SHORT COMMUNICATION

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The "Out of Africa Tribe" (II)

Paleolithic warriors with big canoes and protective weapons

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It is generally difficult to establish a timeline for the appearance of different technologies and tools during human cultural evolution. Here I use stochastic character mapping of discrete traits using human mtDNA phylogenies rooted to the Reconstructed Sapiens Reference Sequence (RSRS) as a model to address this question. The analysis reveals that the ancestral state of *Homo sapiens* was hunting, using material innovations that included bows and arrows, stone axes and spears. However, around 80,000 years before present, a transition occurred, from this ancestral hunting tradition, toward the invention of protective weapons such as shields, the appearance of ritual fighting as a socially accepted behavior and the construction of war canoes for the fast transport of large numbers of warriors. This model suggests a major cultural change, during the Palaeolithic, from hunters to warriors. Moreover, in the light of the recent Out of Africa Theory, it suggests that the "Out of Africa Tribe" was a tribe of warriors that had developed protective weapons such as shields and used big war canoes to travel the sea coast and big rivers in raiding expeditions.

Introduction

Modern foragers today are very diverse in their technological capacities, suggesting that important behavioral and technological changes must have occurred during the hunter-gatherer stage of human social evolution.[1-4] Therefore, an important and unanswered question is at which points did technologies appear and behaviors change, especially during the foraging stage of human cultural evolution.[1-4] This question has been extensively explored by archeologists,[1,2] but, unfortunately, many of the materials used to create tools such as wood, bamboo, feathers or ropes are not easy to recover as fossilized items and the archeological record is scarce.[1,2]

This manuscript is a continuation of previous attempts to describe the culture of the groups of *Homo sapiens* that migrated from Africa to expand all over the world replacing and mixing with previous hominids.[4] The approach is driven by a three step combination of experiments:

First, a genetic tree is built based on mtDNA data from modern hunter gatherers. Second, the cultural traits of those existing hunter gatherers are displayed along that genetic tree. Finally, the resulting tree and the time-line of cultural innovations is analyzed.[4,5]

One potential problem with this approach is that diffusion of technologies could occur across populations, and, therefore, in the presence of information exchange, we may not be able to reliably infer the time of origin of certain technological traits from the phylogenetic arrangement of genes within the populations. However, recent evidence suggests that genetic transfer is either as common as cultural transfer or even easier than cultural transfer.[4,6] Moreover, to further minimize the problem of horizontal transfer of cultural information among genetically distinct groups, we follow two approaches: First, we reduce the number of populations to be considered selecting those for which more isolation has been described, minimizing as much as possible the risk of technology transfer. Second, I implement stochastic character mapping using a probabilistic approach, using the most up-to-date human mitochondrial DNA (mtDNA) phylogeny,[7] rooted to the Reconstructed Sapiens Reference Sequence (RSRS). This is useful because it has been shown that the degree of genetic relatedness correlates with cultural transmissions.[4,6] In other words, culture is normally transmitted along with genes, therefore this method could be considered a phylogenetically appropriate comparative method, capable of testing implicitly the hypothesis of diffusion or independent invention of technologies. In summary, this study relies on two assumptions: (1) that the set of tribes selected represent the most isolated possibly found and studied;[1,2] (2) that culture and genes are co-transmitted.[4,6] Both assumptions are crucial to consider this approach as a valuable alternative to direct archeological studies, which, as previously mentioned, have their own limitations.

The conclusions obtained are:

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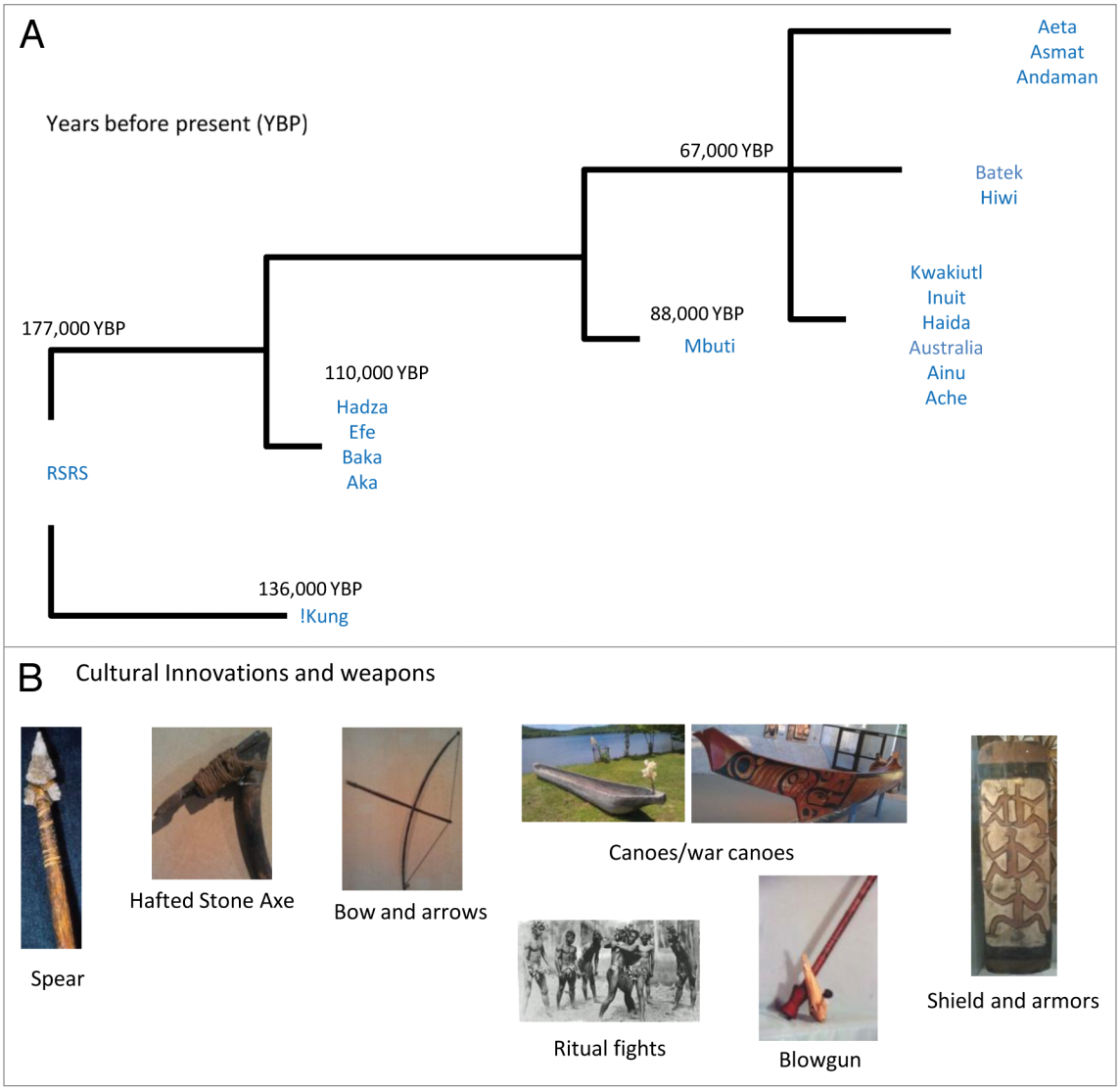

Figure 1. Stochastic character mapping of discrete traits on human mtDNA phylogenies. (**A**) A mtDNA phylogeny rooted to the RSRS sequence. The phylogenetic tree generated and used here is based on mtDNA data from foragers. (**B**) List of cultural innovations and weapons analyzed.

(1) Spears and hafted stone axes are the most ancestral weapons, invented more than 140,000 years before present (YBP) and likely predates the appearance of modern humans.

(2) Use of bows and arrows is likely to be ancestral, but seems to be a technology that can be easily lost by competing more modern weapons, such as the blowgun.

(3) The use of shields is estimated to appear 120,000 to 60,000 YBP. Before that, there is a total absence of defensive weapons and correlates with the appearance of ritual fights and war canoes

(4) The blowgun, on the contrary, is a more recent development (less than 60,000 YBP) and do not correlate with war-prone behaviors

(5) Finally, the timeline drawn by the genetic tree and the stochastic character mapping using mtDNA phylogenies suggests the existence of a cultural transition from hunting societies to war faring societies, marked by the correlated appearance of ritual fighting, the invention of protective weapons and war canoes 90,000 to 70,000 y before present.

Results

The RSRS[7] is a hypothetical mtDNA sequence, constructed by creating a phylogenetic tree (**Fig. 1A**) including all known human mtDNA haplogroups, and working back toward the basal branches of the mtDNA tree until their common ancestor, the RSRS. Therefore, the split between *sapiens* and *neanderthalensis* predates the appearance of the RSRS (**Fig. 1A**).

Using this approach, all mtDNA haplogroups are linked by shared common ancestry and distributed relative to their ancestral vs. derived status,[7] which I used to allocate forager tribes[1-4] along the phylogenetic tree[7] (**Fig. 1A**).

The tree from **Figure 1A** can now be used to superimpose cultural traits[1-4,8-10] and the use of material technology, due to shared common ancestry.

The list of social behaviors and weapons analyzed here (**Fig. 1B**) were divided into seven categories: (1) spears, defined as any shaft with a sharpened end, either for thrusting or throwing, and used for hunting, fishing or fighting. (2) bow and arrows, defined as a shaft of flexible material (bow) which uses a string to shoot aerodynamic projectiles (arrows); (3) ritual fights, any type of battle between males, including wrestling, stick fights or raiding and headhunting expeditions; (4) shields and armor, defensive weapon either carried as a dress (armor) or as an object (shield). Armors are used mainly by foragers in colder environments;[2] (5) stone axes, a stone tool fixed to a wooden shaft; (6) blowguns, hollow tube used for firing light projectiles or darts using the force of one's breath; and (7) canoes and war canoes. The distinction between small canoes and war canoes is important. War canoes were probably one of the most dangerous military advantages among hunter-gatherers and they are often named and treated by them as a different object with respect to small canoes. Each hollowed out of a single tree and manned by 50 or 60 warriors, those vessels were able to transport several warriors at large speed to attack a village before they could prepare for the attack and leave equally fast, and will be advantageous in warfare near the seacoast, rivers or lakes.

Simmap 1.5[5,6] was used to estimate whether two characters are correlated using mutational maps (sample size > 2,000, predictive sample size > 1,000). Ancestral State Reconstruction was also performed using MrBayes and SIMMAP 1.5 using a Bayesian approach. Using this analysis (**Fig. 2**), it is found that the use of spears and hafted stone axes (blue, **Fig. 2A**) is common to all tribes.[8] Use of bows and arrows (blue, **Fig. 2B**) seems to be also ancestral but lost in some tribes (red). Finally, the practice of ritual fights (red, **Fig. 2C**), is opposed to ritual gatherings that only involve storytelling and dancing (blue, **Fig. 2C**).

All these results taken together suggest that the ancestral state of *Homo sapiens* included a hunting "toolkit" composed of stone axes and spears (**Fig. 2A**), bows and arrows (**Fig. 2B**), and that ancestral hunter gatherers performed ritual gatherings that involved music, dancing and storytelling but no ritual fights (**Fig. 2C**). Interestingly, those early weapons differed in their persistence, for example, use of bows and arrows (blue, **Fig. 2B**) is less persistent than the use of spears or hafted stone axes (blue, **Fig. 2A**), because it is lost in some derived groups (red, **Fig. 2B**).

Interestingly, tree-length branches based on the mtDNA molecular clock suggest a transition from ritual gatherings that involve singing, dancing and story-telling to ritual fighting at 90,000 to 70,000 y before present (YBP), according to the dating based on the RSRS analysis[7] (**Fig. 2C**). This transition correlates ($p < 0.05$) with other cultural traits analyzed here, such as the invention of protective weapons like shields and/or armors (**Fig. 2D**) and the use of dugout canoes as war canoes (**Fig. 2E**). The use of shields (red) is estimated to appear 120,000 to 60,000 YBP. Before that, there is a total absence of defensive weapons (**Fig. 2D**, blue).

Next, I analyzed the distribution of canoes, including war canoes. War canoes are probably one of the most dangerous military advantages among hunter-gatherers living near the seacoast or the rivers. Those vessels were able to transport several dozens of warriors very fast. Such a mechanism of fast transport for up to a hundred warriors was unthinkable by land before the domestication of the horse and may have been comparable to the Vikings of more modern times. War canoes allowed humans to make lightning raids against which their enemies had little defense. I therefore analyzed the non-use (blue, **Fig. 2E**) or use of small dugout canoes (green) or war canoes (red). The use of war canoes (red, **Fig. 2E**) is estimated to appear 90,000 to 60,000 YBP, and correlates with the appearance of ritual fights and protective weapons.

Finally, other weapons analyzed, like the blowgun (**Fig. 2F**, use of blowguns in red) is a more recent development (less than 60,000 YBP) and do not correlate with war-prone behaviors. Interestingly, the appearance of more modern hunting tools like the blowgun seems to correlate with the replacement of the bow and arrows, suggesting that those are, to some extent and under certain circumstances, competing weapons. This reflects the fact that the blowgun and the bow are targeted against similar preys, small birds or mammals, which need to be hunted at a distance, potentially becoming redundant weapons.

Discussion

Prior to the Neolithic revolution all humans were foragers,[1-4,8-10] meaning that 90% of human evolutionary history occurred as hunter-gatherers.[1-4,8-10] Moreover, behavioral changes must have occurred during the hunter-gatherer stage.

Here, I have tried to model this cultural process combining human mtDNA phylogenies[7] and stochastic character mapping.[5]

The timeline drawn by this model reveals an ancestral culture formed by groups of foragers that used spears and hafted stone axes and, most likely, bows and arrows. The blowgun, on the contrary, appears to be a more recent hunting weapon. Interestingly, the bow and arrow and the blowgun seem to be competing weapons, because tribes that adopt the blowgun have a higher tendency to lose the bow and arrow. Likewise, the Boomerang of the Australian aborigines, not included in this study, may also be a competing weapon with the bow and arrows (data not shown).

Most importantly, this model of cultural evolution suggests an increase in warfare overtime (**Fig. 3**). This is revealed by the correlated appearance of defensive weapons and ritual fighting as well as the development of large war canoes from initial small canoes. In other words, the timeline draw by the genetic tree and the stochastic character mapping using mtDNA phylogenies suggests the existence of a cultural transition from hunting societies to war faring societies, marked by the correlated appearance of ritual fighting, the invention of protective weapons and war canoes 90,000 to 70,000 years before present (**Fig. 3**).

Interestingly, the timeframe of this cultural transition predates the Out of Africa migration proposed by the recent Out of Africa theory, supporting the view that the Out of Africa Tribe may have been a group of migrant warriors.[4] The results

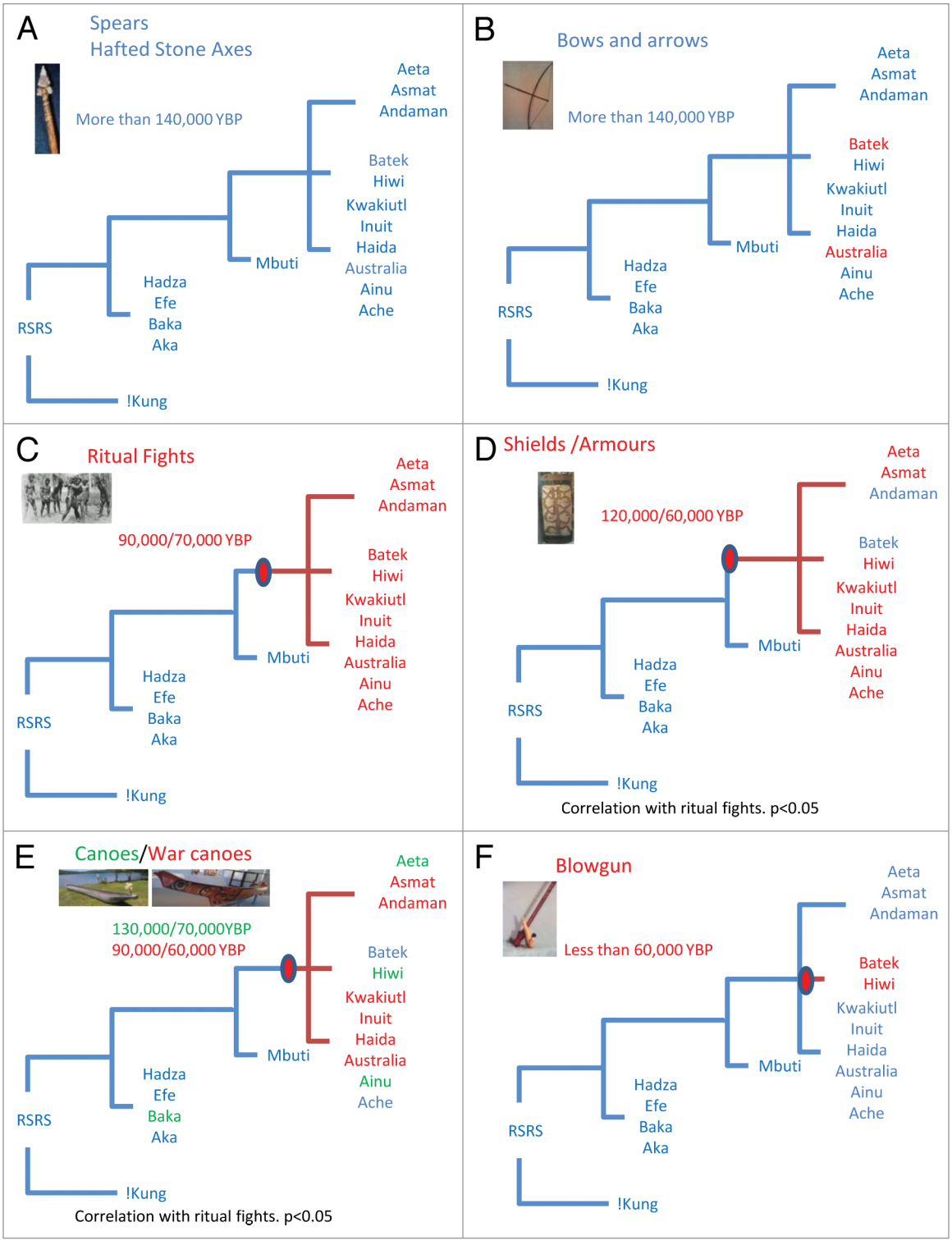

Figure 2. A timeline for the invention of weapons and social traits during early human evolution. (**A–F**) Stochastic character mapping of discrete traits on human mtDNA phylogenies. (**A**) Use of spears and hafted stone axes (blue) is common to all tribes. (**B**) Use of bows and arrows (blue) is ancestral but lost in some tribes (red). (**C**) The practice of ritual fights (red) as opposed to ritual gatherings that only involve storytelling and dancing (blue). (**D**) Use of shields and/or armor (red) or lack of defensive weapons (blue). (**E**) Non-use (blue) or use of small dugout canoes (green) or war canoes (red). (**F**) Use of blowguns (red) is a more recent development.

presented here further suggests that such a tribe may have been able to use big canoes to expand through the coastal routes of Arabia, India, China and the South Pacific toward Australia. It may be important to note that there are African cultures that

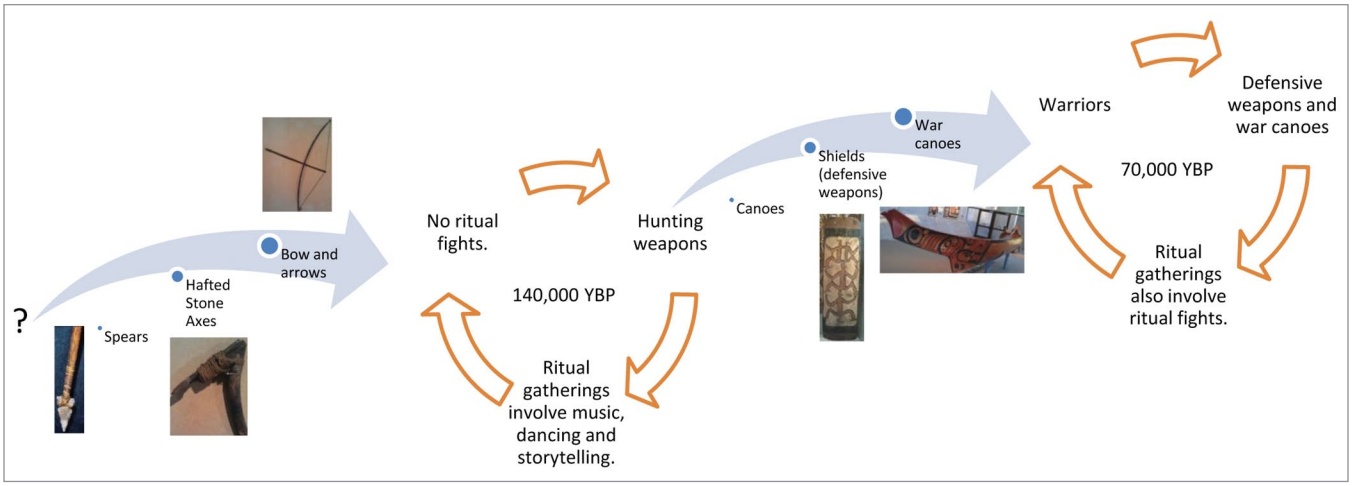

Figure 3. Cultural transitions during the human paleolithic. Prior to 140,000 YBP, the toolkit of hunting weapons (spear, bow and arrow, hafted stone axe) has developed. Around 70,000 YBP a cultural transition occurs that involves the use of defensive weapons, ritual fights and war canoes. The trigger for this transition may be linked to increased competition.

do not fall under the forager category but that do have ritual fights,[4] suggesting that the Out of Africa tribe may have also expanded within Africa before or at the same time as the Out of Africa expansion, as supported by the "within Africa" expansion of L3 mtDNA lineages.[11] In the future it will be interesting to explore whether the "within Africa" expansion of those tribes also occurred along the coasts and rivers, potentially highlighting the use of big canoes.

The technological developments achieved by the "Out of Africa Tribe," such as the war canoes and the protective weapons, could have given them a competitive advantage[12] over other coexisting hominids such as the Neanderthals or the Denisovans,[13-15] and help them expand,[4] specially along the coast and the big rivers of South Asia, Africa and Oceania.[16-18] More recent weapons, like the boomerang or the blowgun, could either be subsequent local innovations or inherited from preexisting groups of hominids from south Asia and/or Australia, during the process of replacement and admixture between the "Out of Africa Tribe" and preexisting hominids.[13-20]

Materials and Methods

The trees were generated using MrBayes (http://mrbayes.sourceforge.net), which is the most widely used (bayesian) approach for phylogenies.[21] Then I used the program Simmap 1.5 (www.simmap.com/) which allowed to perform the filtering. SIMMAP 1.5 will also estimate whether two characters are correlated (or associated) using mutational maps. Most ethnographic data was obtained from the The Cambridge Encyclopedia of Hunters and Gatherers (Cambridge University Press, 1999) and by examining the ethnographic collections at the University of British Columbia's Anthropology Museum, National Anthropology Museum and the Ainu Village of Poroto Kotan. Photographs were also taken at those sites.

Each correlation analysis was configured to have an observed sample size > 2,000 and a predictive sample size > 1,000 and was performed as in Huelsenbeck et al. (2003). D ($D = \Sigma i = 1n\Sigma j = 1m||dij|||$) is the overall association between character i and j. d is a measure of the association between the individual states of each character. a is the observed (o) or expected (e) association between character state i and j (n is the number of states for character 1 and m is the number of states for character 2. The association between one state and another is the frequency of occurrence of states on the phylogeny and was given a p-value for correlated evolution significance. It is important to note that some cultural traits may be more prone to change than others,[4,8] and for this reason stochastic character mapping is an ideal choice, because this method allows one to measure the probability that a trait changes in a unit of time and, therefore, it also can estimate how "stable" vs. "prone to change" a character is. The null hypothesis is that characters evolve independently of each other and that associations are the result of chance rather than correlated evolution. Since the phenotypes are Boolean data and the number of phenotypes was not too high (< 10) I drew random trees from the genetic data and then filter them using the phenotypes. Ancestral State Reconstruction was also performed using Mr. Bayes and SIMMAP 1.5 using a Bayesian approach. The tree(s) and model parameters were derived from an external program (Mr. Bayes).

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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