and Collard [21] we used an archaeological textile
203 assemblage—the Pazryk collection—as an outgroup to infer the likely ancestral states of
204 the textile characters in our analyses. The Pazryk collection was recovered from ice-filled
205 tombs of a nomadic population that inhabited the Altai Mountains of Siberia 2400-2300
206 years ago [51]. The age and quality of preservation of these textiles provide the best

207 available information on the historical roots of weaving among Central and Western
208 Asian nomadic pastoralists [52].

209

210 *2.2 Simulation of horizontal transfers within a hierarchically integrated system*

211 The hierarchically integrated system hypothesis predicts that rates of evolution should
212 differ for the pile-weave design characters versus the technique and flat-weave design
213 characters. To establish whether the rates for the pile-weave design characters would be
214 expected to be higher or lower than the non-pile characters we carried out a set of
215 character simulations.

216 We simulated traits on a Grafen transformation [53] of the parsimony tree
217 topology (no branch lengths) inferred previously from the same data set [21]. The
218 simulation process required branch lengths that are roughly proportional to time, which
219 means using an ultrametric tree in our case because all the tribes exist in the present day.
220 The Grafen transformation is a standard way to generate an ultrametric tree in the
221 absence of good temporal information. It sets the age of each node equal to one less than
222 the number of descendant taxa (Figure 3). We did not use the branch lengths from our
223 Bayesian analysis (described below) because this would have introduced circularity into
224 the simulations.

225 We simulated the evolution of 100 characters, each with an instantaneous
226 transition rate of 0.123. This transition rate was the median transition rate of the empirical
227 dataset when optimized via maximum likelihood on the Grafen transformed tree. For
228 these calculations, we used functions `fitDiscrete` and `simchar` in the R package ‘`geiger`’
229 [54]). We did not allow for any horizontal exchange of these 100 characters, making

230 them analogous to our hypothesized evolutionary process for the non-pile-weave design
231 characters.

232 Under the hierarchically integrated system hypothesis, pile-weave design
233 characters are peripheral elements that should exhibit a different rate of evolution from
234 the non-pile-weave design characters that belong to the core tradition. To create
235 comparable simulated pile-weave design character sets, we generated 100 sets of 30
236 characters under three horizontal transfer processes. Under the local borrowing condition,
237 each tribe had a 30% chance of adopting the character state of one of its sister tribes on
238 the tree. Sister tribes were those separated by only one internal node. We also conducted
239 an anti-local borrowing condition in which each tribe had a 30% chance of adopting the
240 character state of any tribe separated by two internal nodes. Under anti-local borrowing,
241 sister tribes never borrowed character states directly from one another. Lastly, we
242 simulated a global borrowing condition in which each tribe had a 30% chance of adopting
243 a character state from any of the other tribes on the tree. All transfers occurred among the
244 terminal taxa after vertical evolution along the tree topology. This simulation process is
245 similar to that of Greenhill et al. [32].

246 We eliminated characters that were invariant, because such characters are not
247 typically included in cultural and morphological data sets for phylogenetic analysis. After
248 eliminating the invariant characters, we were left with simulated datasets of 25 to 30
249 characters to compare with the 100 characters that experienced no horizontal transfer,
250 which is comparable to our empirical dataset of 24 pile-weave design characters and 98
251 non-pile-weave design characters. We then used the same maximum likelihood estimator
252 (function `fitDiscrete` in 'geiger' [54]) to infer the rates of evolution of the characters,

253 which was repeated for each of the three types of horizontal transfer. We assessed the
254 effect of each form of horizontal transfer on the median rate of evolution by comparing
255 the simulated sets of pile-weave design characters to the 100 simulated non-pile-weave
256 design characters that did not experience any horizontal transfer.

257

258 *2.3 Bayesian phylogenetic inference*

259 Bayesian phylogenetic inference proceeds by assessing consecutive ‘proposals’ of
260 combinations of a dataset and a model of evolution. The model consists of a number of
261 parameters, the most basic being: a tree topology, a set of branch lengths and an
262 evolutionary model for character change. The latter is modeled as the probability of
263 instantaneous change between character states, e.g. from 0 to 1 and 1 to 0. Branch lengths
264 are proportional to the amount of evolutionary change occurring along them. A likelihood
265 score for each character is then calculated, based on the changes that must take place in
266 order to observe the distribution of that character’s states on the proposed topology and
267 branch lengths.

268 After calculating the likelihood of each character given a particular model
269 proposal, the likelihoods for all characters are combined to obtain the likelihood score for
270 a single proposal of a tree and parameter values. The parameters and likelihood score are
271 recorded, and the process is repeated in the next iteration. The iterations take place
272 through a Markov Chain Monte-Carlo (MCMC) process. The MCMC then explores the
273 likelihood landscape by adopting new parameter values in a search that favors parameters
274 that give a higher likelihood. This distribution of trees samples the topologies and branch
275 lengths such that phylogenies with higher support are sampled to a greater extent. The

276 investigator can summarize this posterior distribution by producing a consensus tree of
277 the highest-frequency clades and mean branch lengths in the sample, with nodes
278 annotated with their clade credibility value (i.e., the probability that the node appears in
279 the posterior sample).

280

281 *2.4 Initial model exploration*

282 We used MrBayes b3.1.2 [55,56] to infer phylogenetic trees. During model selection, we
283 used the harmonic mean of the MCMC chain to determine the model with the highest
284 marginal likelihood [50]. We assessed harmonic means after an empirically determined
285 burn-in period. For subsequent analyses, we termed the model best supported by the data
286 the ‘base model’.

287 We modeled the transition rates in each textile character between 0 (absent) and 1
288 (present). Our first parameter characterized whether rates of gain (0 to 1) and loss (1 to 0)
289 were equal, which enabled us to test whether our data were best described by symmetric
290 or asymmetric transition rates. Our second parameter characterized the amount of rate
291 variation across all characters—that is, whether some textile characters evolved faster
292 than others, or if rates were similar across the set of characters. Although our data
293 consisted of presence-absence codes, we tested for rate asymmetry by coding the data as
294 ‘standard’ rather than as binary. We did this because binary data are interpreted by
295 MrBayes as analogous to genetic ‘restriction sites.’ The restriction site model in MrBayes
296 is a direct application of a model for rate asymmetry in DNA data. Known as the F81
297 model, this model uses character state frequency to derive one invariant rate asymmetry
298 for all characters. This assumed invariance of rate asymmetry across characters is

299 unrealistic for anatomical characters because, unlike DNA, no single underlying
300 mechanism causes the asymmetry [57]. Similarly, we had little reason to think a single
301 mechanism produces transition asymmetry for design motifs, weaving techniques, or
302 even that the asymmetry for different design motifs should be invariant. Lewis [57]
303 suggested solving the analogous problem for anatomical data by drawing rate
304 asymmetries from a Beta distribution. This invokes the same number of new parameters
305 as the F81 model, but allows for variance in asymmetry across sites. We considered this
306 model to be more realistic for our data, and we implemented it as the symmetric Dirichlet
307 hyperprior for ‘standard’ data in MrBayes.

308 We used a ‘gamma parameter’ to test for variation in evolutionary rate across
309 sites. This parameter does not adjust the rate asymmetry for sites. Rather, it adjusts all
310 rates for a site by a multiplier that allows for rate heterogeneity. We used a standard
311 setting that approximates (for computational efficiency) the gamma parameter value by
312 fitting four discrete rate categories. Like anatomical data sets used in phylogenetic
313 studies, cultural data sets exhibit a bias in the types of characters coded. Specifically,
314 characters are only included in a dataset if they have been observed in at least one taxon
315 in the sample. This corresponds to the MrBayes code ‘noabsencesites’, in which no single
316 character can have an absent state for all taxa. MrBayes modifies its likelihood equation
317 to account for this bias.

318 These model parameters were not simply imposed on the analysis, but were tested
319 statistically with a likelihood score to assess whether the additional parameters are
320 justifiable on statistical grounds. Bayesian analyses do not always favor more
321 complicated models, because simpler models can actually achieve higher marginal

322 likelihoods [58]. Under an initial assumption that treats all models as equally probable
323 ('flat priors'), our posterior belief in one model over the other model is reflected by
324 differences in the harmonic mean likelihoods generated by each model [50].

325 To search the parameter space efficiently, we used multiple MCMC chains per
326 run. We ran three 'hot chains' that proposed large parameter changes in order to explore
327 parameter space more expansively. A single 'cold' sampling chain periodically adopted
328 the hot chain states and continuously recorded the states of the chain. Large sampling
329 intervals are usually required to reduce autocorrelation between states in the chain, but
330 here the small number of taxa allowed us to sample trees (i.e. record the parameter values
331 and tree topology) every 100 generations. We conducted six such MCMC runs of
332 100,000-iterations for each analysis.

333 The length of the burn-in period was determined empirically such that results
334 obtained prior to the likelihood reaching stationarity were discarded. We took the final
335 900 trees of the post-burn-in from each of six chains to compile the posterior distribution
336 of 5400 trees per analysis. From this distribution, we constructed a consensus
337 phylogenetic tree and assessed how it compared to the bootstrapped parsimony tree
338 inferred by Tehrani and Collard [21].

339

340 *2.5 Hypothesis testing*

341 *2.5.1 The hierarchically integrated system model*

342 After determining through simulation whether horizontal transfers would increase
343 or decrease evolutionary rates, we tested the appropriate prediction through two analyses.
344 First, we modified the base model by partitioning the data set into the pile-weave and

345 non-pile-weave design characters. We then unlinked the rate parameter for each partition
346 and re-ran the MCMC analyses. Unlinking a parameter across partitions allows it to take
347 on different values for each partition, while constraining the other parameters to be the
348 same across all characters. We assessed the support for the partitioned model relative to
349 the base model with a Bayes factor comparison based on the harmonic means of the
350 model likelihoods. The harmonic mean is a standard approximation of the marginal
351 likelihood, the latter being required for Bayes factor analysis [59]. Unlike the frequentist
352 approach, which rejects a null hypothesis, Bayes factors represent a summary of the odds
353 for one model over another. Based on Kass and Raftery's [58] logarithmic scale for
354 interpretation, Bayes factor values between 0 and 2 are barely worth mentioning, values
355 between 2 and 5 represent positive evidence, values between 5 and 10 are strong
356 evidence, and values greater than 10 constitute very strong evidence.

357 Second, we tested for a difference in rates by examining the results for our
358 gamma model for character evolution (see above). The gamma model allows characters
359 to have different rates of evolution, and the posterior sample of these rates produces a
360 unique rate for each character. We used our simulations to justify our prediction of higher
361 or lower rates for the characters with more horizontal transfer. We then compared the
362 inferred rates of the pile-weave design characters (hypothesized to have more horizontal
363 transfer) to the rates of the non-pile-weave design characters (hypothesized to have less
364 horizontal transfer) with a Mann-Whitney U test.

365

366 *2.5.2 The many coherent units model*

367 The second hypothesis predicts that a partitioned Bayesian analysis should support
368 different phylogenies for pile-weave design characters as compared to the non-pile-weave
369 design characters that include both flat-weave designs and weaving techniques. To test
370 this, we allowed different classes of traits to produce different evolutionary histories, that
371 is, we unlinked the topologies across partitions of the data. This method of unlinking
372 topologies for *a priori* partitions has precedence in genetic studies that have investigated
373 topological incongruence due to different descent histories of different genes [49,50,60-
374 63]. For example, Suchard et al. [49] unlinked topology between partitions and used
375 Bayes factors to estimate model support in order to infer the horizontal transmission of
376 viral types among HIV patients. As Gray et al. [5] have suggested, this approach should
377 also be appropriate for studying cultural traits that are potentially learned and transmitted
378 in different ways.

379 By unlinking tree topology during Bayesian tree inference, each partition was
380 allowed to have an independent tree. MrBayes recorded the trees for both partitions
381 during each sampled generation. We calculated the marginal likelihoods of the post-burn-
382 in posterior distribution for each partition and used Mesquite [64] to generate the two
383 consensus trees. If patterns of descent in pile-woven designs differ from other textile
384 traits, we predict positive Bayes factor support for the topologically partitioned model, as
385 compared to the base model.

386 The primary empirical and simulation support for this statistical test comes from
387 Galtier and Daubin [63], who showed that a maximum likelihood (ML) difference metric
388 that is similar to the Bayes factor exhibited more evidence for multiple gene trees in
389 bacteria than in metazoa. This result was consistent with theoretical predictions given the

390 facility with which some bacteria share particular genes across species lineages. Galtier
391 and Daubin [63] also obtained consistently high ML differences for simulated gene
392 evolution on completely unlinked gene-trees. Thus, both their empirical and simulation
393 results indicate that the ML difference reliably detected topological incongruence.

394

395 **Results**

396

397 *3.1 Initial model exploration*

398 A simple model with a symmetric rate and no cross-site rate variation yielded the best
399 posterior probability as reflected by the harmonic mean likelihoods across the MCMC
400 chains (Table 1). Support for the simple model was positive when compared with a
401 model that added the gamma parameter. A model without any rate asymmetry was
402 preferred over all other models, each Bayes factor for comparison comprising ‘very
403 strong evidence’ under Kass and Raftery’s [58] categories. Model fit was worsened by
404 the inclusion of either rate asymmetry or a gamma parameter (Tables 1 and 2). We
405 therefore used the simple model with a symmetric rate of character change and without
406 gamma as the base model. Using the base model and with the complete data set, our final
407 posterior distribution comprised a sample of 5400 trees. This set of trees produced a
408 highly resolved consensus topology (Figure 4a).

409

410 *3.2 Hypothesis testing*

411 *3.2.1 Hierarchically integrated system model*

412 The simulation experiments indicated that horizontal transfers increased inferred
413 evolutionary rates on the Grafen transformed tree topology (Figure 3). The characters
414 were all generated with a rate of 0.123 changes per unit branch length. The median
415 inferred rate for the 100 characters simulated without any horizontal transfer was 0.19,
416 but the mean was a highly divergent 7.04. The distribution of inferred rates is highly non-
417 normal (Figure 5), so the median is the preferred measure of central tendency in this case.

418 We simulated 100 sets of 30 characters that all experienced local independent
419 horizontal transfers (transfers among sister taxa). Of these simulations, 97% exhibited
420 higher median rates of evolution than in the characters without horizontal transfer. We
421 also conducted 100 simulations of 30 characters each that experienced anti-local transfers
422 among taxa separated by 2 internal nodes on the phylogeny. Under this condition, 98% of
423 simulations exhibited greater median rates than did the characters without horizontal
424 transfers. Lastly, we simulated 100 sets of 30 characters each that experienced global
425 transfers that were equally probable among any of the taxa. Under global transfers, 94%
426 of the simulations exhibited greater median rates than the median rate for characters
427 without horizontal transfers.

428 Given the simulation results, we predicted that pile-weave design characters
429 would exhibit higher median evolutionary rates than the other textile characters if they
430 had experienced more independent horizontal transfers as peripheral elements of a
431 hierarchically integrated system. This prediction was not supported by the model with
432 partitioned transition rates for pile-weave and non-pile-weave design characters.
433 Allowing different rates for each character partition slightly worsened the harmonic mean

434 likelihood compared to the base model (-510.13 versus -509.36, Bayes factor = 1.48 in
435 favor of the base model).

436 Furthermore, the analyses revealed no support for the gamma model, which
437 allows for rate variation over the base model without gamma (Table 2). Within this
438 gamma model, however, we found significant support for a small difference in the
439 median rate of character evolution (Mann-Whitney U test, $p = 0.03$, median rate of
440 change per unit branch length for non-pile-weave design characters = 0.997, median rate
441 change per unit branch length for pile-weave design characters = 1.000).

442

443 *3.2.2 Many coherent units model*

444 Unlinking the tree topology for the pile-weave and non-pile-weave design characters
445 produced a substantially improved likelihood and positive Bayes factor support (10.44 in
446 favor of different topologies, ‘very strong evidence’). The consensus tree from the non-
447 pile-weave design characters had the same topology as the consensus tree inferred from
448 the complete data set, and clade credibility values were all equal to or greater than 0.85
449 (Figure 4a). The pile-weave design characters produced a less resolved topology for some
450 nodes, but for one node they supported a different topology than the non-pile-weave
451 design characters (Figure 4b). This node puts the Papi in a basal position relative to the
452 Boyer Ahmad, Bakhtiari, and Qashqa’i. The latter three tribes are linked in a
453 monophyletic clade with credibility support of 0.89. We also found positive Bayes factor
454 support for this node by comparing the inferred topology shown in Figure 4b to a
455 topology that constrained the Papi as sister to the Bakhtiari for the tree of pile-weave
456 design characters (5.88 in favor of the inferred topology). These findings suggest that the

457 pile-weave design characters have a different descent history compared to the non-pile-
458 weave design characters. This difference can be seen in Figure 4 and is consistent with
459 the hypothesis that these traits comprise a cultural component that was borrowed by some
460 or all of these groups from a non-ancestral source.

461

462 **Discussion**

463 Using Bayesian phylogenetic approaches, we inferred independent evolutionary histories
464 for two sets of Iranian textile characters, enabling us to test models about the underlying
465 processes of culture change. The simple base model inferred a robustly supported
466 consensus tree that matched the consensus bootstrap parsimony tree obtained previously
467 from these data [21]. We also obtained the same tree, with similar clade credibility
468 values, from less favored, more complex models (unpublished results).

469 The analyses provided very limited support for the idea that a history of
470 commercial trade produced a different rate of inter-tribe transmission of individual pile-
471 weave design characters. Based on our simulations, such a process should have resulted
472 in a greater median transition rate for pile-weave design characters in the gamma model.
473 While we found significant support for the predicted increased rate, the amount of rate
474 increase was minimal (an increase of 0.003 changes per unit branch length compared to
475 the overall rate). The small magnitude of increase is probably why Bayes factors did not
476 support either the partitioned model or the gamma model, both of which allowed for rate
477 variation. Because the magnitude is small, it is of little consequence to the likelihood of
478 the data. Horizontal transfers may occur more frequently in the pile-weave design

479 characters, but the increased rate is extremely small and has little impact on the
480 distribution of character states among the tribes.

481 We note that it is also conceivable that horizontal transfers would increase the
482 variance of inferred evolutionary rates without affecting their central tendency. This
483 effect was difficult to assess with our particular simulations given the boundary
484 conditions of the maximum likelihood estimation procedure. The empirical data,
485 however, showed no support for different variances of the pile-weave design and other
486 textile characters (F-test, ratio of variances = 1.04, $p = 0.96$, numerator $df = 97$,
487 denominator $df = 23$; nonparametric Fligner-Killeen test, median $\chi^2 = 0.15$, $p = 0.70$, $df =$
488 1). These findings are consistent with Tehrani and Collard's [21] cladistic analyses of the
489 textile traits, which found no significant differences in the retention indices of pile and
490 non-pile characters. We can therefore conclude that there is little evidence to suggest that
491 Iranian tribal weaving traditions evolve in line with the "hierarchically integrated system"
492 model.

493 In contrast, the results of the analyses are strongly consistent with the multiple
494 coherent units model. This model proposes that pile-weave design characters transfer as a
495 group and do so separately from the other characters—a process that produces separate
496 transmission histories. Consistent with the coherent units model, we found positive
497 support for different topologies for non-pile-weave design and pile-weave design
498 characters. The clade credibility values for these trees are reduced (Figure 4), but this is
499 understandable given the concomitant reduction in the number of characters used to infer
500 each tree. A single clear topological disagreement is manifest in the comparison of the

501 non-pile-weave and pile-weave trees: that being the position of the Papi textiles relative
502 to the Boyer Ahmad, Bakhtiari, and Qashqa'i.

503 A caveat about the Bayes factor test for multiple tree topologies exists on
504 mathematical grounds [50,61]. When the model for character evolution on a single tree is
505 overly simple compared to the actual process of character evolution, the Bayes factor test
506 for different trees is thought to produce spurious positive results due to model
507 misspecification. Positive results for multiple trees may be suspect when the underlying
508 data are fit best by the most complex character model available, as this might indicate
509 that the character model is insufficiently complex to describe how the characters truly
510 evolved. In our study, however, the simplest model for character evolution was favored in
511 the model exploration for a single tree topology. So, the caveat does not apply.

512 Two potential explanations may account for the topological difference between
513 the best-fit phylogeny for the pile-weave design characters, and the best-fit phylogeny for
514 the other characters. One is that the Boyer Ahmad, Bakhtiari, and Qashqa'i adopted pile-
515 weave design characters from a common external source, leaving the Papi in a basal
516 position. The other is that the Papi adopted pile-weave designs from the Yomut and/or
517 Shahsevan, which would have the effect of shifting the Papi to a more basal position.
518 Given that the Papi currently live hundreds of miles away from the Shahsevan and Yomut
519 (~300km and ~800km, respectively, over deserts and mountainous terrain) and there is no
520 evidence that the Papi were ever neighbors of the Shahsevan or Yomut, the second
521 scenario seems unlikely. In contrast, the first scenario is consistent with ethnographic and
522 historical data. To reiterate, the main media for the introduction of pile designs from
523 foreign sources—workshops and cartoons—are both linked to commercial rug

524 production. Commercial rug production has a long history among the Qashqa’i, Bakhtiari
525 and Boyer Ahmad. For example, pile rugs attributed to the Qashqa’i were being traded in
526 urban and export markets as early as the mid-eighteenth century [52,65]. A distinctive
527 feature of these groups’ commercial weavings is the extent to which they imitate well-
528 known urban and courtly designs. For example, the Bakhtiari ‘kheshti’ (brick) pattern
529 appears to be based on the classical ‘four garden’ design, which was popularized during
530 the Safavid Dynasty (1507 – 1732). Other common imitations of urban designs include
531 the so-called Herati pattern, medallion ornaments and Shirazi prayer rugs [66].

532 We suggest that the topology of the pile-weave design tree reflects the
533 involvement of the Qashqa’i, Boyer Ahmad and Bakhtiari in commercial textile markets,
534 such that they each adopted pile-weave designs from an external source common to all
535 three. This transfer would have facilitated the spread of commercially popular tribal and
536 urban designs. Because women belonging to different tribes would have been competing
537 within a single regional market, they would be expected to adopt the designs that were
538 most popular among consumers. Design popularity and their physical co-occurrence on
539 design cartoons may be the mechanism that produced the package-like transfer of these
540 traits and resulted in the observed topological differences.

541 This explanation is consistent with the exclusion of the Papi from the clade
542 linking the pile designs of the Bakhtiari, Qashqa’i and Boyer Ahmad. The available
543 historical evidence suggests that the Papi began commercial production much later than
544 the other three tribes, compared to whom they were both geographically and politically
545 remote. Lacking a coherent centralized leadership structure, the Papi were much less
546 integrated into the political economy of Iran than the Qashqa’i, Bakhtiari and Boyer

547 Ahmad. The leaders of the latter groups, the ‘khans’, were major players on the national
548 stage, with the power to levy taxes and raise armies. They provided an important cultural
549 and economic link between ordinary tribe members and wider Iranian society. In the case
550 of rug weaving, the khans actively encouraged commercial production as a means of
551 increasing tax revenues, and even set up their own workshops that were managed by their
552 wives [67]. So-called ‘bibibaff’ rugs (‘woven by ladies’) were specifically produced for
553 urban consumers and aristocrats, and are today valuable antiques [68]. The absence of
554 comparable institutions among the Papi might explain why they relied more on their own
555 traditional patterns, rather than borrowing from outside the tribe.

556

557 *Conclusions*

558 Our study highlights a new approach for investigating a fundamental question in cultural
559 transmission and evolution: Do cultural traits exhibit different histories of transmission?
560 If so, can assemblages be characterized as “hierarchically integrated systems” comprising
561 “core” and “peripheral” traits, or as “multiple coherent units”? While both these models
562 have been widely discussed [5,46-48], few techniques have been developed to infer them
563 from comparative ethnographic and archeological data. Our study demonstrates that
564 Bayesian phylogenetic inference provides a statistically rigorous framework to
565 investigate these possibilities.

566 Our analyses of Iranian tribal textile assemblages found that the transmission
567 histories of pile-weave design characters differ from other textile characters. They do not,
568 however, represent a collection of peripheral traits that move freely between the branches
569 of a single “core” phylogeny. Instead, it appears that the textile characters comprise two

570 distinct and phylogenetically coherent packages. Crucially, this kind of analysis cannot
571 be easily carried out with the parsimony methods used in previous studies of material
572 culture evolution [6-10, 21]. This is because, unlike the harmonic mean likelihood,
573 parsimony statistics such as the retention index can only be used in reference to a single
574 topology. Thus, our Bayesian approach advances this field by rendering open to scientific
575 inquiry a hypothesis that was previously untestable with the sort of comparative data used
576 in this study. We anticipate that this approach will be useful for many other types of
577 cultural data, including language, behavior, and material culture.

578

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- 747

748 **TABLES**

749

750 TABLE 1. Harmonic means of log likelihoods (lnL) for different evolutionary models.

model	lnL
symmetric transition rate (S)	-509.36
symmetric transition rate + gamma (SG)	-509.96
asymmetric transition rate (A)	-544.76
asymmetric transition rate + gamma (AG)	-543.03

751

752

753

754 TABLE 2. Bayes factor comparison of evolutionary models described in Table 1.

	S	SG	A
SG	1.20	-	-
A	70.80	69.60	-
AG	67.34	66.14	-3.46

755

756 Note: Bayes factors were calculated as $2 * (\text{column harmonic mean } \ln \text{ likelihood} - \text{row}$
 757 $\text{harmonic mean } \ln \text{ likelihood})$. Positive Bayes factors indicate support for the model in
 758 the columns across the top, negative values for the model in rows to the left. S:
 759 symmetric transition rates without gamma, SG: symmetric transition rates and gamma, A:
 760 asymmetric transition rates without gamma, AG: asymmetric transition rates and gamma.

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771 FIGURE LEGENDS

772

773 Figure 1. Asymmetric hybridization hypothesis developed by Tosi et al. [43] to explain
774 incongruent gene trees in Asian macaque monkeys (genus *Macaca*). Asymmetric
775 hybridization is shown by arrows that indicate when males of one species breed with
776 females of another. The male and female hybrid offspring then breed back with the
777 maternal species only. The Y chromosome is a contiguous DNA fragment inherited
778 solely through the paternal lineage. Because of chance processes or female preference,
779 the admixed Y chromosomes become typical of the descendent species, resulting in the
780 bottom phylogeny for Y chromosomes. Note the shifted positions of *Macaca fascicularis*
781 and *Macaca sinica*. This evolutionary process can take multiple generations and involves
782 multiple transmission events. The physical linkage of Y chromosome DNA is the
783 mechanism that produces the transfer of Y chromosomes as a coherent unit and the
784 resultant gene-tree incongruence. Analogously, any mechanism in cultural transmission
785 that produces a necessary linkage of traits during transmission events could result in
786 similar forms of tree incongruence. (modified from [43])

787

788 Figure 2. Section of a Bakhtiari saddle-bag illustrating examples of the technical and
789 decorative traits used in the analyses

790

791 Figure 3. The Grafen transformation of Tehrani and Collard's [21] parsimony tree of the
792 textile data. Character evolution was simulated along the branches of the tree and
793 independent horizontal transfers of individual characters were simulated at the tips.

794

795 Figure 4. Consensus trees from the Bayesian phylogenetic analysis of Iranian textile
796 characters. Numbers at nodes show clade credibility values, which reflect the proportion
797 of trees in the posterior probability sample that share a given node. Panel A shows the
798 tree inferred from all characters (credibility values outside parentheses) and from non-
799 pile-weave design characters (credibility values inside parentheses) using the base model.
800 Panel B shows the tree inferred from pile-weave design characters using the base model.
801 Note the shifted position of the Papi.

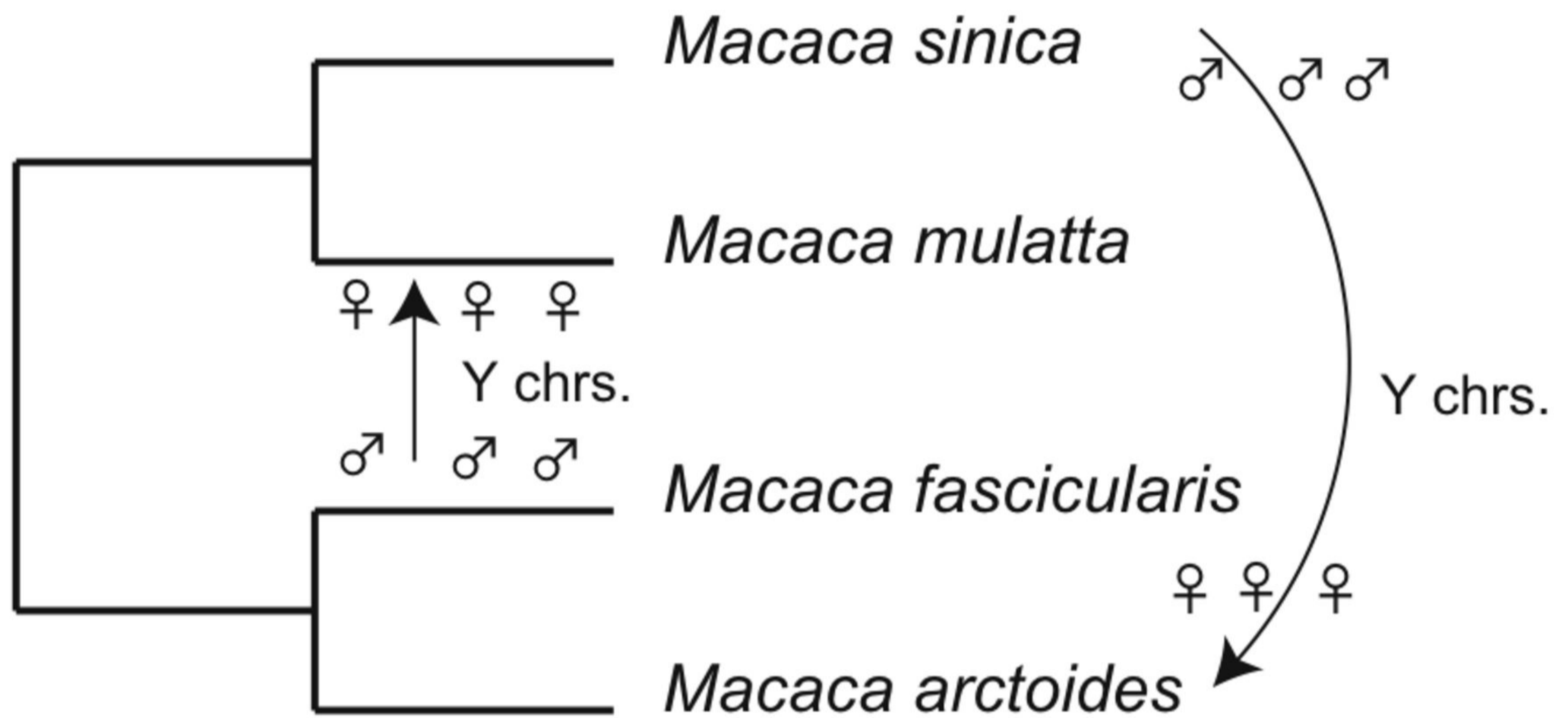
802

803 Figure 5. Histogram of inferred rates of evolution for 100 characters simulated without
804 horizontal transfers. This non-normal distribution also was characteristic of the rates
805 inferred under the horizontal transfer conditions.

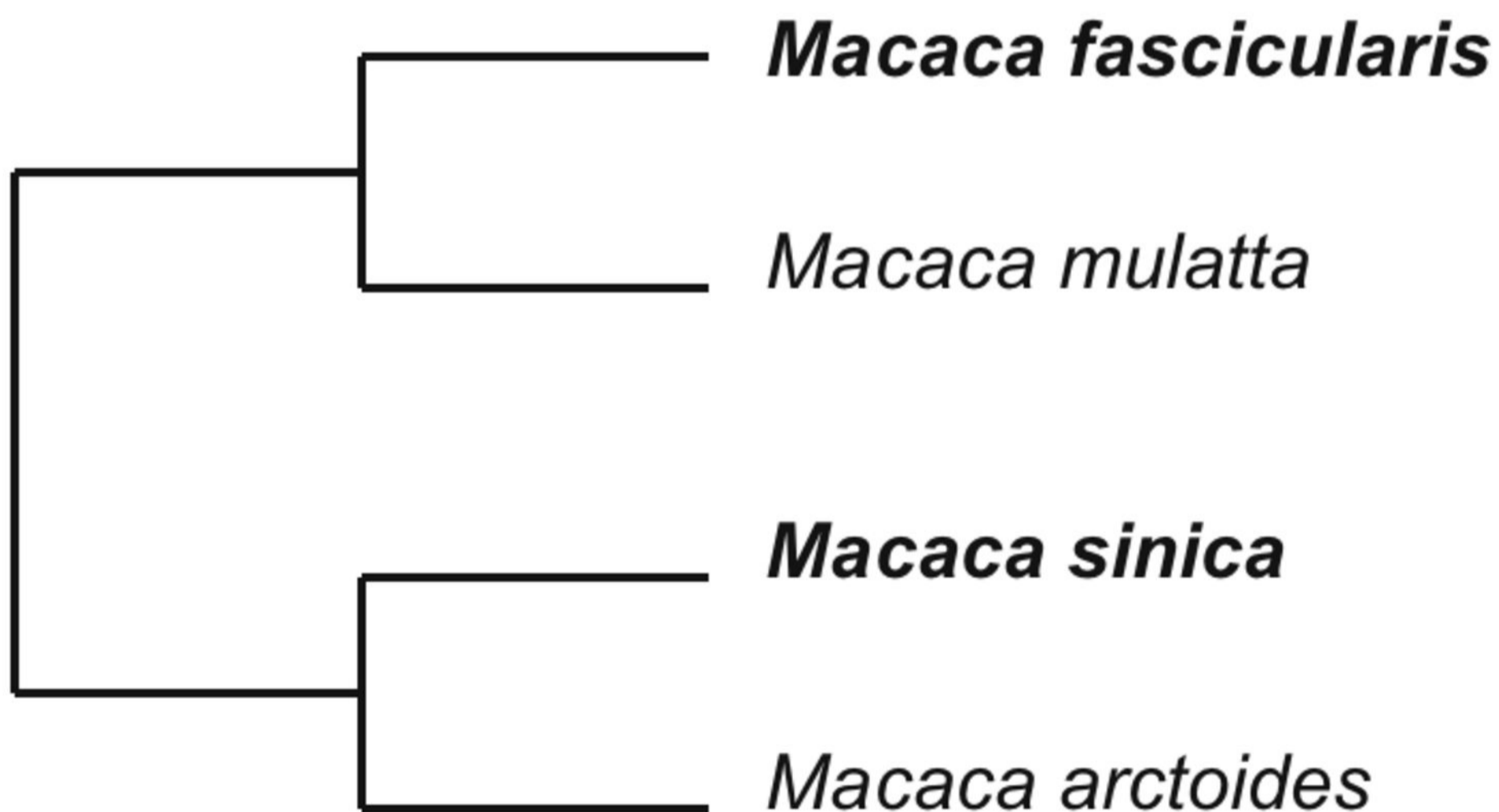
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807

Species history (reflected by majority of genome)



Resultant Y chromosome history





Plain-weave

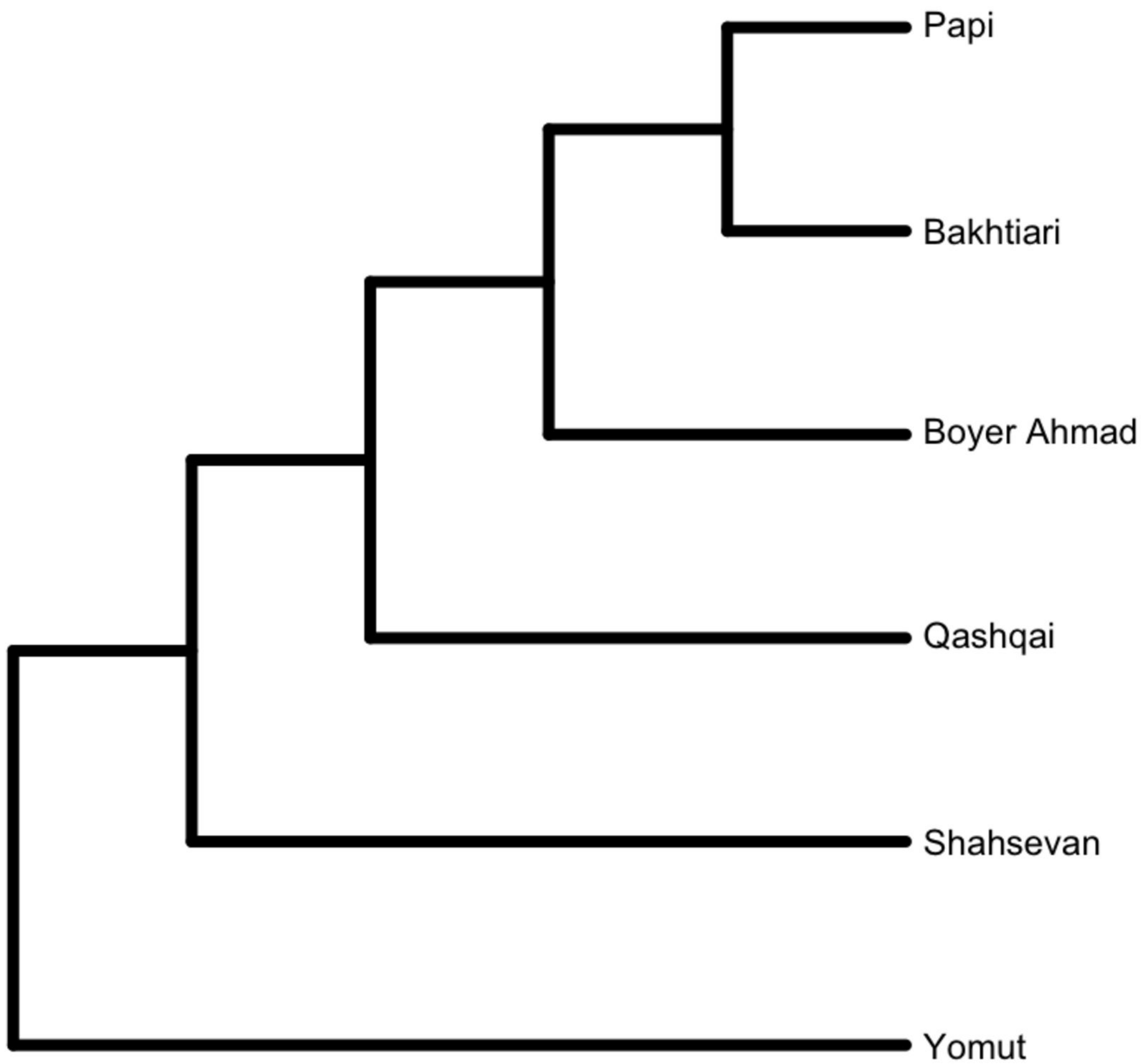
Weft-wrapping

Pile-weave technique

"Infinite knot" motif

"Rooster" motif

"Jagged border"



Papi

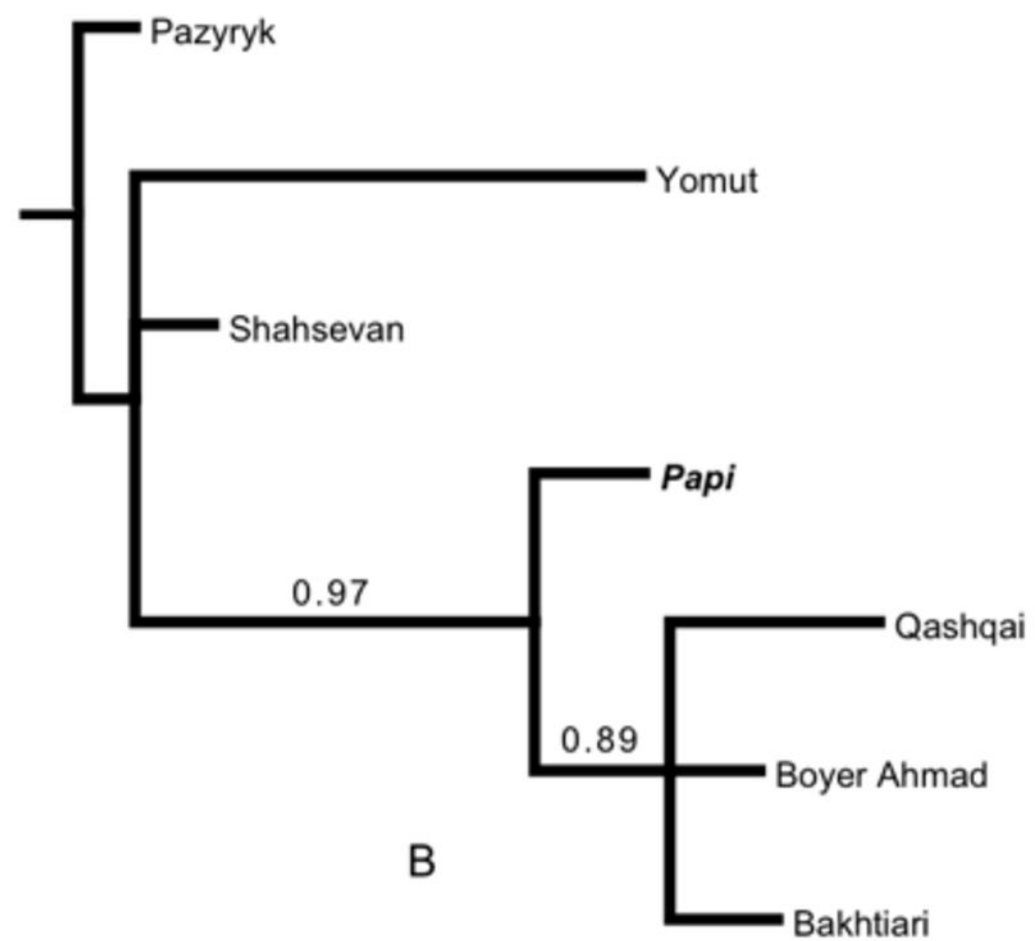
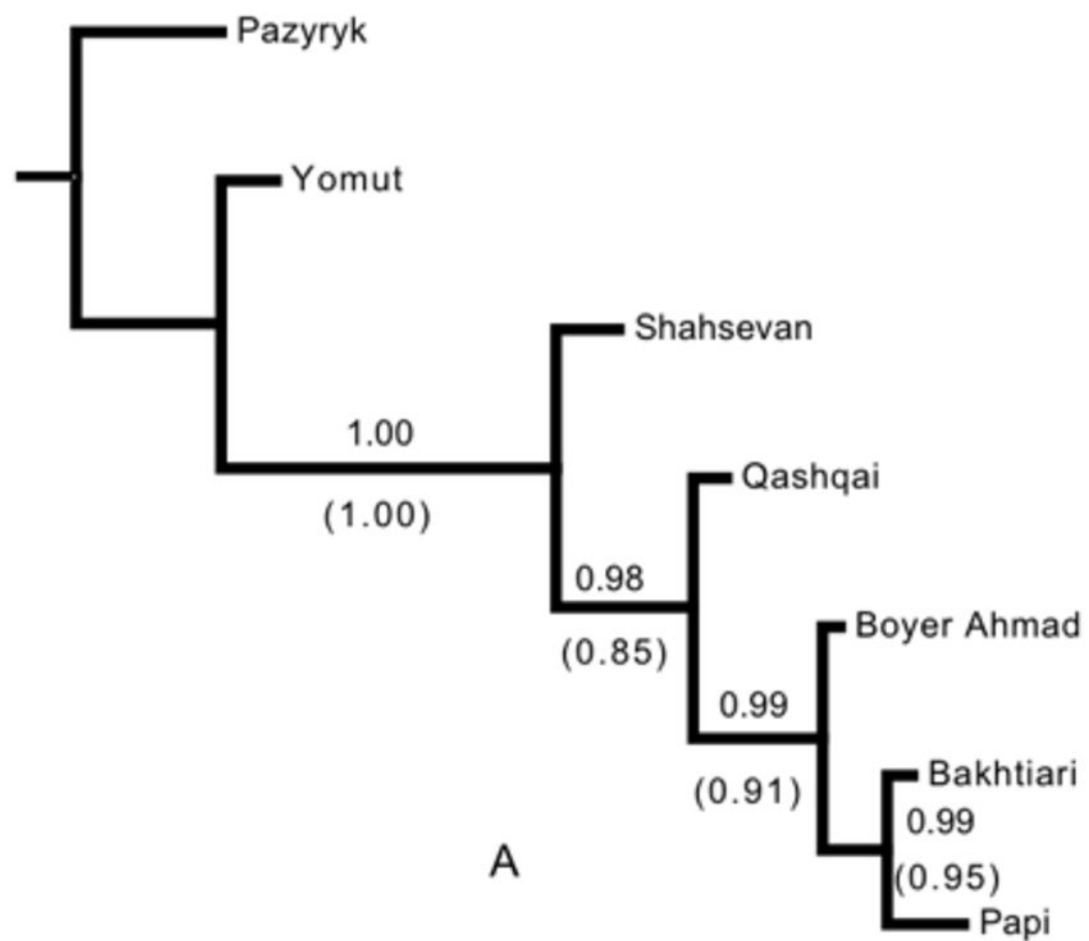
Bakhtiari

Boyer Ahmad

Qashqai

Shahsevan

Yomut



Percentage of simulated characters

