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Human Origin Sites and the World Heritage Convention in the Americas

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The Mitochondrial Genome and the Origin of Native Americans: Structuring Variability in South America's Initial Settlements, Moving Forward Toward Integrated Research Approaches

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Abstract

The mitochondrial DNA (mtDNA) is perhaps the most widely studied genetic marker in human populations. Due to its fast mutation rate and lack of recombination, it provides a straightforward way of identifying different genetic lineages and their associated geographic distributions. In the case of Native Americans, the five founding lineages originally identified based on the sequence of mtDNA 'control region' – a short and hyper variable segment of less than 1,000 base pairs – have been recently expanded into more than ten lineages thanks to the increased resolution provided by complete mtDNA genome sequencing. 'Pan-American' lineages, that is, those occurring all over the Americas, seem to have undergone a strong and fast expansion, possibly around 15 thousand years ago (kya), which is usually associated with a fast migration southwards following the Pacific coast. Nonetheless, there is a general lack of strong genetic structure between North and South America, which is illustrated by the fact that most founding lineages entering the Americas through Beringia eventually reached South America. In this sense, mtDNA studies tend to make inferences on migration routes based on haplotype frequency in different geographic regions. However, inferring such a process from mtDNA alone is problematic. Sampling issues aside, because all mtDNA genome is non-recombining, it gives us a single genealogy, which in turn tells us a single history. Because a single genealogy can be highly influenced by stochastic processes, the major problem is that this specific history may not be representative of the true population history we are trying to reconstruct. To overcome these issues, it is important to use multilocus (or genomic) approaches to study the peopling of the Americas and, more specifically, the peopling of South America. Large genetic datasets, such as those composed by microsatellites (STRs) or single nucleotide polymorphisms (SNPs) genotypes in many individuals across a wide geographic area are good alternatives to mtDNA in understanding the evolutionary history of human populations. On a broad geographic scale, these approaches are helping us to understand the strength of genetic exchange between Native Siberian and Native American populations suggesting that a 'single wave' model is too simplistic to explain the Peopling of the Americas properly. This general conclusion seems to be robust across different analytical frameworks, including model-free analyses or approaches based on explicit evolutionary scenarios. In conclusion, those of us interested in the peopling of the Americas have learned important lessons from mtDNA in the last decades. However, a necessary next step is using multilocus analyses to refine our understanding about migration routes and population structure, more specifically in South America.

Mitochondrial DNA (mtDNA) is probably the most studied molecular genetic marker in animals, including humans. Since the initial descriptions of how and when all living human populations shared a common ancestor in the past (Cann et al., 1987; Vigilant et al., 1991), mtDNA in general, and its control region (mtDNA-CR) in particular became the genetic markers of choice for other studies. Of course, there are many reasons for this. MtDNA is relatively easy to characterise as it is present in several copies in every cell type having mitochondria, and it is thus much easier to extract and amplify mtDNA than nuclear markers. It lacks recombination, which is difficult to model and complicates several evolutionary/population genetic analyses. In addition, as only women can transmit it to the offspring, it has a smaller effective population size compared to autosomes (one quarter, to be precise), which makes it easier to detect genetic structure among populations. Finally, it has a fast evolutionary rate, which results in the accumulation of new substitutions in a short amount of time. This feature, coupled with methods based on the molecular clock (for instance, the assumption that the DNA molecule accumulates difference linearly in time), is extremely useful for dating recent events (in evolutionary time) such as those associated with human evolution (see Witas and Zawicki, 2004; Pakendorf and Stoneking, 2005).

This history of success also translates into another advantage. MtDNA datasets are usually large and, therefore, it is relatively easy to compare many individuals (and sometimes many populations) in a single analysis. For example, in September 2014, using the taxonomy browser in the Genbank (www.ncbi.nlm.nih.gov/taxonomy/) and 'mitochondrion' as the keyword resulted in about 35,000 matches. Moreover, there is a growing systematic effort to name related mtDNA sequences into haplogroups (Hg) or sub-Hg (www.phylotree.org; van Oven and Kayser, 2009), which allows the discovery of shared/private patterns among populations and the comparison of mtDNA haplogroup frequencies in space.

MtDNA and the peopling of the Americas

Schurr (2004) provides an excellent review of the initial studies of mtDNA variation in Native Americans. In summary, five major Hgs, termed A-D and X, were identified and strongly suggested a close affinity with Central Asian/Siberian populations. Each of these Hgs would have contributed to a single 'founding type' for the Native American gene pool. The earlier studies witnessed a hot debate concerning the timing and number of different 'migration waves' from Asia to the Americas. The timing of these migration waves were usually inferred based on the coalescence time of each Hg (for instance, the time when all different haplotypes find a common ancestor). For example, Bonatto and Salzano (1997) suggested that HgA-D all show an excess of low-frequency haplotypes, which is typical of populations which underwent demographic expansion. Under these circumstances, the coalescence time is connected to the expansion time. The close similarity of the coalescence times for these four Hgs made these authors suggest a single wave for the peopling of the Americas after a period of population growth in Beringia. This explanation would fit well with the dates obtained (>25 thousand years ago [kya]), which were much older than those reported for archaeological sites in the Americas (Goebel et al., 2008). On the other hand, the origin of HgX was harder to pinpoint, as this was a rare Hg, later shown to be absent from extant South American indigenous populations (Dornelles et al., 2005). Some authors took the more recent coalescence time estimates as evidence of a second migration, perhaps even from a different route (Brown et al.,1998), even though these estimates could be due to the small sample size for this haplogroup. Another lesson from the older studies was that the different Hgs were unevenly distributed across the continent. HgX was not restricted to North America, but Hg frequency could also change among regions (see Figure 2 in Schurr, 2004), possibly indicating the importance of regional movements or different demographic histories among regions.

The development of faster and cheaper DNA sequencing devices in the early 2000s allowed researchers to move from the mtDNA-CR perspective to the full mtDNA genome perspective (for example, Ingman et al., 2000). The full mtDNA genome has ~16,000 base pairs (bp), compared to the ~1,000 BP of the mtDNA-CR. However, as important as the availability of more DNA sequences to refine the picture of mtDNA Hg classification was the estimation of a more accurate calibration of the evolutionary rate for the mtDNA, which is essential in molecular clock analyses. Because the mtDNA-CR evolves faster, it is more difficult to control for multiple-hits when comparing the human sequence with the chimpanzee. In other words, it is very hard to know precisely how many mutations have occurred since these two species diverged ~6,500 kya and, of course, this affects how well the molecular clock would work. The remaining of the mtDNA genome, which codes for proteins or contain genes for rRNA and tRNA (therefore usually called the 'mtDNA coding region'), evolves a little slower and therefore allows for better resolution and better dating.

New studies based on complete mtDNA sequences initially confirmed some of the findings of the earlier studies, such as the importance of Beringia in the development of specific Native American mutation motifs, but also reserved several new results (Tamm et al., 2007; Achilli et al., 2008; Fagundes et al., 2008; Mulligan et al., 2008). For instance, they suggested that coalescence times were actually more recent than previously thought, between 15-20 kya and, therefore, that the population expansion previously associated to the standstill in Beringia was actually better reconciled with an expansion into the New World following the Last Glacial Maximum (LGM) around 16-18 kya. Also, new founding types were proposed and the rapid expansion suggested that the initial settlers followed a Pacific route, as by that time there would be glaciers into the continent blocking any passage to the south. Finally, it was also clear that while HgX could have taken part of the same 'wave' together with the other four major Hgs, some other sub-Hgs with more restricted distribution, especially in northern North America, such as HgD2a, would have arrived later, reflecting new migrations affecting these regions only.

Continued research on complete mtDNA genomes has revealed a growing number of founding types, which now sums almost 20 of them (Saint Pierre et al., 2012; Achilli et al., 2013). Arguably, several of these (see Achilli et al., 2013) may have distributions restricted to North America (but see below) and especially those restricted to Arctic populations may represent secondary waves from north-east Asia into the Americas after the major expansion occurring after the LGM. In addition, as long as more populations are being studied, the geographic distribution of mtDNA Hgs allows different interpretations of the mtDNA data. For example, Perego and colleagues (2009) and Hooshiar Kashani and colleagues (2012) claim that the geographic distribution of haplotypes C4c and X2a suggest a secondary entry route onto the continent possibly through an inland ice-free corridor. In this case, two, rather than a single major 'wave' from Beringia, would have affected mtDNA variation at the continental level.

MtDNA and the peopling of South America

When we turn our focus to South America, much of the job is to understand what happened in North America, as all genetic data available so far suggests that Beringia was the only entry door for the earliest Native Americans. Brown and colleagues (1998) suggested a putative 'western Eurasian' link with the Americas based on the presence of mtDNA HgX, but the sub-Hgs present in Native Americans, west Asians and Europeans are actually quite different. In agreement, the recent ancient genome from a 24 kya skeleton from central Siberia showing mixed affinities with both western Eurasians and Native Americans suggest some population replacement (with gene flow) in central Siberia, not alternative entry routes for the Americas (Raghavan et al., 2014).

An excellent review of models for the peopling of South America was recently presented by Rothhammer and Dillehay (2009). In short, they proposed some sort of genetic continuity from the north (for instance, coming from the Panama Strait), with a major entry route following the Pacific coast, with secondary migration waves flowing east of the Andes to the Amazon, Chaco, Patagonia and the Brazilian Plateau. Indeed, we should not forget that the oldest archaeological site in the Americas, Monte Verde, lies in southern Chile (Dillehay, 1997) and the evidence from mtDNA does suggest an extremely strong and fast demographic expansion, which can be reconciled with the Pacific route (for example, Fagundes et al., 2008). Another interesting feature is that the number of rare founder sub-Hgs is much lower in South America than in North America (Achilli et al., 2013). This is expected as a migrating population loses genetic variation as it moves on geographically, creating the known pattern for humans of loss of diversity as one moves out of Africa (for example, Ramachandran et al., 2005).

Though mtDNA studies based on several complete genomes from Native South Americans are lacking, two studies focused on mtDNA haplotypes found in southern South America (Bodner et al., 2012; Saint Pierre et al., 2012) suggest some interesting features. Firstly, they suggest that some sub-Hgs found (so far) only in South America are old enough to play the role of a founding type. According to this idea, sub-Hgs D1g, D1j and B2l could be present in low frequencies in the expansion wave and then expanded (in frequency) locally in South America, but were subsequently lost by genetic drift in Central and North America. This in an exciting finding, as it suggests that new founder types could be found locally in South America given that enough sampling effort is taken in characterizing these sub-Hgs. Secondly, they suggest that at least in southern South America, the Andes do not act as a barrier to gene flow. At first sight, this is in contrast to the scenario proposed by Rothhammer and Dillehay (2009). However, it is well known that some Patagonian populations such as the Mapuches crossed the Andes frequently (see Bodner et al., 2012 and references therein) and it is hard to know if the pattern for the southermost part of the continent would be representative of the overall picture.

Interestingly, another well-known continental pattern in South America is also related to the Andes. Tarazona-Santos and colleagues (2001), based on Y-chromosome data, suggested that populations in the Andes (or in western South America) would have higher connectivity and larger population sizes, while populations from lowland (or eastern) South America would have smaller population sizes and would be more

Figure 1. Major patterns of mtDNA variation in South America. The dark blue square represents the standing genetic variation in North America, and the thick blue arrow represents the major ancient (~15 kya) migration through the Pacific coast associated with some loss of genetic variation, as indicated by the color gradient in light blue. Two additional blue arrows in Northern South America (identified with a question mark) represent two putative alternative ancient migration routes. The major east/west difference in genetic variation is represented as follows: Populations from Western South America (Andes) are generally characterized by larger population sizes, higher connectivity due to gene flow and low values of genetic structure. This is represented by the large circles in shades of red, and the thick bidirectional arrows. Populations from Eastern South America (Amazon, Chaco and so on) generally have smaller population sizes, low connectivity and consequently higher genetic structure. This is represented by the small circles in different tones, and bidirectional arrows with broken lines. Putative connections between East and West 'components' are represented by bidirectional arrows. A black unidirectional arrow in Northern South America represents possible migration movements towards Central America, as may be the case for the Chibchan language group.

isolated. This pattern would result in more genetic diversity and less genetic structure in the Andes, and in less genetic diversity and more genetic structure in the lowlands. Fuselli and collaborators (2003) corroborated this general pattern using low resolution mtDNA data.

In a different study including protein genetic markers, Fagundes and collaborators (2002) focused on a sample containing many populations from the Amazon region and suggested that genetic drift was stronger than migration to create patterns of genetic structure, in agreement with the scenario suggested above (Tarazona Santos et al., 2001; Fuselli et al., 2003). They also suggested that language, rather than geography, was the best proxy of the genetic relatedness among populations (Fagundes et al., 2002). Other mtDNA patterns usually reported involve high/low frequency of specific Hgs, such as high frequency of HgC in Brazil or high frequency of HgB in the Andes (see Figure 2 in Schurr, 2004) but these data are usually based on low resolution mtDNA. Clearly, more complete mtDNA genomes from all around South America would be important to critically evaluate the relevance of the scenarios proposed by Tarazona-Santos and colleagues (2001) and by Rothhamer and Dillehay (2009). The major patterns of mtDNA variation in South America are summarised in Figure 1.

Limitations of the mtDNA as a molecular marker

Despite all we have learned from mtDNA studies, there are at least two major drawbacks of maintaining it as some sort of 'gold standard' for molecular anthropological studies worldwide. The use of the coding region of mtDNA in studies of complete genomes should have allowed a more reliable clock estimate compared to mtDNA-CR studies and a common choice was based on the estimate for the coding region of 1.26×10^{-8} substitutions/site/year from Mishmar and collaborators (2003). However, there are several technical issues related to mtDNA evolutionary rate calibration. Thus, the first and more technical concern is related to the tricky exercise of calibrating this.

Bromham and Penny (2003) and Kumar (2005) present two useful reviews for those unfamiliar with the molecular clock history and basics. In short, the idea of using a molecular clock is that if one has some 'calibration' for the clock rate, then it is possible to estimate any event affecting clades or populations. This 'calibration' can be provided by fossils or biogeographic data, as is common practice in phylogenetic studies. However, for recent human evolution, one usually has to rely on a direct estimate of the molecular clock obtained from previous studies (probably based on fossil data). This leads to an overestimation of coalescence time due to the 'time-dependency' effect, which occurs when estimation and calibration operate in very different time periods (Ho and Larson, 2006; Ho et al., 2011). In addition, rate variation among lineages and among mtDNA sites is also challenging for having a perfect molecular clock (Endicott and Ho, 2008).

More recently, Soares and colleagues (2009) suggested a method for correcting the effects of the ongoing purifying selection on standing variation which is one of the major causes in the overestimation of coalescence times (Kivisild et al., 2006), suggesting different rates for different mtDNA partitions. Using their method, these authors estimated the expansion of a Native American major founder Hgs ~15 kya, which is slightly later than the original estimates (see above). Although most recent studies do use this corrected evolutionary rate, it is important to keep in mind that even this 'best rate' cannot account for some of the complexities of mtDNA evolution and, therefore, associating specific mtDNA Hgs to a specific points in time is far from a trivial task.

The second limitation of the mtDNA as a marker, however, is more theoretical/philosophical and less technical. This also means that this limitation might be harder to overcome. To try to illustrate it in a didactical way, I will take an example from the arts. *Rashomon* is a classic film by the Japanese director Akira Kurosawa. In the movie, we are shown different versions of the same story told by different characters. Naturally, in the end the spectators are left with the feeling that no single story could be trusted as a single 'truth'. How does the *Rashomon* film connect with the concerns of population genetics and molecular anthropology? In some sense, mtDNA has been the sole 'story teller' molecular anthropologists are relying upon. It has several advantages, as previously mentioned, but it is still a single story teller. What about other stories? What about other genes?

Coalescent theory has revolutionised the field of population genetics since the 1980s (Kingman, 1982; Hudson, 1983; Tajima, 1983) by providing a way of describing the genealogy of a sample of genes taken from a population of size *N* (for a recent review, see Wakeley, 2008). Importantly for us, coalescent theory showed explicitly that the genealogy of any gene is highly stochastic and thus, that the genealogies of two independent genes taken from the same population can be different. More or less like *Rashomon* in molecular genetic terms, it means that the story of a single gene may not be representative of the history of the populations where it was drawn. In other words, relying on a well resolved and accurately dated mtDNA genealogy might be misleading as it may be very different from other genealogies which are also conditioned in the same demographic history. Rather than interpreting 'THE' mtDNA genealogy, we should interpret a set of genealogies derived from our samples.

Rather than asking if 'THE' mtDNA genealogy corroborates or refutes a given hypothesis, we should ask if a set of genealogies corroborates or refute our hypothesis. For molecular anthropologists, this is a major change in thinking.

MtDNA and multiple loci studies in testing hypothesis about the peopling of the Americas

Among the classical hypotheses proposed to explain the Peopling of the Americas, it is important to understand how much support they receive from genetic data (mtDNA and multiple loci studies), as well as some of the limitations of these studies. In the following paragraphs, I will present the tripartite hypothesis of Greenberg and colleagues (1986), the dual component hypothesis based on morphology (for example, Neves and Pucciarelli, 1991; Neves and Hubbe, 2005) and the recurrent gene flow model of Gonzales-José and colleagues (2008).

The first major multidisciplinary hypothesis for the origin of Native Americans is the tripartite hypothesis of Greenberg et al. (1986), who proposed three distinct migration waves corresponding to the three linguistic phyla identified by J. Greenberg, namely, Amerind, Na-Dene and Eskimo-Aleut, with Amerind being the first wave and Eskimo-Aleut the last. In this model, we would expect a strong genetic structure associated with the linguistic phyla and, ideally, expansion or divergence dates associated with the corresponding phylum would be congruent with the order predicted in the original hypothesis. A second major (continental-level) hypothesis that could be tested with genetic data was proposed, among others, by Neves and Hubbe (2005), based on craniofacial morphology. According to these authors, there is a major shift in craniofacial shape in the Americas, where the early skeletons are much more robust and without many derived traits (so-called Palaeo-American), while extant populations and more recent skeletons (later than ~7 kya) have many derived features associated with a so-called 'Mongoloid' phenotype. In this hypothesis, the first Palaeo-American populations would have been replaced by more recent settlers or at least admixed with them causing the change in morphology. In this hypothesis, we would expect evidence of two distinct waves or, at least, a temporal structure between recent and old samples if the old settlers were completely replaced. More recently, Gonzalez-José et al. (2008) proposed a different interpretation of the morphological data suggesting, upon review of mtDNA and Y-chromosome studies, that the morphological transition could have occurred due to recurrent gene flow between Asia and Americas in the Arctic following a major initial Pleistocene colonization. In this case, we would predict evidence of gene flow between the two continents and only a subtle temporal structure comparing recent and old samples. Importantly, the hypothesis of Greenberg et al. (1986) is impossible to test with only South American samples, as the second and third migration waves only affected North America. However, the dual component hypothesis could be tested with only South American samples, as the morphological change would have occurred at the whole continent level. Indeed, a more recent analysis of craniofacial morphology lends support to the gene flow hypothesis (De Azevedo et al., 2011).

Current interpretation of mtDNA data suggests that, except for northern North America, one or two major migrations would explain well the observed level of variation (see above). On the other hand, the pattern for northern North America could be interpreted as evidence of recurrent gene flow from Asia. Another possible interpretation could be that these data support, at least in part, the three wave scenario of Greenberg et al. (1986) - even though a strong genetic distinction between Na-Dene and 'Amerind' (sensu Greenberg) populations in not very clear (for instance, Bonatto and Salzano, 1997; Achilli et al., 2013). On the other hand, there is not much evidence for a marked temporal structure in the continent (for example, Raff et al., 2011), lending little support to scenarios involving population replacement, such as those suggesting that more earlier 'Palaeoindian' populations were replaced by more recent 'Mongoloid' settlers on a continent-wide scale. Indeed, a recent study found mtDNA HgD1, typical of modern Native Americans, in an ancient Palaeoamerican skeleton from Mexico dating between 13-12 kya (Chatters et al., 2014) suggesting genetic continuity between 'Palaeoamerican' and 'Mongoloid' populations.

It should be no surprise that based on mtDNA alone it is difficult to distinguish rigorously among the different hypotheses that have been proposed to explain the big questions about the peopling of the Americas. MtDNA is just a single story teller. What about studies based on multiple markers? Hey (2005) and Kitchen and colleagues (2008) presented some results suggesting that gene flow with Asia could be important for explaining the patterns of genetic diversity in Native American populations, but neither study tested if gene flow provided a better fit to the data compared to a model of no gene-flow. On the other hand, Wang and colleagues (2007) suggested a single major colonization from Siberia but, again, did not test explicitly for the hypothesis of gene flow between the two continents. In an attempt to address this issue in a more formal way, Ray and colleagues (2010) used part of the Wang et al. dataset (401 out of 678 STR markers) to test hypotheses using an ABC framework (see Bertorelle et al., 2010; Csillery et al., 2010 for detailed reviews of this method).

Roughly speaking, the ABC framework is based on running many (millions) simulations based on coalescent theory for any arbitrary demographic model, which should be defined in advance. For example, one can choose to simulate a 'single wave' scenario for the peopling of the Americas by defining two populations (for example, pop1, representing Asia and pop2, representing the Americas) and forcing a major migration from pop1 to an empty pop2 by 15 kya. Following each demographic simulation, genetic data mimicking the observed data is generated and summary statistics for this data are recorded. Thus, if the real dataset contains 401 STR loci, exactly 401 STR loci are generated after each simulation and the same set of observed summary statistics calculated for the real data are recorded for the simulated dataset, such as the average number of alleles, average heterozigosity and so forth. The important point here is that the level of genetic diversity in the simulated data would be conditioned on the demographic story (thanks to coalescent theory). The last step is comparing the summary statistics generated from the simulations with the same summary statistics calculated on the real dataset. Simulated scenarios close to the true demographic history should generate summary statistics very close to that obtained from the real dataset. When different scenarios are simulated, the scenario better supported by the data will be the one resulting in simulated summary statistics closer to the observed than the real data. The ABC framework is an interesting alternative for comparing different scenarios explicitly when likelihood methods cannot be used.

Ray and colleagues (2010) tested three hypotheses: a single wave hypothesis, a two-wave hypothesis and the recurrent gene flow hypothesis. However, because the dataset contained only one Na-Dene speaking population and no Eskimo-Aleut population, no formal test of the Greenberg hypothesis could be done. The authors also decided to test hypotheses considering North and South America together or considering each subcontinent separately. This was important because if the two-wave scenario were better for North America only, for example, it could be better interpreted as reflecting the distinctiveness of the Na-Dene population, rather than something related to a morphological transition that occurred in both continents. The results clearly supported (with a relative posterior probability of ~1.00) the recurrent gene flow hypothesis for both North and South America. This result corroborates the importance of recent migration between Asia and the Americas, and suggests that gene flow with Asia was an important evolutionary factor even for South American populations, in general good agreement with the model proposed by Gonzales-José et al. (2008).

Another important study is that of Reich and colleagues (2012), who typed ~365,000 genetic markers in 17 Siberian and 52 Native American individuals from the three major linguistic phyla. These authors used a different approach compared to the one described before (Ray et al., 2010), in that no alternative scenarios were formally contrasted. Instead, they generated a population tree allowing for genetic admixture among populations. Their results also suggest that a single migration wave scenario would be too simplistic to account for Native American genetic diversity. They suggested three independent streams of Asian gene flow. While native South Americans would derive their ancestry from a single stream, Na-Dene and Eskimo-Aleut populations would be admixed between the first stream and subsequent ones. This sounds much like the original Greenberg et al. (1986) hypothesis, except that the subsequent migration waves would have admixed with the 'First Americans' as they reached the New World. It would be quite ironical if the Greenberg hypothesis, which has been strongly criticised by linguists (for example, Matisoff, 1990), shows to be accurate in terms of genetic ancestry (Amorim et al., 2013).

It is not easy to compare the results from the studies by Ray et al. (2010) and Reich et al. (2012). Except for the obvious convergence that a single wave does not adequately explain genetic diversity of Native Americans, the differences in methods and datasets makes other comparisons problematic. For example, based on the Reich et al. (2012) dataset, would a recurrent gene flow model perform better than a single wave model for South America? Would the scenario proposed by Reich and colleagues for the whole continent be better supported than the recurrent gene flow model of Ray and colleagues? If having multiple genetic story tellers alleviates the issues of relying on too much on mtDNA results, it clearly adds a new layer of complexity for our analysis and data interpretation.

Concerning South America, the study by Ray et al. (2010) suggests we would need to recognize the impact of recurrent gene flow with Asia as a possible player in the microevolutionary change of South American populations. Other major patterns can be also distinguished based on multiple loci studies. For example, Wang et al. (2007) corroborate the West vs. East pattern also found for the Y-chromosome (Tarazona-Santos et al., 2001) and mtDNA (Fuselli et al., 2003). However, genomic data also suggest that even this major pattern is not absolute, as the case of the Inga, in Colombia, whose genome seems to be admixed between Amazonian and Andean groups (Reich et al., 2012). Also, the connection of Chibchan-speaking groups in South and Central America (Wang et al., 2007; Reich et al., 2012) is important to show that even though South America is usually considered the endpoint of a migration process moving southwards, there were important back migrations from South to Central America.

Moving forward

MtDNA will probably maintain its role as a major molecular tool for generating and testing anthropological hypothesis. The fact that it is much easier to find good quality mtDNA in old samples is also a major technical advantage of this marker. However, rigorous hypothesis testing based on mtDNA alone is difficult because it represents a realisation of the genealogical process and a single genealogy may be compatible with several different historical scenarios. On the other hand, the recent trend of genomic studies will also bring new challenges for how we analyse, interpret and frame our anthropological hypotheses in ways that can be suited for testing using genetic markers.

Nevertheless, anthropologists interested in using genetic markers must keep in mind that population genetics models are simplifications of the real demographic processes and, as such, might be unable to fulfil the level of detail and precision that would be important for anthropologists. An instructive example is the very concept of 'effective population size', which is the size of an ideal population that behaves as an observed real population. Anthropologists might be interested in census population size (for instance, how many individuals are/were there?), but, in this case, population genetics models might be unable to answer this question satisfactorily. On the other hand, population genetics models are useful when they can predict results or when they can integrate results in a coherent and synthetic manner. Given all we have learned from population genetics models applied to the peopling of the Americas, I think that the new era of genomics will show major advances in refining our understanding of the peopling of the New World, in general, and of South America, in particular.

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Molecular Approaches to Colonization and Population History in the North American Arctic

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Introduction

Scholarly interest in the Arctic has a long and diverse history. From research into the ecological diversity of the extreme environment of the Arctic to human biological and cultural adaptations to those same ecological conditions, the reasons for academic interest in the Arctic are manifold. With respect to the UNESCO World Heritage thematic programme of Human Evolution: Adaptations Dispersals and Social Developments, our interest in the North American Arctic has four major elements: 1) via Beringia, the former land bridge linking North America and Asia, it represents the entry point for dispersal of human populations to the Western hemisphere, 2) the region of the North American Arctic has seen three major dispersals of colonizing populations within the last 15,000 – 20,000 years, and, therefore, 3) serves as a geographic model for the population dynamics of human colonization and dispersal that may be relevant to similar human dispersals in other parts of the world, and at other temporal depths. Finally, 4) the recency of human dispersal and adaptation in the North American Arctic provides an opportunity to more clearly assess the merger of the archaeological and genetic records as ways of unveiling past human activity. By assaying both the archaeological record of human occupation of high latitudes and the signature of human demographic history recorded in the genetic variation carried by both modern and ancient populations of the region, we can more directly identify the strengths and weaknesses of both records, and begin to merge them into a powerful, coherent approach to the study of the past.

The archaeological record of the North American Arctic has been accumulating for several decades and its broad outlines are well known to archaeologists and prehistorians (for example, Morrison and Pilon, 1994, and papers therein). The genetic record is of much more recent vintage, with information on modern molecular variation in Arctic populations having been accumulating for only a decade or so. As a result, it is more fragmentary and less well known than the archaeological record. Accordingly, a few words on the basic tenants of human evolutionary genetics are warranted. It has long been recognized that the demographic history of human populations is archived in the patterns of genetic variation exhibited by individual populations. With the advent of molecular genetic techniques, based on our ability to detect individual base differences in DNA sequences, the resolution of the genetic record, the observed pattern of sequence variation between individuals, has increased dramatically, as has our ability to read the history of a population in its genome. This has made it possible to estimate population sizes of earlier populations, date the divergence of populations from an ancestral population and begin to evaluate alternative histories based on both the archaeological and genetic records. Most recently, this has been facilitated by our ability to also assess molecular variation in prehistoric populations through the analysis of ancient DNA (aDNA) (see Tackney et al., 2014 for a review of aDNA studies in the Arctic).

Each individual possesses two genomes. The nuclear genome is very large, containing ~3 billion bases organized into 23 pairs of chromosomes. This genome, as the name implies, is found in the nucleus of a cell and each member of a pair of chromosomes is contributed by either the father or mother. Thus, the nuclear genome is biparentally inherited. The second genome each individual possesses is the mitochondrial genome. This genome is located not in the nucleus of the cell, but in multiple organelles in each cell's cytoplasm. The mitochondrial genome is a single, circular molecule of DNA approximately 16,500 bases in length and each of the many mitochondria in each cell may contain from tens to hundreds of these molecules. Thus, while the nuclear genome is very much larger than the mitochondrial genome and, hence, harbours much more variation overall, there are many more copies of the mitochondrial genome, a fact which has led to its intense study in ancient samples, where the likelihood of recovery of mitochondrial DNA (mtDNA) is much higher than nuclear DNA (nDNA) due to the initial higher copy number.

Unlike the biparentally inherited nuclear genome, mtDNA is inherited solely from the mother. Thus, tracking changes in mtDNA lineages is the equivalent of tracking maternal lineages through time. Many such maternal lineages have now been identified in populations around the world, although only a few are known from the indigenous populations of the Americas. The ancestral mtDNA lineage is termed L3 and is known primarily from Africa. It gave rise to two daughter forms, M and N lineages, which were carried out of Africa during the initial human dispersal and each subsequently gave rise to the large number of lineages known worldwide today. Although at least 15 founding mtDNA lineages have been identified in Native American populations (Perego et al., 2010), all belong to five larger groupings known as haplogroups. The individual lineages known in the Americas belong to haplogroups A, B, C, D and X. Arctic populations have an even more reduced

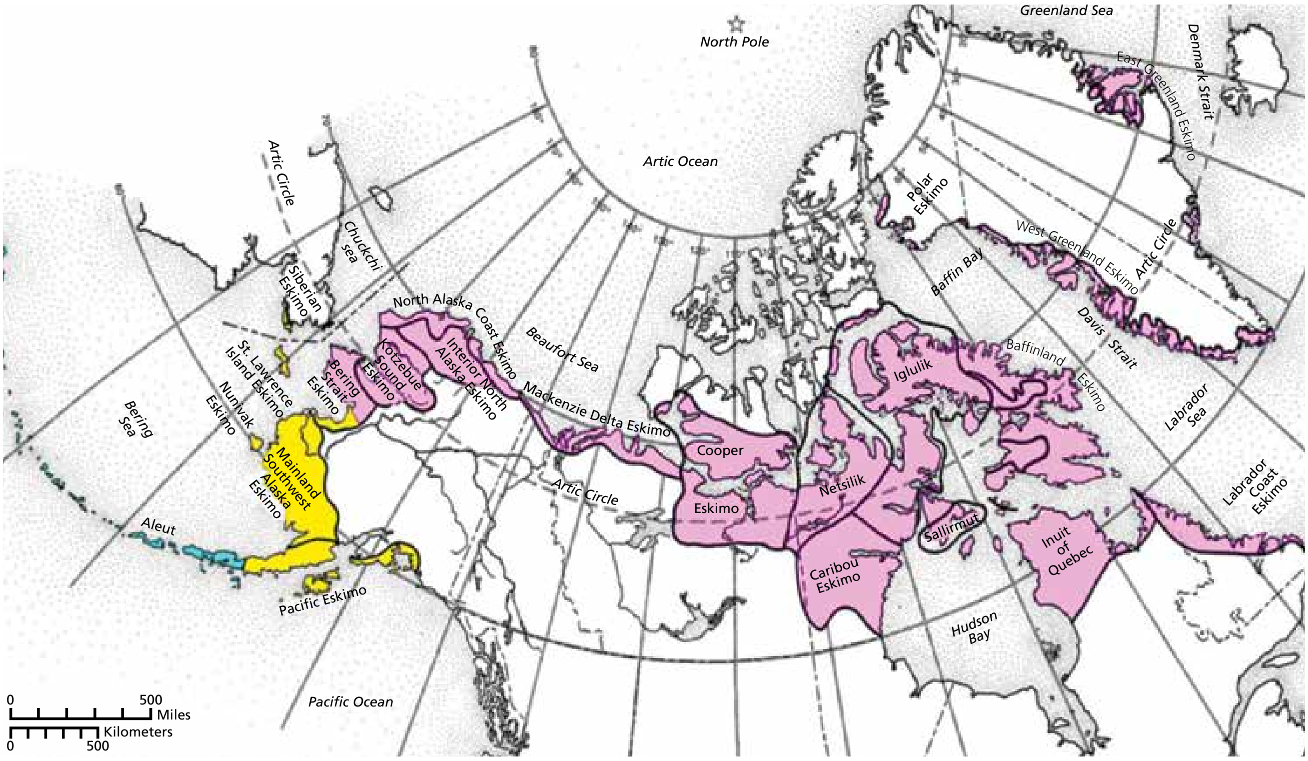

Figure 1. Geographic location of three regional arctic population studies reviewed in text.

number of mtDNA lineages, exhibiting lineages in only haplogroups A and D. Lineages of the other three Native American haplogroups are unknown in the Arctic, except as they can be accounted for by recent migration to the region.

Regional Studies

With this brief primer of molecular genetics, it is now possible to begin to evaluate our state of knowledge of the genetic record of Arctic populations against the backdrop of the archaeological record to attempt to provide a greater resolution to our understanding of the prehistory of Arctic colonization and dispersal. Three regional studies will serve as examples of how molecular and archaeological data can be jointly employed to provide a clearer picture of prehistoric population dynamics and testing of hypotheses regarding population history. The three regional studies, where the archaeological record is augmented with both modern and ancient genetic studies are the Aleutian Islands, the Eastern Canadian Arctic and the Alaskan North Slope (Figure 1). In each area, the questions of interest, originally derived from the archaeological or osteological records, relate to colonization and population replacement in prehistory. For example, in the Aleutian case, Hrdlička (1945) hypothesised on the basis of perceived changes in cranial morphology that a population replacement occurred in the region approximately 1,000 years ago, despite archaeological continuity. In the Eastern Canadian Arctic, the archaeological record indicated a population replacement of Palaeo-Eskimo groups by Thule whalers, also approximately 800-1,000 years ago (McCartney, 1977; McCullough, 1989; Maxwell, 1985), while the morphological characteristic of the two groups did not appear to differ. In both cases, modern and ancient DNA studies are employed to test these contrasting hypotheses of human population dispersal and replacement. The Alaskan North Slope provides an opportunity to track the story of one of these replacement hypotheses back in time to attempt to examine the source of the migrants and therefore provides additional detail and resolution to our understanding to this period of Arctic history in North America.

The Aleutian Islands

Archaeological evidence indicates that the eastern Aleutians were first inhabited 9,000 - 8,000 years ago, that the archipelago was settled from east to west and that the region is characterised by near archaeological continuity since colonization. Nevertheless, based on an observed shift in cranial morphology from dolicocranic to mesocranic[1], Hrdlička (1945) postulated a migration of the immediate ancestors of modern Aleuts (Neo-Aleuts) into the archipelago approximately 1,000 years ago, replacing an earlier resident population (Palaeo-Aleuts). We reasoned that if such a migration occurred, the earlier and later populations would likely differ genetically.

Accordingly, we undertook an ancient DNA study of the original human skeletal material recovered by Hrdlička (1945) and used in formulating his replacement hypothesis. The samples used in the aDNA analysis (Hayes, 2002; Hayes et al., 2003, 2005; Smith et al., 2009) came from the burial caves on Kagamil and Shiprock Island and Chuluka midden in Nikolski on the island of Umnak. AMS ^{14}C dating of each sample indicated an age range of >3500 – 750 BP (Coltrain et al., 2006), spanning the time period of the replacement event proposed by Hrdlička (1945). A total of 80 individuals from the three sites were studied, with two-thirds of those that yielded analysable DNA (n=61) characterised by mtDNAhaplogroup D and one-third by mtDNAhaplogroup A (Table 1A). These lineage frequencies were indistinguishable from the mtDNA lineage variation found in modern Aleut populations (Rubicz et al., 2003; Zlojutro et al., 2009), nor was there any significant difference between the lineage frequencies between Palaeo- and Neo-Aleuts, leading to an initial inference of no evidence for a migration or replacement event (Hayes, 2002; Hayes et al., 2003, 2005). Rather the results seemed to confirm the archaeological record of population continuity.

Table 1. mtDNA lineage frequencies in prehistoric Aleutians and Eastern Canadian Arctic

The Aleutians - According to Smith et al., 2009

Sites	N	%A	%D
Kagamil	32	25	75
Ship Rock	12	17	83
Chaluka	36	48	52
Total	80	34	66
Hrdlička's Morphological Groups			
Paleo-Aleut	42	53	47
Neo-Aleut	38	19	81
Total	80	36	64
Temporal Groups			
Pre-1000 AD	11	73	27
Post-1000 AD	52	23	77
Total	63	32	68
The Eastern Canadian Arctic - After Hayes 2002			
Dorset	3	0	100
Thule	20	100	0
Sadlermiut	19	56	44

Closer examination of both the archaeological, radiometric and genetic data however, revealed additional information. The oldest samples came from the Chaluka midden site and all had been classified by Hrdlička as Palaeo-Aleuts. The majority of individuals recovered from Shiprock and Kagamil caves dated later in time (<1000 years old) and were classified by Hrdlička as Neo-Aleuts. Samples dating to after 1,000 BP at Chaluka were a mixture of Palaeo- and Neo-Aleuts as described by Hrdlička. This would seem to contradict Hrdlička's (1945) postulate of Neo-Aleuts as a replacement population, since both morphologically defined groups existed together at Chaluka for several hundred years. There is heterogeneity in lineage frequencies among the three sites and between Hrdlička's morphological groupings, but they proved to be statistically non-significant. However, when we examined the mtDNA lineage distribution in the pre- and post-1,000 year old material,

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[1] Dolicocranic: a skull with a breadth c. 75% of the length; brachycranic, a skull with a breadth c. 80-85% of the length; mesocranic, a skull with a breadth/length ratio intermediate between dolicranic and brachycranic.

significant differences emerged. The samples predating 1,000 years BP (all from Chaluka) were predominantly mtDNA lineage A, with only a quarter lineage D. In the post-1,000 year old cohort, the frequencies were reversed, with only a quarter lineage A. These lineage frequency differences were much more substantial and statistically significant than any observed in any other grouping of the samples. Using the computer simulation program of population dynamics, *Nsitu* (Cabana et al., 2008), we could eliminate continuity and change via stochastic drift as an explanation of the observed temporal pattern in lineage frequencies (Smith et al., 2009). The data did support the arrival of some new individuals at ~1,000 years ago that differed from the earlier population of the Aleutians, although it did not appear to be an actual replacement event. In this regard, Hrdlička (1945) was at least partly correct.

In an effort to determine the source of the new genetic information and new migrants to the eastern portion of the chain, we undertook additional aDNA studies on human skeletal material from various sites on the Alaska Peninsula (Raff et al., 2010). The results indicated that more mitochondrial diversity existed on the peninsula than in the archipelago in prehistory, at least so far as our samples were adequate to judge. Two individuals from the Brooks River region (Dumond, 1981), both predating European contact by several hundred years, were found to be mtDNA lineage B. While common further south in both North and South America, this lineage had not been reported before in prehistoric Arctic or subarctic populations (Raff et al., 2010), confirming a genetically complex prehistory of the region than earlier studies on modern populations had indicated.

The Eastern Canadian Arctic

The Thule expansion across Arctic North America is one of the most well-known and dramatic migration/replacement events in prehistory. The archaeological record indicates that Thule whalers dispersed across the North American high Arctic from somewhere in north-west Alaska or coastal Chukotka around 800 – 1000 BP, reaching and colonizing western Greenland in a span of 200 years or less (Friesen and Arnold, 2008). The Thule, immediate ancestors of modern Inuit/Iñupiat peoples, supplanted an earlier population in the eastern Arctic, the Palaeo-Eskimo groups known by various archaeological traditions depending on time and place. Despite what seems a clear archaeological record of migration and replacement, some argued that the Thule might have been a local innovation from a Palaeo-Eskimo source population in the east, while others suggested that the Palaeo-Eskimo population, always small and dispersed, had disappeared centuries before the Thule arrival (for example, Park, 2000). Still another archaeologically derived hypotheses was that some of the Palaeo-Eskimo populations did not originate in the west and disperse east in an earlier migration, but rather originated from American Indian populations living south of the Arctic in the middle Holocene (for example, Birket-Smith, 1929). Again, we attempted to test these various hypotheses with molecular genetic data.

With the support of local native communities and the Canadian Museum of Civilization, we obtained skeletal samples from the only three Dorset (Palaeo-Eskimo) remains then available. All came from the region of northern Hudson Bay and Southampton Island. We also secured access to prehistoric (that is, pre-contact) Thule samples from two archaeological sites on the north-west coast of Hudson Bay, Silimiut and Kamarvik (McCartney, 1977). The aDNA results provided strong support for the archaeologically inferred Thule migration and replacement (Table 1B). All of the Thule were found to be mtDNA lineage A, while two of the three Dorset samples were mtDNA lineage D (Hayes, 2002; Hayes et al., 2003, 2005). The third Dorset sample could clearly be shown to not be any of the other known Native American lineages, but the key sequence to confirm lineage D proved impossible to characterise (Hayes, 2002). Nevertheless, the differences in mtDNA lineage frequency strongly suggested separate origins for the Palaeo- and Neo-Eskimo groups and a plausible replacement interpretation.

This inference was given added weight with the analysis of another group of samples from Sadlermiut on Southampton Island. This population was known historically and became extinct in the early twentieth century due to contagious disease introduced by European sailors. The Sadlermiut were known to differ in many cultural traditions from modern Inuit, spoke a language unintelligible to modern Inuit, and lacked many of the components of the modern Inuit tool kit. Indeed, some early ethnographers suggested this population was a remnant Palaeo-Eskimo (Dorset) population that escaped replacement upon arrival of the Thule. The genetic analyses of this population seemed to confirm this suggestion, since the population was composed of nearly equal frequencies of mtDNA lineages A and D, as might be expected in an admixed population (Table 1B). However, recent genomic analyses of a series of Palaeo- and Neo-Eskimo individuals, in addition to ten Sadlermiut samples, clearly demonstrated that the lineage of haplogroup D present in the Sadlermiut (D4b1a2a; formerly a lineage of haplogroup D3) was not shared with any of the Palaeo-Eskimo samples (Raghavan et al., 2014). Indeed, the new genomic data indicated the Sadlermiut were more closely aligned genetically with Neo-Eskimo (Thule) populations rather than Palaeo-Eskimo (Dorset) populations. Thus, the earlier inference of the Sadlermiut being the result of admixture between Dorset and Thule populations is no longer supported (Raghavan et al., 2014).

The results of these analyses confirmed the archaeological inference that the modern Inuit are directly descended from the Thule migrants and that the Palaeo-Eskimo are genetically distinct from the Thule, and could not have given rise to them. Moreover, while it initially appeared that the Sadlermiut were an admixed population of both Dorset and Thule ancestry (Hayes et al., 2003, 2005), higher resolution genomic data from the same populations demonstrates this is most unlikely (Raghavan et al., 2014). At least some of these conclusions were confirmed by Gilbert et al. (2008) who obtained the full mtDNA genome sequence of a Palaeo-Eskimo from western Greenland (dated to >3500 BP). This individual of the Palaeo-Eskimo Saqqaq archaeological tradition was mtDNA lineage D2, the haplogroup D lineage found at high frequency in modern Aleut populations, and at moderate frequency in early Aleutian populations, but not present in the intervening geographic area of the Arctic. This would seem to confirm the west to east migration and dispersal of Palaeo-Eskimo groups rather than an origin in eastern subarctic Indian populations. But the absence of molecular data to inform the archaeology of the central Arctic and northern Alaska was problematic.

A geographic gap - The Alaskan North Slope

These and other genetic studies of North American Arctic populations (for example, Helgason et al., 2006; Raff et al., 2010) clearly demonstrate that while prehistoric populations were occasionally genetically more variable than contemporary populations, modern Arctic populations are nearly monomorphic for mitochondrial lineage A2, reflecting substantial reduction in genetic variation among Arctic populations. Lineage A2 has two sublineages, A2a and A2b, which have distinct geographic distributions. A2a has higher frequencies in the western North American Arctic, where it is nearly fixed among Aleut populations, while A2b is typically higher in frequency in the eastern Arctic. Inuit/Eskimo populations also occasionally have a minor frequency of mtDNA lineage D4b1a2a (generally <3%), while this lineage is absent in Aleuts, where lineage D2 predominates, as it does among the Palaeo-Eskimo samples analysed to date. The origin of these regional patterns is not clear. All appear to be related to the early dispersal of Aleut and Palaeo-Eskimo groups, and later Thule populations, from the north or north-west coast of Alaska – an area for which molecular genetic data is lacking.

Consequently, with M. G. Hayes of Northwestern University and Anne Jensen of the Ukpiagvik Iñupiat Corporation, we initiated ancient and modern DNA studies of the Iñupiat populations of the North Slope of Alaska. Hayes is assaying molecular genetic variation in all of the Iñupiat communities on the Arctic slope of Alaska, while our group at Utah has collected samples from Anne Jensen's archaeological excavations at the Nuvuk village site at the tip of Pt. Barrow, AK. Nuvuk was an Iñupiat village that appears to have been continuously inhabited for well over a thousand years; through the Classic Thule period until nearly the middle of the twentieth century. With the support and encouragement of the local Iñupiat community, the ancient burials that are now eroding into the Arctic Ocean due to increased erosion from storms caused by global climate change, are being identified, carefully excavated and studied prior to re-interment safely inland. This large collection provides an invaluable comparative base for other ancient and modern genetic studies of the region, and not only broadens the geographic coverage of such genetic samples, but covers a critical time period, as well. Most of the burials recovered for molecular sampling date between the tenth and fourteenth centuries.

This large project is not yet complete, but a few early inferences can be made. Based on analyses completed to date, the ancient mtDNA lineages match those found among the modern population of the region. The constellation of mtDNA lineages is consistent with the region being the source for both the Palaeo-Eskimo and the Thule migrations and colonizations of the North American high Arctic, with both A2 lineages being present in frequencies consistent with the known geographic clines in these lineages, and the presence of both mtDNA D lineages, not typical in other Arctic regions, where one or the other is present, but not both. As additional population analyses are completed on this project, we expect to provide additional clarification to the origin of dispersing populations in the American Arctic, and more clearly understand the population dynamics of colonizing populations in this challenging environment that will be useful in reformulating our views on continental colonizations at earlier points in time.

Lessons learned

Several important insights have been obtained by using molecular genetic methods to test archaeological hypotheses. Reduced genetic variability is often the result of a restriction in population size, a bottleneck, at some time in the past. The fairly dramatic reduction in the number of mtDNA lineages in the North American Arctic might suggest a population bottleneck at founding, that is, at colonization, that could indicate a general pattern of bottleneck and genetic variation loss in other colonization contexts. However, Marchani et al. (2007), examining the reduction of mtDNA variability in the American Arctic relative to the greater diversity found in potential source populations in north-east Siberia found that a dramatic founder effect was not a requirement for lineage loss. The effects of a bottleneck on genetic variation are measured by the Severity Index (SI), which is the ratio of the duration of the bottleneck to the effective population size during the bottleneck. Marchani et al. (2007) found that the SI for early Thule populations ranged between 0.10 – 0.44 under realistic demographic parameters that were consistent with ethnographic and archaeological evidence. This is only a mild to moderate bottleneck, indicating that extreme population reduction is not necessary for lineage loss in migrating colonizing populations. Indeed, the loss of mtDNA lineage variation was consistent with effective population sizes of ~250, perhaps more. Census size would be substantially larger, indicating that fairly large populations may have been involved in both the migration and colonization of the Arctic, but nevertheless associated with a reduction in genetic variation. While this is counter-intuitive from a genetic perspective, it is consistent with the archaeological evidence of much larger effective sizes among the prehistoric Thule whalers than among the less economically specialized Palaeo-Eskimo populations that preceded them.

This lesson is echoed in a recent study of aDNA analyses conducted in the Americas. O'Rourke et al. (2000) reviewed the then limited set of aDNA studies in the Americas and found that 1) there was little evidence of reduced genetic variation in the ancient samples, measured by nucleotide diversity, compared to modern population genetic samples and 2) the strong geographic structure to mtDNA lineage variation was present even in the earliest aDNA samples studied. This implied that the geographic structure of modern indigenous populations of the Americas is of considerable antiquity. But this early review was based on only six aDNA studies published to that time and the oldest samples were barely 1,500 – 2,000 years in age. Raff et al. (2011) updated this analysis by examining over 60 aDNA studies conducted in the Americas over the previous decade and concluded that the geographic structure in mtDNA lineages is even stronger than suspected (Figure 2) and that there is little evidence to indicate that the ancient samples are any less variable at the DNA sequence level than modern samples. Indeed, it may be that earlier populations were slightly more genetically variable than modern populations and that apparent loss of variability may have less to do with founding populations at colonization than with loss of variation as a result of demographic collapse at contact. Moreover, an Analysis of Variance of the lineage frequencies in these aDNA studies indicated that while there was no discernable temporal effect on genetic variation at the continental level (nor any temporal x regional interaction), the geographic effects on lineage distribution was highly significant (F-10.286; $p<0.001$; Raff et al., 2011). These general trends will not hold for every population (for example, some regions exhibit lineage diversity increases over time, others diversity loss and still others show no change over time), but the general patterns of regional structure are well established and of long standing. In the present context, it is worth noting the placement of the Arctic populations at some distance from other regional populations of the Americas in Figure 2, and the similarity in the lineage distributions between the ancient and modern Arctic populations examined. These observations highlight the separate and later entry of colonizing populations into the North American Arctic compared to the Native American populations living at lower latitudes. Finally, it is worth emphasizing that the temporal frame covered by Raff *et al.*'s (2011) review is over 4,000 years, substantially extending the origin of the geographic structure of mtDNA lineage variation in the Americas.

These lessons are not unique or specific to the Arctic. Much debate has occurred as to the importance of small founding populations at the initial colonization of the Western Hemisphere by populations migrating through or along the Beringian land bridge (Goebel et al., 2008; Perego et al., 2010; O'Rourke and Raff, 2010; O'Rourke, 2011; Hoffecker et al., 2014). In the traditional view of American colonization, very small founding populations moved south between receding ice sheets to rapidly colonize the two continents. Almost by definition this model of colonization would require founding bottlenecks that would result in a substantial reduction of genetic variation. At first blush, the data reviewed above would seem to be consistent with this interpretation. But all of the data presented here is based on mtDNA, a single, uniparentally inherited genome that is particularly susceptible to intergenerational sampling error, genetic drift and hence, loss of lineages over time, even in moderately sized populations. A better measure of changes in effective population size and genetic variation comes from the nuclear genome. Unfortunately, we have only a very limited amount of nuclear genomic data on indigenous American populations at present. But this, too, is changing. Genomic screens by Wang et al. (2007) and Reich et al. (2012) indicate that there is only minimal reduction in genetic variation among Native American populations (for example, <7% in Wang, et al., 2007), drawing into question the assumption of small populations at founding. Perhaps this should come as no surprise, since Ward et al. (1991) suggested early on that there was little evidence of a bottleneck in even mitochondrial DNA sequence data even if some lineages had been lost. Thus, the lessons learned by studying the latest long-range migration and colonization event in the North American Arctic may well provide a foundation for how we view the original colonization of the Americas and the population dynamics associated with that momentous event.

Conclusions

The use of newer, higher resolution genetic data, in conjunction with the constantly growing archaeological record, is a powerful inferential approach to the past. It facilitates both the refining of hypotheses of prehistoric population dynamics, and their more effective and efficient test, as well. Indeed, there is little reason to stop at the use of human molecular data.

Understanding the population dynamics of human prey species and resource items via similar molecular genetic analyses can tell us much about their human consumers (for example, Broughton et al., 2012). Not only can archaeo-faunal and archaeo-botanical materials tell us much about their human consumers, obligate human pathogens are also accessible via aDNA analyses and serve as effective proxies for human movement in the past. For example, genomic variation in a number of obligate human pathogens, including JC virus (Sugimoto, et al., 1997) and *H. pylori* (Ghose et al., 2002; Moodley et al., 2009), would seem to only be consistent with two or more independent colonization events, rather than the single one often favoured by modern geneticists (but see Reich et al., 2014 for an alternative genetic view). In the case of *H. pylori*, the existing genomic variation is consistent with a founding greater than 12,000 years ago and with no bottleneck (Ghose et al., 2002). How this translates to the population dynamics of the human host at introduction remains to be fully elucidated, but raises questions with respect to the standard view of American colonization.

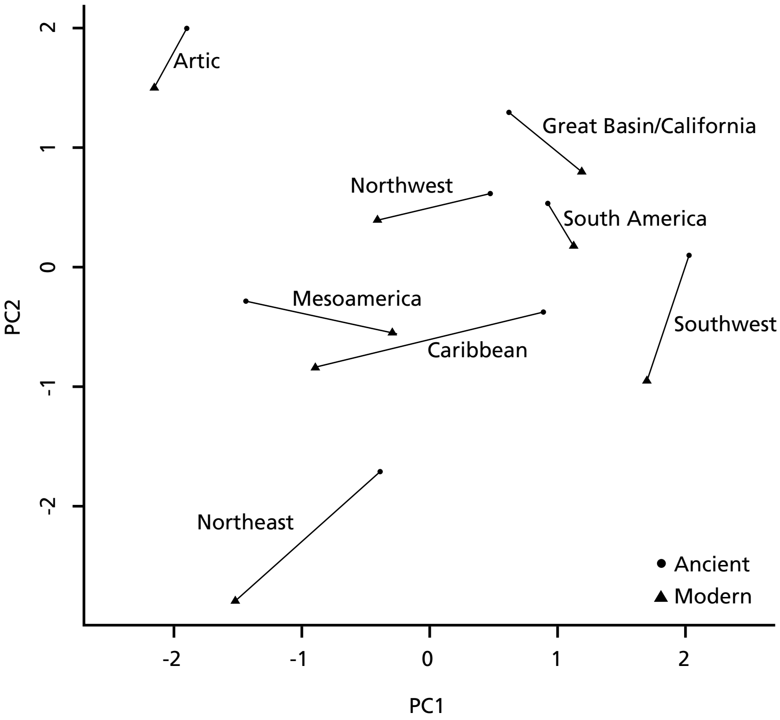

Figure 2. Plot of first two principal components of modern and ancient mtDNA lineage frequencies in the Americas. Filled circles represent plot of modern population mtDNA diversity while filled triangles reflect the position of the same diversity observed in ancient samples. Source: Raff, et al., 2011.

It has not been possible here to review another important area of research that also impacts the reconstruction of prehistory using molecular and chemical approaches. Isotopic analyses of human remains, as well as archaeo-faunal and archaeo-botanical material, is an important adjunct especially for aDNA analyses (Coltrain et al., 2004). Inferences are stronger and more robust with a combined aDNA/isotopic analysis that either provides alone. Incorporating faunal and botanical analyses can also clarify questions of dietary composition, local adaptive strategies and in specific contexts, aid in refining AMS ^{14}C dating (for example, calibrating the marine reservoir effect, Coltrain et al., 2006).

As useful as I think such combined molecular and archaeological approaches are for both regional history and continental level colonization models, all such inferences are based on an oversimplification of the relevant environments in which early populations lived. Palaeo-environments and palaeoclimates were not uniform, but temporally and spatially heterogeneous (Hoffecker et al., 2014). As newer methods of palaeoecological reconstruction provide increasing resolution to our view of early landscapes and human environments, the integration of these environmental reconstructions with the archaeological and genomic records of humans and their resource bases, and their pathogens, will lead to a true science of the past.

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Human Skeletal Evidence for the Peopling of North America: A Palaeoanthropological and Historical Perspective

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Introduction

In addition to his pioneering observations on altitude sickness, geology and history in Peru and Mexico, the Jesuit priest, José de Acosta (1539-1600), was the first to formally assert that Native Americans must have derived from Asian populations (Burgaleta, 1999). In his book, *Historia natural y moral de las Indias* (*Natural and Moral History of the Indies*), published in Seville in 1590, de Acosta marshalled biological and cultural observations made on Native Americans during his fifteen years in the New World to support his assertion and even suggested a land crossing across what would now be considered the Bering Strait land bridge (de Acosta, 2002). The Asian ancestry of Native Americans was firmly established in the literature by the beginning of the twentieth century and is evident in influential works on human biology, based largely on anatomical features of living and skeletal populations, throughout the century (for example, Deniker, 1909; Hrdlička, 1925; Hooton, 1932; Eickstedt, 1934; Coon, 1965; Stewart, 1960, 1973; Laughlin and Harper, 1979). Analysis of dental morphology, particularly the presence of shovel-shaping of the incisors (Hrdlička, 1920), has been emphasised in this context (Scott and Turner, 1997). The Asian-Native American connection has been further solidified by increasingly greater genetic knowledge based on autosomal, mitochondrial and Y-chromosome DNA (Crawford, 1998; Goebel et al., 2008; O'Rourke and Raff, 2010; Reich et al., 2012; Raghavan et al., 2014), including human DNA extracted from Palaeoindian-aged coprolites (Jenkins et al., 2012).

The exact age of the appearance of Native American ancestors in the New World has long been a matter of some debate (see discussion in Meltzer, 2009 and Klein, 2009). While today it is generally accepted that humans did not arrive in the New World until toward the end or after the Late Glacial Maximum or LGM (recently dated to between 26,500 and 19,000 years ago – Clark et al., 2009), that was not always the case. In the nineteenth and early twentieth centuries, arguments for the existence of 'Pleistocene Man' or even earlier forms, in the New World were not uncommon; and some examples are considered later in this review. With this in mind, I assess the record of the earliest North America human skeletal remains from the perspective of palaeoanthropology, rather than bioarchaeology. A baseline for this consideration will be my 1976 review of the earliest skeletal evidence for humans in North America (Smith 1976). I will illustrate how and why the list of early remains is far different today than forty years ago. Additionally, I provide some historical perspective on certain debates concerning the nature of Native American origins, including the role of Aleš Hrdlička's often misunderstood or misrepresented views on the age of humans in the New World.

European Challenges

A relatively recent challenge to the Asian derivation, or at least total Asian derivation, of Native Americans has arisen from data suggesting that the earliest people in the New World were not specifically Asian in cranial morphology. This interpretation was particularly highlighted by the original interpretations of the Kennewick skeleton, found along the Columbia River in Washington in 1996. This virtually complete skeleton was initially analysed by Chatters (2000) who noted that the skull did not exhibit typically Asian features. In some early discussions of the material, the skull was described as 'Caucasoid' by Chatters, but he later noted that this was not the most appropriate terminology (Chatters, 2001). The European character of the skull actually was emphasised more by early media accounts than by scientists, but Chatters also notes that he and others who initially examined the specimen were doing so from more of a forensic anthropology paradigm than an evolutionary one (Chatters, 2001). This certainly led to an emphasis of the apparent non-Asian features of the specimen.

From a historical perspective, and in the context of more typological constructs, it should be noted that even living Native Americans were generally considered to be a somewhat distinctive 'type' of Asian. For example, in describing Native Americans a half-century ago, Coon (1965, p.152) wrote that they are Asians '… of a peculiar kind, just as they would be Caucasians of a particular kind had the New World been peopled by a small band of Upper Palaeolithic Europeans…'. Coon also noted that Native Americans differed from other Asians in aspects of the central face, some of the same features that

Chatters relied on. Even before Kennewick's discovery, analyses by Steele and Powell (1992, p.140) demonstrated that pre-Holocene North American Palaeoindian crania - with their long, narrow cranial vault and short, narrow faces – fell '…at the periphery of modern north Asian and North American Indian populations and near the Australian and southern Pacific rim populations.' Several other analyses have confirmed the morphological distinctions between Palaeoindian crania and those of later Native Americans (for example, Neves and Pucciarelli, 1991; Lahr, 1995; Jantz and Owsley, 2001, 2005; Powell, 2005). Most recently, Jantz and Spradley (2014) specifically demonstrated Kennewick's affinities to Pacific Rim, particularly Polynesian, populations on the basis of cranial morphometrics and Gill (2014) came to the same conclusions on the basis of discrete traits. Brace and colleagues (2014) found close morphometric relationships between Kennewick and the Ainu and Jomon peoples of Japan. Hubbe and colleagues (2011) found that several early New World crania (not including Kennewick) showed close morphological affinities with a sample of late Palaeolithic specimens from Europe, west Asia and China. They concluded that early Native Americans were part of a regionally mostly undifferentiated sample of early modern humans that existed prior to the emergence of regionally specific morphological features. These studies show that pre-Holocene Palaeoindians are part of a more 'generalised' cranial morphological pattern that characterizes some recent eastern Pacific Rim populations but lack many of the more recently-evolved features characteristic of recent modern Native Americans and north Asians. The similarity to Polynesians is taken as support for a coastal route as a major factor in populating the Americas (Jantz & Owsley 2001, 2005; Jantz and Spradley 2014), which might help explain the very early dates for human presence in South America (see Gibbons, 2014).

Extraction of a high-coverage genome from the Clovis-associated Anzick 1 male infant, dated to between 12,556 and 12,707 years BP (calibrated ^{14}C), adds additional strong support for the Asian derivation of Native Americans, as does the genome of a ~24,000 year old individual from Siberia (Rasmussen et al., 2014) and the recent genomic analysis of the Kennewick skeleton itself (Rasmussen et al., 2015). Results of a genome-wide analysis comparing Anzick 1 to 143 non-African modern populations demonstrated that Anzick 1 showed statistically significant closer relationships to all 52 Native American groups than to any of the Eurasian samples examined (Rasmussen et al., 2014). Furthermore, the Anzick infant reflects distinct evidence of gene flow from the ~24,000 year old individual (MA-1) from the Siberian Upper Palaeolithic site of Mal'ta (Raghavan et al., 2014). The Mal'ta genome is described as 'basal' to western Eurasians, closely related to Native Americans, but lacking strong connections to recent east Asians (Raghavan et al., 2014, p.505). The Kennewick "Ancient One" demonstrates closer genetic similarity to Native Americans than to any other group, but interestingly is more related to Native American lineages to the south than in the northern regions of North America (Rasmussen et al., 2015).

The connection of Siberia to western Eurasians is not really surprising. Fifty years ago, the palaeoanthropologist, Andor Thoma (1964, 1973), pointed to distinct similarities between west Eurasian Neanderthals and Palaeosiberians, leading him to suggest what could be termed a 'European' connection between these regions in deep time. The Palaeosiberians, in Thoma's model, reached southern Siberia and there '…under strong selection pressure of the new environment, they were transformed into the proto-mongoloids' (Thoma, 1973: 531). Although the terminology is archaic, the 'Palaeosiberians' and 'proto-mongoloids' reflect the generalised structure and midfacial features that characterize the pre-Holocene Palaeoindians and other groups discussed above. In addition to the Mal'ta gemonic evidence, Thoma's model has been strengthened by recent morphological and genetic studies that demonstrate a Neanderthal presence in south-western Siberia (Krause et al., 2007; Prüfer et al., 2014). Thus, if pre-Holocene Palaeoindians and even recent Native Americans can trace as much as a third of their ancestry to 'western Eurasia' (Balter, 2013), the explanation for this is a pattern of population movement from western Eurasia to the east that occurred, or at least began, long before human migrations across Beringia. This means the 'European' features that have confused understanding of the ancestry of Palaeoindians result from deep-time population history of north-western Asia, not from a more direct European source.

Such a more direct possible source for European impact on Palaeoindians has taken the form of a model positing a trans-Atlantic origin for Palaeoindians (Bradley and Stafford, 2004). Termed the Solutrean hypothesis, this model sees strong similarities between Palaeoindian lithic technology and that of the Solutrean. The Solutrean is a European Upper Palaeolithic complex that is found in south-western Europe from about 21,000 to 16,500 years ago and is characterized by precisely flaked leaf points and other points of various sizes and shapes (Klein, 2009). Fossil human remains clearly associated with the Solutrean are rare, fragmentary, and/or of uncertain context (for example, see Smith et al., 1999), thus precluding systematic skeletal comparisons with Palaeoindians. Thus, the Solutrean hypothesis is based primarily on the lithics and some other indirect evidence (Stafford and Bradley, 2012). An analysis of the lithic and other arguments is beyond the scope of this review, but it is noteworthy that these Solutrean/Palaeoindian connections have been suggested before (see Fiedel, 2004) and rejected on both archaeological and other grounds (for example, Straus et al., 2005; Fiedel, 2004). Certainly there are no biological data to specifically support the Solutrean hypothesis and any 'European' biological aspects of Palaeoindians are easily explained by the deep-time connections presented above.

Age of the initial appearance of humans in the New World

The primary evidence germane to human appearance in the Americas has traditionally been the archaeological record and the earliest widespread evidence is the Clovis culture, dated to between 13,600 and 12, 800 years ago and found in the continental United States (Walters and Stafford, 2007). Dates for well-established non-Clovis complexes in Alaska go back to about 14,000 BP and begin to exhibit considerable variation soon thereafter (Goebel et al., 2008). Sites with tools or evidence of human cultural activity purported to be earlier are not compelling - including Calico Hills, Tule Springs, Old Crow and Bluefish Cave (see review in Goebel et al., 2008). However, evidence for pre-Clovis occupations south of Alaska and Beringia is steadily increasing in both quantity and quality (see Gibbons, 2014) as is the evidence for non-Clovis groups generally contemporaneous with Clovis (Jenkins et al., 2012). Still, the oldest of these approaches an age of about 15,000 years ago. Genetic estimates also support a split between Native American and north Asian populations during or just after the LGM, with estimated coalescence dates for three subclades of the C1 mitochondrial haplotype falling between 16,600 and 11,200 years ago (Goebel et al., 2008).

However, this relatively late date for human emergence in the New World has not always been so clear. Specimens such as the Trenton crania, Calaveras skull, Natchez os coxae, Nebraska 'loess' skulls and numerous others were suggested as likely candidates for a much earlier presence of humans in North America (see review in Hrdlička, 1907). Florentino Ameghino (1879) claimed great antiquity for human skeletal remains in South America, especially in Argentina, and ultimately developed a phylogeny of human evolution that derived humans from fossil monkeys he discovered, also in Argentina (Ameghino, 1910, 1911). Finally, the so-called Nebraska man, actually based on a single molar and named '*Hesperopithecus haroldcookii*' in 1922, was touted as a North American anthropoid, indicating that ape (and possible human) evolution could have played out in North America as well as the Old World (Osborn, 1922). Five years later, it was demonstrated that the tooth was from a peccary (Gregory, 1927). Still these arguments regarding human evolution in the New World created a bit of a theoretical and methodological crisis for American anthropology at the time. It is in this framework that the work of Aleš Hrdlička, one of the founders of systematic and scientific biological anthropology in the United States (Spencer, 1979), is best understood and the misconceptions concerning his ideas best addressed.

Aleš Hrdliča's model for 'peopling of the world'

Hrdlička's view on the origin of Native Americans is not an isolated idea but rather one aspect of his perception of the origin and spread of modern humans throughout the world. These views are presented in a number of publications (for example, Hrdlička, 1920, 1921, 1930, 1939) but sometimes are a bit difficult to isolate from other aspects of his detailed publications (see Spencer and Smith, 1981). Hrdlička basically viewed the origin and spread of modern people in four stages (Hrdlička, 1921). The first was a dispersal of Neanderthals throughout Europe and North Africa, terminating in the emergence of the earliest modern humans, which he termed 'western Palaeolithic man.' Unlike most of his contemporaries, Hrdlička saw the Neanderthals as the logical ancestor of modern humans and believed that early modern specimens, like those from Předmostí (now in the Czech Republic) represented transitional forms between Neanderthals and later modern people (Hrdlička, 1927, 1930). In the second phase, 'western Palaeolithic man' diversified into specific racial types and for the first time established a foothold in Asia. The third phase witnessed populations entering Asia and moving north and east, eventually populating Siberia and then the Americas. The fourth phase in Hrdlička's scheme was the populating of the Pacific islands and the differentiation of peoples in the Old and New World into the current pattern of human biocultural variation.

Hrdlička's insistence that humans did not have a deep ancestry in the New World is fully understandable in light of this model and his insistence on rigorous scientific evidence to support ideas about humans in the past. Between 1898 and 1912 he made a detailed study of all the available evidence attributed to early humans in the New World. He argued strongly that careful analysis of the stratigraphy and context of human skeletal remains, as well as of the skeletal remains themselves, was critical to claims for antiquity and he found that such analyses were unfortunately often inadequate in the case of the purported early American remains (Hrdlička, 1907, 1912). Because of his experience with Neanderthals and earlier fossil humans, Hrdlička felt that evidence of archaic morphology, as well as geological antiquity, was necessary to establish deep antiquity for human skeletal remains. For example, in 1918 (p. 36) he wrote that '…anthropology has a right to expect that human remains of whatever nature assigned to great antiquity should show some adjustment in structural type to such antiquity.' His examination of specimens in the Americas purported to derive from the Pleistocene yielded no such evidence of 'primitive' features - no evidence of anything like Neanderthals in Europe (Hrdlička, 1907, 1912, 1937). At the conclusion of his 1907 monograph, Hrdlička wrote that '…in every instance where enough of the bones is preserved for comparison the stomatological evidence bears witness against their geological antiquity and for their close affinity to or identity with those of the modern Indian' (Hrdlička, 1907, p.98). He goes on to note that this does not preclude the possibility that earlier humans were in the Americas but only that definitive morphological and geological proof thereof was not available in 1907. Such proof never materialised during his career (Hrdlička, 1937).

Hrdlička was perhaps too zealous in his insistence that the earliest American skeletons did not differ significantly from more recent Native Americans. However, it is important to remember the framework in which these pronouncements were made. Although he never specifically declares this to be the case, Hrdlička is clearly approaching the study of these early American remains from an evolutionary perspective. Yes, he was a taxonomic 'pigeon-holer' when it came to recent human crania and in assessments of these purportedly early skeletons he does make reference to specific racial groups recognized at that time. However, it is also the case that his primary perspective on these particular specimens was to assess their antiquity and their evolutionary relationships. In other words, were they modern humans or some archaic human form? Hrdlička's analyses clearly pointed to the former, and I contend that his equating of these early specimens with 'the modern Indian,' as he often wrote, was primarily a means of underscoring their basic modernity and less about their specific affinities within modern humans. It is that same evolutionary viewpoint that characterizes Stewart's perspective on these earliest American skeletons (Stewart, 1973) and my own similar statements three years later (Smith 1976). As Chatters comments concerning his use of 'Caucasoid' to describe Kennewick, I should have been more precise by clearly attributing the morphology of remains known in 1976 to modern humans and not comparing them specifically to more recent Native Americans. In the conclusion, I did state that '…from a morphological point of view, the earliest suggested American Indian remains do not align them with any hominid form other than *Homo sapiens sapiens*' (Smith, 1976, p.140). As I believe was largely the case for Hrdlička, my perspective on the material was palaeoanthropological (evolutionary), not a forensic or bioarchaeological one.

SITE (STATE)	DATE (METHOD)	PORTIONS PRESERVED (SEX/AGE)
Arlington Springs (California)	10,000 + 310 (A) 10,000 + 200 (B)	femoral and other postcranial fragments (?/adult)
Brown's Valley (Minnesota)	8,000 – 10,000 (C)	cranium and mandible (♂/adult)
Gordon Creek (Colorado)	9,700 + 250 (A)	cranium, mandible, partial postcranium (♀/adult)
Laguna Beach (California)	17,150 + 1,470 (A)	fragmentary cranial and postcranial bones (?/adult)
Los Angeles (California)	23,600 + 1,100 (A)	fragmentary calvaria and postcranial bones (♀/adult)
Marmes (Washington)	10,687 + 215 (B)	cranial, mandibular and postcranial fragments (?/adult)
Melbourne (Florida)	Late Pleistocene (C)	cranial, mandibular, and postcranial fragments (♀/adult)
Midland (Texas)	7,100 + 100 (B)	fragmentary cranium, some postcranial elements (♀/adult)
Minnesota (Minnesota)	Late Pleistocene (C)	cranium, mandible, mostly complete postcranial skeleton (♀/adolescent)
Natchez (Mississippi)	Late Pleistocene (C)	os coxa (♀/adult)
Rancho La Brea (California)	9,000 + 80 (A)	cranium, mandible, some postcranial elements (♀/adult)
San Diego (California)	48,000; 44,000; 28,000 (D)	three partial skeletons (adults)
Taber (Alberta)	30,000 (C)	cranial, mandibular, and postcranial fragments (?/infant)
Tepexpan (Mexico)	11,000 + 500 (A)	cranium, mandible, some postcranial remains (♀/adult)
Vero Beach (Florida)	Late Pleistocene (C)	calvaria, mandible and postcranial fragments (♀/adult)

(A) Direct standard and uncalibrated radiocarbon date on bone collagen from the specimen
(B) Direct standard and uncalibrated radiocarbon dating of associated remains
(C) Dating by geological, faunal, or other relative technique
(D) Amino acid racemization dating

Table 1. Possible Remains of the Earliest Native Americans. This list is a slightly modified version of Table 1 in Smith (1976). The modifications are in how the information on each specimen is presented. The specimens list and dates are unaltered from the 1976 list.

The skeletal remains of the earliest Americans: the 1976 survey

In 1976, I prepared a review of human skeletal remains from North America that were posited to date from the Pleistocene or very early Holocene at that time. Reviews of this evidence were provided on several occasions during the early twentieth century by Hrdlička (1907, 1918, 1937) and by his successor at the Smithsonian Institution, T. Dale Stewart (1960, 1973). By 1976, new chronometric dates were presented for several specimens, some of which suggested older ages than were available to Stewart (Bada and Helfman, 1975; Bada et al., 1974a,b; Berger, 1975; Berger et al., 1971; Bischoff et al., 1976). These results added new skeletal candidates and older dates to the debate which I felt warranted consideration. Table 1 lists the sites and specimens I considered in 1976. I excluded specimens that were dated or thought to younger than 8,000 years BP, as well as specimens for which a Pleistocene age had already been convincingly countered. I did include the Natchez os coxa because of its early discovery date, between 1837 and 1844, but only for historical reasons. I somewhat arbitrarily limited my focus to North America and although I was able to study the material from Minnesota listed here at a later date, the data and observations I made use of in 1976 were extracted totally from the literature.

My overall conclusion, based on the human skeletal material and chronological information available in 1976, was that there was not compelling skeletal evidence of humans in the New World older than between 20,000 and 27,000 years BP and, as noted above, that none of these specimens exhibited anything but modern human anatomy (Smith, 1976, pp.139-140). The date of 20,000- 27,000 years BP was an extrapolation based on a radiocarbon date published for the Yuha site (Bischoff et al., 1976), as well as dates on the Los Angeles and Laguna Beach specimens. I expressed doubts about older ages attributed to skeletal remains in two cases: the Taber infant skeleton – suggested to be ~30,000 years old (or more) and the so-called San Diego skeletons, dated to as much as 48,000 years BP. Table 1 is quite different from subsequent listings of early American skeletal remains (for example, Steele and Powell, 1992; Fiedel, 2004; Lepper, 2014) and an assessment of why the picture has changed so extensively will provide some insights into the problems often faced in accurately determining the age and context of specimens, particularly those actually or potentially of considerable antiquity. Three examples highlight these problems very well.

Taber

The Taber infant skeleton was found in 1961 in south-western Alberta. This fragmentary skeleton was recovered in calcium carbonate-cemented sands that appeared to lie between two glacial tills, the upper one representing the Wisconsin glacial maximum (Stalker, 1969). There were no direct dates on the specimen, but its geologic context suggested an age in excess of 18,000 and perhaps as old as 60,000 years (Stalker, 1969). I chose 30,000 years as a conservative estimate of the specimen's geological age based on the information available in 1976. There were no cultural associations with the skeleton and the young age-at-death of the individual and its fragmentary condition precluded extensive morphological analysis. However, published photographs (Langston and Oschinsky, 1963) show exclusively modern infant cranial features. I noted concerns about the geological context but did not rule out the possibility that a late Pleistocene age might be accurate and thus would represent early biological evidence of a modern human presence in North America (Smith, 1976, pp.129-130).

However, the case for Taber's antiquity began to unravel soon after 1976. In the late 1970s, another team returned to the site to attempt to establish the skeleton's context (Wilson et al., 1983). No further skeletal remains were found, but a series of bone-bearing Holocene sand patches were noted. Analysis of the sand matrix still adhering to the Taber infant were a much closer match in chemical makeup and colour to these Holocene sands than to the Pleistocene alluvial deposits (Wilson et al., 1983). The last blow to a Pleistocene age for Taber came when a small segment of the infant skeleton was dated using the AMS radiocarbon method. The resulting age of 3,550 ± 500 radiocarbon years BP (Brown et al., 1983), places the skeleton in the middle Holocene, far younger than the ages claimed for it previously.

San Diego skeletons

A second example concerns the specimens I listed as the San Diego skeletons in 1976. The San Diego skeletons were remains of several individuals found in and around La Jolla and Del Mar, California. These specimens were studied in detail by Rogers (1963, 1974), whose descriptions clearly establish all of the specimens as anatomically modern. Table 2 gives the dates given estimated for the various specimens. These dates, ranging between 48,000 and 27,000 years ago, were all determined by amino acid racemization dating, a technique that measures the rate of protein diagenesis in bone or shell (Bada and Helfman, 1975). Amino acid racemization was the new rage in the mid-1970s and appeared to hold great promise for dating of skeletal remains. One reason there was so much excitement about the techniques was that it provided the possibility of determining chronometric ages for human remains, both biological and cultural, that were older than the range of radiocarbon at that time. The period from 40,000 BP back to 100,000 years ago or so was a bit of a black hole in terms of accurate chronometric dating at that time, and this was a critical period for understanding the pattern of modern human origins and the role of various archaic human forms, like the Neanderthals, in that process. The San Diego dates emerged in the context of this enthusiasm about amino acid racemization's potential impact on the study of human evolution. These dates are still the earliest chronometric dates ever associated with early Native American skeletal remains and they created quite a stir in the 1970s.

Although in today's world of better chronology for the appearance of modern humans, 48,000 years BP might not seem so problematic, but in mid-1970s there was no compelling evidence that modern humans existed anywhere earlier than perhaps 40,000 to 45,000 years ago (see Smith, 1985). So a claim of an age of as much as 48,000 years for modern humans anywhere in the world back then was a really big deal, but it was especially so in North America. Because amino acid racemization was a relatively new technique, there was concern that various factors (most prominently temperature during burial or in areas where remains were stored after excavation) could affect the ages determined and such concerns were expressed regarding the age estimates for these burials (Protsch, 1975; see also discussion in Smith, 1976). Also for some specimens, there were already standard radiocarbon dates on associated material of the La Jollan culture ranging from 5,460 ± 100 to 7,370 ± 100 radiocarbon years BP (Rogers, 1963) that cast a shadow of doubt on the older dates. Subsequently, a series of AMS radiocarbon dates on the same skeletal specimens produced ages that range from 4,820 to 6,330 radiocarbon years BP (Bada et al., 1984a; Taylor et al., 1985). The AMS dates are comparable in age to the standard ^{14}C dates on the La Jollan cultural material; and while this antiquity is certainly respectable for North America, the San Diego skeletons are certainly far younger than they were claimed to be in the 1970s.

Table 2. Amino Acid Racemization Dates for the San Diego Skeletons in 1976 (adapted from Bada et al. (1974a: p.791) and Bada and Helfman (1975, Table 7).

Specimen No. – Location	Date
W-34A – Del Mar	48,000 BP
W-34A – Del Mar	47,000 BP
W-34A- Del Mar	41,000 BP
W-2 – South of Scripps	44,000 BP
W-2 – South of Scripps	27,000 BP
W-12A – North of Scripps	39,000 BP
W-12A – North of Scripp	27,000 BP
W-99 – Batiquitos Lagoon	45,000 BP

Laguna Beach, Los Angeles and Yuha

Single specimens from these three sites represented the other remains purportedly dated around 20,000 years ago back in 1976. Both Laguna Beach and Los Angeles are partial crania that are fully anatomically modern and were dated to 17,150 ± 1470 and >23,600 radiocarbon years ago, respectively (see Plhak, 1978, 1980). The Los Angeles specimen also yielded an amino acid racemization date of 26,000 BP (Bada and Helfman, 1975). Both specimens lack archaeological associations. As with the San Diego skeletons, subsequent direct AMS radiocarbon dating has determined ages of 5,100 radiocarbon years for Laguna Beach (Bada et al., 1984) and 3,560 for Los Angeles (Taylor et al., 1985). These dates indicate that the Los Angeles and Laguna Beach specimens are mid-Holocene, not Pleistocene, in age.

In the case of the Yuha burial, caliche covering one of the bones of burial was dated to 21,500 ± 1,000 years BP by standard radiocarbon analysis (Bischoff et al., 1976) and an age of 23,600 ± 2,600 BP was later determined based on amino acid racemization (Bischoff and Childers, 1979). However, doubts about the dating were quickly raised, based primarily on the cultural similarity of the Yuha burial to Holocene cairn burials in California deserts (Wilkie, 1978). Subsequent AMS radiocarbon dating directly on the skeleton yielded dates of <4 Ka BP, supporting the mid-Holocene age for the Yuha burial (Stafford et al., 2004).

What's left and what's new – a concluding perspective

All of the human skeletal specimens suggested in 1976 to demonstrate an age of more than 12,000 years for humans in North America have been shown to be much younger than they were then claimed to be. Even the Tepexpan skeleton (Mexico) is no longer considered 11,000 years old (or older), but rather about half that age based on a uranium series date of 4,700 ± 200 years BP (Lamb et al., 2009). Comparison with the most recent compilation of dates for early material in North America (Lepper, 2014) shows that only seven specimens from my 1976 list are still considered to exceed 8,000 years of age. These specimens and the ages available for them in 1976 and now are given in Table 3. The oldest of these, Arlington Springs, is now dated almost 1,000 years earlier than in 1976. Gordon Creek and Rancho La Brea still use the same dates that were available in 1976. The Browns Valley and Minnesota (Pelican Rapids) skeletons from Minnesota had estimated ages in 1976, but these estimates have been generally confirmed by direct ^{14}C dates (O'Connell et al., 2013). Midland is considered about 10,000 years old, but this is not based on chronometric dating; and the Marmes specimens now have ^{14}C dates that are about 1,000 years less than in 1976. Of course, there are now several other specimens not known or recognized in 1976, so that the sample size for specimens dated earlier than 8,000 years BP is now much larger and more informative (Fiedel, 2004; Powell, 2005; Lepper, 2014). Still, it is important to note that no specimen dates earlier than 13,500 radiocarbon years BP and most are less than 11,000 radiocarbon years BP. Thus, my two major points from 1976 remain basically supported by these new and improved data: skeletal remains in North America belong to modern *Homo sapiens* (*H. s. sapiens*) and there is no skeletal evidence for humans older than 27,000 years on this continent. In fact, current evidence demonstrates that I was too generous in my estimate, as there is no such evidence older that about 16,000 calendar years BP.

Several of the specimens added to the list of earliest Native Americans were recovered in Mexico, including most recently the Hoyo Negro specimen, dating to 10,960±20 radiocarbon years BP (Chatters et al., 2014). Although gracile, this female skeleton exhibits the generalised Palaeoindian morphological pattern discussed previously and does not demonstrate specific affinities to more recent Native Americans; and its D1 mitochondrial DNA haplotype, while derived from Asians, is unique to Americans (Chatters et al., 2014). The Hoya Negro specimen, along with other Mexican remains of comparable age (see Lepper, 2014: Table 1.1) shows that the distinctively generalised morphology indicated for Kennewick and other Palaeoindian age-equivalent remains in the United States and Canada also extends into Mexico. Work by Neves and colleagues (Neves and Pucciarelli, 1991; Neves and Hubbe, 2005; Hubbe et al., 2010, 2011) demonstrates the extension of this morphological pattern into South America as well.

Table 3. Specimens from Smith (1976) considered to date earlier than 8,000 BP. See Table 1 for the basis of the 1976 dates. All dates are uncalibrated. For details of the Pelican Rapids and Browns Valley dates, see O'Connell et al. (2013). For the remainder of the 2014 dates and a complete list of specimens now considered 8,000 years old or older, see Lepper (2014).

Site/Specimen	1976 Date	2014 Date
Arlington Springs	10,000+310	10,960+380
Brawns Valley	8,000-10,000	9,049+82/-72
Gordon Creek	9,700+250	Same as 1976
Marmes	10,687+215	9,870+50; 9,430+40
Midland	7,100+100	c. 10,000
Minnesota (Pelican Rapids)	Late Pleistocene	7,840+70
Rancho La Brea	9,000+82	Same as 1976

In a general sense, the fact that these early Americans do not show a clear indication of more derived Asian morphological features is easily understandable in a broader evolutionary perspective. In fact, prior to the mid-Holocene there are very few skeletal specimens that can clearly be aligned with any modern so-called 'racial' morphological pattern (see Lahr, 1995). An excellent example of this is the case of the three Zhoukoudian Upper Cave or Shandingdong crania first studied by Weidenreich in the 1930s. Although seven individuals were identified in the sample, only the three relatively complete skulls were the subject of careful study. Weidenreich (1938-39, 1946) believed the three skulls had affinities with three different populations (Melanesians, Eskimos, primitive Mongoloids) but he did not note any specific connections with modern north Asians. In fact, he noted that modern north Asian skulls were higher and shorter than those from the Upper Cave but also that this recent pattern likely evolved from the Upper Cave form. The lack of close association between the Upper Cave and recent north Asian cranial has been reaffirmed by multivariate cranial analyses that find a more generalised form (Kamminga and Wright, 1988; Lahr, 1995; Hubbe et al., 2010, 2011) or perhaps affinities with Polynesians (Howells, 1989). A detailed morphometric study that included Pleistocene-aged modern human remains found that specimens like Upper Cave and Minatogawa 1 (Japan -16,400-18,250 years BP) exhibited some recent north Asian features but generally have '…not developed the modern "Mongoloid" configuration, which does not appear until the mid-Holocene' (Habgood, 2003, p.229). Howells (1989) also found that Upper Palaeolithic specimens from Europe were not appreciably closer morphologically to modern Europeans than the Ainu were; and Grine and colleagues (2007) determined that the 36,000 year old skull from Hofmeyr (South Africa) was more like Upper Palaeolithic Europeans than recent Africans.

Of course all these specimens are older than the early American material, although Minatogawa is only slightly so. However, similar patterns are observed in more recent specimens. Howells (1989, 1995) found that some Mesolithic (early Holocene) European samples were only marginally related to more recent Europeans and the ~11,000-16,000 year old Iwo Eleru specimen from West Africa is more similar to archaic Africans than to recent ones (Harvati et al., 2011). It seems that recent modern morphological patters do not appear to have much in the way of a Pleistocene time depth anywhere. Seen in the light of this evolutionary perspective, the fact that the earliest Americans (Palaeoindians), at least those older than ~ 8,000 years ago, exhibit a more generalised morphological form, differing from more recent Native Americans, is really not that unusual at all.

However, these differences do not mean that Palaeoindians were not pivotal in the ancestry of recent Native Americans, but rather that there are some evolutionary changes that mark the later development of recent Native American variation. This is aptly reflected by the recent demonstration that Kennewick is clearly allied with Native Americans genetically but not so unequivocally in cranial form (Rasmussen et al., 2015). There has been a tendency to view the origin of Native Americans in a series of 'waves' from Asia, particularly following the linguistic analysis of Native American languages by Greenberg (1987). Greenberg posited three waves with the last representing the Eskimo-Aleut peoples. Recent cranial morphometric analyses often have argued for a two-wave model, with the earlier Palaeoindian 'wave' representing a more generalised morphology that entered the New World prior to the emergence of classically north Asian features and a later 'wave' of people bearing these north Asian features (Powell, 2005; Neves and Hubbe, 2005; Hubbe et al., 2010, 2011; Jantz and Spradley 2014). However, as Jantz and Spradley (2014, p.486) state: 'These later migrants may have displaced the earlier ones, *or more likely assimilated some,* which would explain the high variability among recent Native Americans' (emphasis mine). As a human palaeontologist who studies the Neanderthals and the nature of their interactions with early modern humans in Europe, I see some potential demographic parallels with the Palaeoindian-recent Native American situation. I am not equating Palaeoindians with Neanderthals in a morphological or evolutionary sense. In fact, I make it clear above that Palaeoindians are modern humans. Still I suspect that Palaeoindians were relatively rare on the landscape, much as was certainly the case for Neanderthals (Smith, 2013, in press). Thus, one could make the case that, in a parallel fashion to Neanderthals, Palaeoindian contributions to recent Native American biology were relatively small, not because of any type of inferiority but just because there were not many of them to be assimilated.

A stumbling block to the 'two- wave' model comes from genetics. The primary mt DNA and Y-chromosome haplotypes, and some autosomal DNA, indicate that all Native Americans descended from a single ancestral gene pool (see reviews in Goebel et al., 2008; Hoffecker et al., 2014; but see Reich et al., 2012 and below). In 2007, Tamm and colleagues suggested that this population existed in Beringia, halting here after migrating from Asia in what is termed the Beringia standstill hypothesis. According to Tamm and colleagues, the standstill would have provided for the emergence of distinctively Native American mutations and would have been followed by a relatively rapid dispersion of peoples into the Americas beginning around 15,000 to 16,000 years ago. Considerable biological diversity, including cranial variation (Roseman and Weaver, 2004), would follow from this rapid dispersion and the subsequent adaptations of small populations to diverse environments and climates (Steele et al., 2007) spread across the New World. While a model derived from stochastic factors, mixed with selection, has robust explanatory power (Powell, 2005), there would appear to be a strong temporal pattern, specifically the Palaeoindian versus later Native American cranial form, that might not fit this model so well, at least not the stochastic aspect of it.

A good, if simple, illustration of this has to do with changing patterns of human head shape from the very late Pleistocene to post-agricultural populations. A good historical discussion of this was provided by Weidenreich (1945), who both reviewed and corrected some racially-based use and misuses of the cephalic or cranial index and provided some insight into its evolutionary significance. This index, determined by dividing maximum cranial breadth by maximum cranial length and multiplying by 100, was first defied by Anders Retzius in 1843 (see Retzius, 1845) and was often used to suggest replacement of one 'racial' group by another, particularly in Europe. Weidenreich showed that such an explanation did not fit the temporal pattern of cranial index change over time and suggested that the general shift from more long-headed people, which began with fossil human forms, towards more round-headed people among recent populations in many parts of the world resulted from evolutionary changes '…whose exact nature is unknown…' (Weidenreich, 1945, p.50). Weidenreich termed this trend the brachycephalization (round-headedness) of recent mankind.

Since Weidenreich's day, several factors have been shown to have impact on the cranial index in humans. One of these is climate, but climate clearly is not the primary factor since the trend toward brachycephalization occurs regardless of climatic circumstances (Beals et al., 1983, 1984). Much more significant is likely the impact of changes in functional demands on the masticatory apparatus. Carlson and Van Gerven (1977, p.495) noted that among Nubian skulls the shift to cereal grain agriculture '…led, secondarily, to an alteration of the growth of the maxillomandibular complex such that the face became progressively less robust and more inferoposteriorly located relative to the cranial vault.' Carlson and Van Gerven go on to suggest that increases in relative breadth and height of the cranial vault resulted from the reduced size and less prognathic nature of the face, which was the more direct result of reduction of the masticatory apparatus (see also Larsen, 2014). Such changes have been repeatedly documented for European and some Asian populations (see Weidenreich, 1945; Henneberg, 1976) and for certain North American groups (Newman, 1962; Steele and Powell, 1992). Palaeoindian crania tend toward being long-headed with lower vaults, with some intermediate specimens but no classically round-headed ones (Smith, 1976; Steele and Powell, 1992), but as agriculture dominates subsistence in certain regions, the cranial index and cranial vault height tend to increase. For example, in the Tennessee Valley, Archaic crania, from a hunter-gatherer population, tend toward lower indices (long-headed). Woodland people (incipient horticulturalists) are intermediate and Mississippian people, who are maize agriculturalists, tend strongly toward high indices (round-headed) (see Steele and Powell, 1992, p.318; Smith, unpublished). Interestingly, geographic groups where this trend to higher indices (round heads) is not so strong are areas where agriculture did not have an impact, for example in the Eskimo (Steele and Powell, 1992) and parts of southern Africa (Henneberg and Steyn, 1993).

While it may seem old fashioned to invoke head shape in the current world of geometric morphometrics, I believe that the 'brachycephalization' issue may well explain much of what happened from Palaeoindian times to the advent of recent Native American variation patterns. Of course, accurate explanations for complex biological changes are unlikely to be fully explained by one index of two measurements, but expanding slightly on the cranial index may be useful. If the genetic data are correct in suggesting a single source population for Palaeoindians and recent Native Americans, rather than models positing separate waves of different populations, then the masticatory-functional hypothesis of Carlson and Van Gerven may hold the key. My own data (unpublished) for the three archaeological groups of Tennessee Native Americans show that from the hunting-gathering Archaic people to the agricultural Mississippians, crania get higher (both absolutely and relative to cranial length) and prognathism reduces along with the changes in cranial index discussed above. This is the same general pattern found among the Nubians and a similar pattern characterizes the difference between Neanderthals and early modern Europeans (Bastir and Rosas 2013; Bastir et al., 2007, 2010, Smith 2013; Smith et al., in press), albeit on a different scale. Unlike the examples related to agriculture, the changes in Neanderthal-to-early modern faces involve other selective mechanisms and although the pattern of relationships between cranial breadth, height and length is quite similar, both fossil samples groups remain relatively long-headed. Still the developmental patterns responsible for these changes are likely comparable.

These cranial pattern changes certainly do not explain all aspects of the differences between Palaeoindians and more recent Native Americans. Specifically, they do not explain the development of some of the more north Asian features in the latter group. The comprehensive study of Native American genetic variation by Reich and colleagues (2012) shows that while the vast majority of this variability can be traced to a single migration, two other smaller migration events occurred. If the majority migration represents the Palaeoindians, then these smaller migrations might have introduced the recent features. However, this appears unlikely as these later influences seem relatively small and restricted to groups in the very northern part of recent Native American distribution. As I see it, we are left with the conundrum that genetics generally suggest a single source population for Palaeoindians and more recent Native Americans while many morphometric skeletal studies suggest different source populations.

I find it interesting that Tamm and colleagues (2007), in their presentation of the Beringian standstill hypothesis for the identification of the source population for the peopling of the New World, note something similar in mt DNA to what Reich and colleagues document. They demonstrate a later spread of one mtDNA haplotype into the New World and also the apparent back migration of two mtDNA haplotypes from Beringia into north Asia. Might it be that the Beringian population also gave rise to the emergence of other biological features that are considered characteristic of both north Asian and post-Palaeoindian Native American populations? Like the data presented by Reich and colleagues, these mitochondrial influences appear restricted to northern populations. However, perhaps the morphological features spread much further. Essentially then, all of the variation seen in Palaeoindians, later Native Americans and later north Asians might be derived from multiple migrations from that single Beringian source population. While this idea is speculative at this point, it would appear to offer a possible solution to the morphometric versus genetic view on the peopling of the New World.

Understanding of the peopling of the New World has increased impressively from the 1970s. Today this issue is informed by a tremendous amount of genetic and other biological evidence that both clarifies and complicates the exact nature of the migrations of people into the Americas. Often, there is a certain disappointment that more data do not lead immediately to clear answers to important questions, but the nature of science actually works in a different way. With more data, scholars can ask more detailed question and delve deeper into the intricacies of phenomena, both historic and current. This is the state of the art with the issue of Native American origins. Investigations have moved beyond the simple Asian-origin explanation to more detailed questions of precise population relationships and complex, multidirectional movements and thereby toward a more comprehensive picture of how the Americas were populated. This move to more detailed questions is exactly the same situation that has characterized my area of primary interest, the initial origin of modern people, in recent years. Those of us involved with either of these questions certainly work in exciting, if sometimes confusing, times.

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The Origins and Context of Palaeoamerican Cranial Morphology: Implications for Discussions about Human Dispersal into the Americas

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Abstract

The cranial morphology of the Early Holocene remains from Lagoa Santa, in central Brazil, have attracted the attention of researchers since the mid-nineteenth century and have been a central piece in discussions about the biological origins of early American populations. From the point of view of cranial morphology, these early populations have been described as being different from most of the modern Native American populations, generating a long standing debate about the origins of the early Holocene morphological patterns observed in the continent and its implications for our understanding of the processes of human dispersion into and occupation of the continent. Lagoa Santa (eastern central Brazil) is of high importance for this discussion, due to the high density of Late Pleistocene/Early Holocene sites and hundreds of human skeletons recovered from the local rockshelters and caves. These remains are unique in the continent, for they allow the study of the biological characteristics of early American groups from a population perspective, increasing the reliability of the conclusions drawn from the analysis of this material. This chapter summarises some of the morphometric analyses of this collection in the past decade and how these results address and contribute to the discussions about the settlement of the continent. Recent studies can be divided into two topics: the study of the origins of the morphology that characterizes early South American populations; and the study of how this morphological pattern is related to the morphology that characterizes recent Native Americans. To address the first topic, Early Holocene remains from Lagoa Santa were compared to Late Pleistocene remains from Europe and East Asia, and the results suggest that these populations share a common morphological pattern, for instance, they have closer morphological affinities with each other, despite the geographic distance between them, than with modern populations from their own continents. These analyses indicate that the Palaeoamerican morphology is a retention of the morphological pattern that characterized human populations around the planet by end of the Pleistocene and predates the diversification processes that gave rise to the actual human cranial morphological diversity on the planet. Regarding the second topic, different studies have tried to address the best dispersion models that would explain the diachronic morphological diversity in the continent. In the past decade, studies have defended models that assume 1) two discrete waves of human dispersion into the continent; 2) continuous gene-flow between Asia and the Americas during the Holocene; and 3) local morphological adaptations to new lifestyles and a different climate as possible causes for the observed diversity. However, to date no consensus has been achieved among authors addressing these questions and the debate about the best human dispersion model to explain the cranial morphological diversity across time in the continent is still unresolved. This lack of consensus might be the result of our limited understanding of the biological diversity that existed in the continent in the past, and to solve this problem future studies will have to include more comprehensive collections from the New World.

Introduction

The initial occupation of South America dates to at least 14 cal kyr BP (Dillehay et al., 2008; Dillehay, 2009; Rothhammer and Dillehay, 2009), with the Pacific coast showing the earliest accepted archaeological evidence for human groups on the continent, associated with groups that probably depended heavily on coastal resources (Sandweiss et al., 1998; Dillehay, 2000; Dillehay et al., 2008). Early human evidence on the continent is more common in the Pacific rim and Andean regions (Dillehay, 2008), although there is no doubt that by 11 cal kyr BP most of the continent was already occupied (Salemme and Miotti, 2003), with groups dwelling in forest environments (Roosevelt et al., 1996; Guidon et al., 1998), bushy savannahs (Correal, 1990; Araujo et al., 2008; Araujo and Feathers, 2008;) and cold and semi-arid steppes and plains (Steele and Politis, 2009; Bayón et al., 2011).

These early settlements differ considerably from the early cultures described for North America, especially when compared to the megafauna-specialized Clovis culture (Dillehay, 2000). So far, South America lacks convincing evidence of a systematic exploitation of megafauna (Hubbe, A. et al., 2007; 2009, 2013; Borrero, 2009), although evidence of human and megafauna coexistence through the end of the Pleistocene/beginning of the Holocene has been reported in Brazil (Neves and Piló, 2003; Hubbe A et al., 2009, 2013) and Argentina (Politis et al., 2003; Borrero, 2009). It is probable that South America's occupation followed coastal routes (Rothhammer and Dillehay, 2009), as recently proposed for North America's Pacific coast (Dixon 2001; Erlandson et al., 2011). However, a clear connection between these dispersion movements is still to be established. There is little doubt that these Late Pleistocene/ Early Holocene groups were mobile, covering large territories to meet their subsistence needs. Certainly, the adaptation and colonization of new ecological niches must have posed a challenge to these initial groups, with social and ritual considerations having important roles in the creation of mobility strategies (Dillehay, 2008: 42).

It is likely that the lifestyle of early South Americans changed around 10 cal kyr BP when more permanent settlements start to appear in distinct regions of the continent (for example, Arriaza et al., 2008; Araujo et al., 2008; Dillehay et al., 2003; Dillehay, 2008; Piperno and Stothert, 2003; among others). This shift, which predates the domestication of plants and animals on the continent probably involved the establishment of logistic centres around which mobile groups were organized (Dillehay, 2008). These more permanent settlements can be seen as precursors to the diverse local cultural traditions that developed in the Middle Holocene.

From a biological perspective, little can be inferred about the first millennia of human presence on the continent, since human remains from this period are scant. Excluding a few individual skeletons in North, Meso and South America (Powell, 2005; Waguenspack, 2007; Feathers et al., 2010), osteological remains from the end of the Pleistocene are not found in the archaeological record. Therefore, attempts to reconstruct the biological characteristics and diversity of early Americans depend on estimates based on later material, which so far have been unable to offer a consensus regarding the origins of Native Americans' biological diversity. Early Holocene skeletal samples are more common in South America than in North America (Jantz and Owsley, 2001; Powell, 2005; Waguenspack, 2007) and have been described in Brazil (Hubbe et al., 2004, 2007; Neves and Hubbe, 2005; Neves et al., 2005, 2007a), Colombia (Neves et al., 2007b) and south Chile (Neves et al., 1999), although collections also exist in Peru (Benfer, 1990) and central Chile (Passig et al., 1986). The cranial morphology shared by early skeletons in the continent has been described as presenting a peculiar morphology. Recent studies have indicated that they share a morphological pattern not seen among most of the later Native Americans (Neves and Hubbe, 2005; Hubbe et al., 2010, 2011). Indeed, studies show a wide array of populations that would have closer morphological affinities to them than recent Native Americans: Australo-Melanesians (Powell and Neves, 1999; Jantz and Owsley, 2005; Neves et al., 2007a; Hubbe et al., 2010), Sub-Saharan Africans (Neves and Pucciarelli, 1989; Neves and Hubbe 2005), generalised Asian groups (Brace et al., 2004; Seguchi et al., 2011) or even European populations (Chatters, 2001).

This early morphological pattern, sometimes referred to as Palaeoamerican (Neves and Hubbe, 2005, but see Gonzalez-José et al., 2008 for a critic on its use), is characterized by long and narrow crania, low and projecting faces, and low orbits and nasal apertures (Neves and Hubbe, 2005; Hubbe et al., 2010, 2011). This pattern contrasts with the morphology present among recent Native American groups, that varies around a central tendency characterized by short and wide neurocrania, high and retracted faces, and high orbits and nasal apertures, although there is considerable variation around this central tendency (Gonzalez-José et al., 2003, 2008; Pucciarelli et al., 2006; de Azevedo et al., 2011). Although the Palaeoamerican and late Native American morphological patterns overlap to a great extent when individual variation is taken into account (González-José et al., 2008), when contrasted to modern worldwide variation, these differences are not subtle, being of roughly the same magnitude as the difference observed between recent human populations from distinct continents (Neves and Hubbe, 2005; Neves et al., 2013). When assessed within the comparative framework of worldwide craniometric human variation, early American groups often show stronger morphological affinities with Australo-Melanesian and African samples, while most Amerindian groups share the morphological pattern observed today among recent east Asian populations (Neves and Hubbe, 2005: Hubbe et al., 2010).

The morphological differences between Early and Late American skeletons were initially noticed by nineteenth century scholars studying the skeletal remains from Lagoa Santa, in east-central Brazil. Following the typological paradigm accepted by those scholars, some of these authors deemed the differences between early and late groups large enough to constitute distinct human races, the early 'Lagoa Santa Man' (Rivet, 1908). In fact, the antiquity and the nature of the Lagoa Santa individuals called the attention of many scholars in Brazil, Europe and the United States (Lacerda and Peixoto, 1876; Kollman 1884; Ten Kate, 1885; Quatrefages, 1887; Hansen 1888; Virchow, 1892; Hrdlicka, 1912), especially since their morphological characteristics were so different from recent Native Americans (Lacerda and Peixoto, 1876; Ten Kate, 1885; Hansen, 1888; Rivet, 1908; Imbeloni, 1938). Today, Lagoa Santa is one of the two regions in the entire continent with enough individuals recovered from early contexts that permit their study from a population perspective, allowing for more reliable extrapolations about the biological characteristics of Early American groups. The second region is Bogotá Savannah, in central Colombia, where a series of early skeletons have been recovered from local limestone rockshelters. This material has been covered in detail by Neves et al. (2007b) and represents a collection of ~20 skeletons dated to between 11.5 and 6.5 ky BP, coming from only a handful of sites. No other collection of early specimens presents numbers even close to these (Waguenspack, 2007; Neves et al., 2013).

Even when compared to the Bogotá Savannah, Lagoa Santa is remarkable in terms of its archaeological record. During almost two centuries of excavations in the area over 100 human skeletons dated to between 11.5 and 7.5 14C kyr BP were recovered. Consequently, the Lagoa Santa human remains represent by far the largest series of early skeletal remains from the Americas (Neves and Hubbe, 2005). This material has been repeatedly used in studies about the biological diversity and the mode of dispersion of human groups into the continent (for example, Neves and Pucciarelli, 1989, 1991; Powell and Neves, 1999; Neves et al., 2004, 2005, 2007a, 2013; Powell, 2005; Van Vark et al., 2003; González-José et al., 2008; Hubbe et al., 2010, 2011; de Azevedo et al., 2011; Seguchi et al., 2011), as well as studies dealing with aspects of their lifestyle (Da-Gloria, 2012; Hubbe A et al., 2009; Mendonça de Souza, 1995; Neves and Corneiro, 1997; Neves and Piló, 2003; Prous and Fogaça, 1999).

The main concern regarding the Lagoa Santa remains has been to explain the origin of its peculiar morphological pattern when compared to most recent Native American populations. The existence of two distinct morphological patterns across time indicates that the process of human dispersion into the continent might have been more complex than traditionally assumed. Several studies of early American cranial morphology suggest that the differences observed between early and later American groups are too large to be accommodated into a single expansion event into the continent. Instead these works have argued for two dispersal events into the Americas by populations sharing a common ancestor in East Asia (Neves et al., 2004, 2007a, b; González-José et al., 2005; Neves and Hubbe, 2005; Hubbe et al., 2010). Others, however, consider that the morphological differences between early and late Native American populations result from differences accumulated through time in concert with local microevolutionary forces, such as genetic drift and natural selection, acting on cranial shape (Powell, 2005; Perez et al., 2007, 2010) or were a result of the continuous influx of diversity from Beringia into the continent (González-José et al., 2008; de Azevedo et al., 2011), an interpretation consistent with most, though not all, genetic evidence (Bonatto and Salzano, 1997; Zegura et al., 2004; Tamm et al., 2007; Wang et al., 2007; Fagundes et al., 2008; Rothhammer and Dillehay, 2009; but see Perego et al., 2009; Reich et al., 2012).

Consequently, the study of the origins of the morphological pattern of early Americans, as well as the process through which the morphological diversity seen in the continent along time originated, is key to understanding details about the human dispersion into the New World in the past. Two questions regarding the evolutionary context of the Palaeoamerican morphology have been extensively debated in the literature in recent years, and this chapter summarises the results of some of the recent work on this subject (for example, Hubbe et al., 2010, 2011; Neves et al., 2013). The first question relates to the origin of the Palaeoamerican morphology. More specifically, it addresses the question of whether the Palaeoamerican morphology is unique to the continent or if it can be traced back to ancestral populations outside the continent. Elucidating if the Palaeoamerican morphology is a local development or if it is related to the evolutionary history of modern humans outside the Americas is an essential first step in explaining its origin and how it related to the process of human dispersion into the continent. The second question relates to the origins of the recent Native American morphological pattern and its relationship to the early Palaeoamerican morphology. Many studies have focused on this question, since the definition of the degree of association between these morphological patterns can shed light on the pattern and number of dispersion waves into the New World.

In exploring these questions, Lagoa Santa has been of unique importance, due to the size and chronological frame of its skeletal collections. Therefore, very few studies dealing with early Americans' biological diversity have not included the Lagoa Santa material or parts of it. Due to its preponderance in the studies about the morphological characteristics of Early Americans and its contribution to the discussion about the tempo and mode of the human dispersion into the New World, this chapter will precede the discussion of the morphological analyses of early South American remains with a general description of Lagoa Santa's archaeological background and history of discoveries, complementing it with new data generated by the latest research of the past decades.

Lagoa Santa archaeological record

The karstic region of Lagoa Santa (Figure 1) derives its importance from the studies of early humans in the continent from the long history of palaeontological and archaeological excavations of its caves and rockshelters, and the relatively well preserved archaeological packages dated to the beginning of the Holocene. The region became famous during the nineteenth century thanks to the systematic work of the Danish naturalist, Peter Lund, who explored hundreds of caves in the region between 1835 and 1844 and intensively excavated around 60 of them (Lund, 1844, 1845; Holten and Sterll,

Figure 1. Location of Lagoa Santa and other important archaeological regions with early human remains in South America

1999). Lund was primarily interested in the Quaternary faunal deposits in the region and based on his findings, described several new genera and species of extinct mammals that inhabited the region in the past. However, in the context of this chapter his most significant contribution was the discovery of human remains associated with extinct megafaunal specimens inside Sumidouro Cave (literally 'swallet cave'). The Sumidouro remains, recently dated to a minimum age of ca. 8,500 cal yr BP (Neves et al., 2007a), were among the first evidence of an older presence of human beings in the continent, quickly becoming a major topic of discussion among European and American scholars (for example, Hansen, 1888; Hrdlička, 1912; Lacerda and Peixoto, 1876; Rivet, 1908).

Lund's work certainly inspired many new researchers to explore the caves and rockshelters of the region during the following centuries. Of special interest to this chapter is the work of the French-Brazilian mission (Laming-Emperarie, 1979; Prous and Fogaça, 1999), who recovered the oldest evidence of human evidence in the region: a young female skeleton recovered from Lapa Vermelha IV, a 14 m deep fissure filled with sediment and faunal remains, but with scant evidence of formal human presence. The skeleton was not recovered inside a burial context, being probably the result of a body that was discarded into the fissure. The skeleton was originally dated to 11.4–16.4 cal kyr BP (Laming-Emperaire, 1979), based on its stratigraphic position between charcoal concentrations. New OSL dates agree with the date range of this skeleton, suggesting a range of between 12.7 and 16.0 cal kyr BP (Feathers et al., 2010). Although only one individual, the skeleton from Lapa Vermelha IV is currently one of the oldest in the Americas and attests for the presence of human beings in the region of Lagoa Santa since at least the final millennia of the Pleistocene.

Other research teams during the twentieth century excavated a great number of caves and rockshelters in the region with evidence of early human occupations, and generated relevant collection of early human skeletons. Hurt and Blasi (Hurt, 1960, 1964; Hurt and Blasi, 1969) excavated the Cerca Grande complex, from where 17 burials dated to 9,500 and 8,000 14C yr BP were recovered. Finally, Harold Walter led a team of amateur archaeologists who excavated many different sites, recovering early human remains from Lapa Mortuaria and a high number of skeletons from different sites in the region (see Neves and Hubbe, 2005 for a complete list of well-preserved skulls from Lagoa Santa, and Strauss, 2010 for a discussion of their chronology).

Since 1999, a long term archaeological project in the Lagoa Santa region has been led by Prof. Walter A. Neves (Universidade de São Paulo, Brazil). Over this decade of work, two rockshelters with deep archaeological packages were systematically excavated (Araujo et al., 2008), one of which – Lapa do Santo – has a high concentration of human burials. To date, 32 burials dated to between 9,200 and 7,000 14C yr BP were recovered from Lapa do Santo, showing a wide array of burial practices, including complex secondary ritual manipulation of human remains in a significant part of them (Strauss, 2010, 2011, 2012; Strauss et al., 2011a, 2011b).

The new dates generated for the region showed that Pleistocene individuals are quite rare and only the individual from Lapa Vermelha IV (Luzia) has been dated to before the Holocene. Despite the presence of Pleistocene dates at the bottom of the archaeological record in the rockshelters (for example, Araujo et al., 2008), the systematic use of these spaces as burial ground did not start until ~9,500 14C yr BP, suggesting a possible shift in the cultural background of groups living or moving across the region around this date.

During the last 13 years, the permanent lake shores of the region were prospected and evidence of human presence in the form of lithic artefacts has been recovered dated to *c.* 8,300 14C yr BP (Araujo and Feathers, 2008; Araujo et al., 2013), suggesting a possible increase in the logistic use of the regional resources by populations that established themselves in Lagoa Santa during the beginning of the Holocene. Inside rockshelters, the pattern of secondary burials described in Lapa do Santo contradicts the notion that early groups of Lagoa Santa had simple and homogeneous burial practices (Strauss, 2010, 2011, 2012; Strauss et al., 2011a, 2011b). In fact, the burials recovered from this site show a complex ritual processing of the dead, frequently dichotomizing cranial and postcranial remains by organizing bundles of the later (sometimes of more than one individual) around and/or inside opened skull cases (Strauss, 2010).

The project in Lagoa Santa also excavated palaeontological sites and systematically dated megafaunal remains of the region, through which it was able to show a significant chronological overlap between human groups and extinct megafaunal species. At least the saber-tooth cat (*Smilodon* sp.) and one type of ground sloth (*Catonyx cuvieri*) survived into the Holocene (Neves and Piló 2003), although no evidence of direct interaction between human and megafaunal species have been reported for the region (Hubbe, A. et al., 2009, 2012, 2013), suggesting that these hunter-gatherers were not focusing on large prey. The faunal assemblage recovered from the Lagoa Santa archaeological records is strongly dominated by deer (*Mazama* sp.) with a minor participation of medium and small mammals (armadillos, wild pigs and rodents), as well as birds, lizards and snails. The specialization towards smaller fauna is supported by the lack of a lithic points industry specialized to this end, with the local lithic assemblage being composed mainly of small and micro flakes made out of quartz, with only minor changes observed over the more than 3,000 years of occupation of the local rockshelters (Araujo et al., 2008). The diet of these populations appears to have included a larger amount of cariogenic items (rich in carbohydrates) than typical hunter-gatherer populations, which resulted in unusually high prevalence of dental caries among the local groups (Neves and Cornero, 1997; Neves and Kipnis, 2004; Da-Gloria, 2012).

In summary, the early archaeological sites of Lagoa Santa show the presence of humans by the end of the Pleistocene, who progressively increased their use of the landscape, developing a specific cultural tradition that clearly reflects their adaptation towards the local landscape. The local cultural development, reflected in their technology, treatment of the dead and even dietary practices, contrast sharply with the typical image of early American groups elsewhere in the continent and favour the idea that by the beginning of the Holocene the Americas were occupied by diversified groups that developed specific and unique ways to handle the landscape around themselves (Dillehay, 2008).

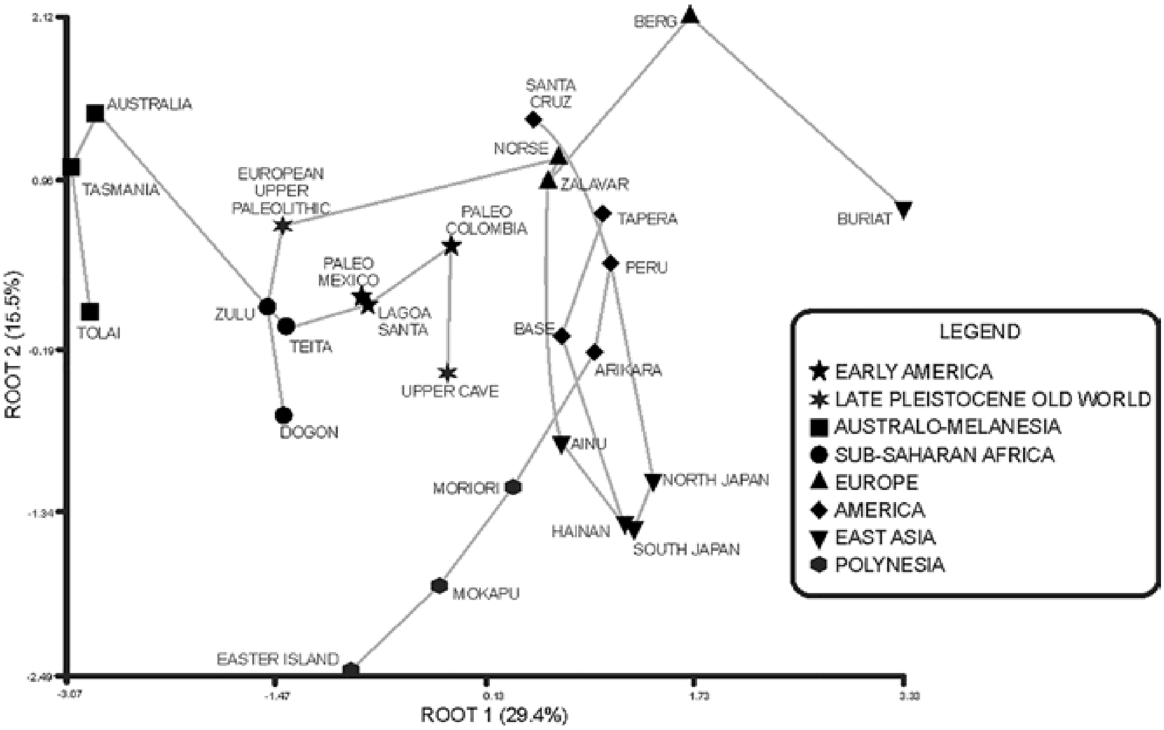

Figure 2. Cranial morphological affinities between early American and Late Pleistocene Old World series in reference to modern human worldwide morphological variation.

Palaeoamerican morphology in its late Pleistocene context

As presented above, the early human groups that inhabited Lagoa Santa during the first millennia of the Holocene share a distinct cranial morphological pattern when compared to most of the late Native American populations. These differences might denote important biological differences as well as important levels of diversity in the continent during the Holocene, which might be a product of the complex processes of human dispersal into and occupation of the New World in the past. To explore the origins of this morphological diversity in the continent, two lines of research have been followed in the past decades. The first, resumed in this session, refers to the origins of Palaeoamerican morphology. The second, addressed in the subsequent session, addresses the origin of the Late Native American morphological variation and how it relates to Palaeoamerican morphology.

The main goal of the studies dedicated to understanding the origin of the Palaeoamerican morphology has been to contextualise this morphology in the continent as well as on the planet, to elucidate if this morphological pattern is unique to the Americas or if it can be seen in the context of the evolutionary processes that characterize modern human cranial morphology worldwide. Although this morphological pattern is better observed among Lagoa Santa populations, due to its large sample size, it is not unique to this region, being found widespread in South America by the end of the Holocene. In fact, every human skull dated to more than seven thousand years BP, compared so far with Lagoa Santa, shows high morphological affinities with this population and share the Palaeoamerican morphological pattern. In South America, it has been described in samples from east-central Brazil (Lagoa Santa; Neves and Hubbe, 2005; Neves et al., 2007a) and Colombia (Bogotá Savannah; Neves et al., 2007b), as well as in isolated specimens from south-east Brazil (Capelinha; Neves

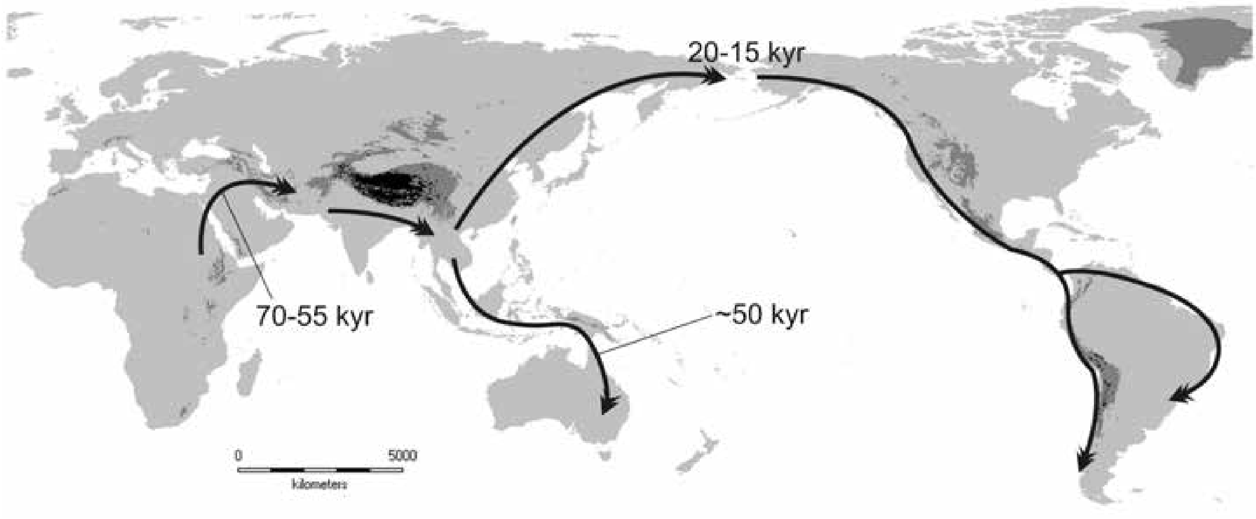

Figure 3. The morphology of early American groups might result from retention of the morphology of the first human groups, which left Africa between 70 and 55 kyr BP. *In this sense, the settlement of the New World can be seen as a direct extension of the human dispersion out of Africa into Southeast Asia and Australia. Dates presented are an approximation based on the recent literature (Mellars, 2006; Dillehay, 2009; among others).*

et al., 2005), north-east Brazil (Toca dos Coqueiros; Hubbe et al., 2007) and southern Chile (Palli Aike; Neves et al., 1999). However, distinct cranial morphology has also been observed in early skulls from Mesoamerica (Mexico; Gonzalez-José et al., 2003) and North America (Jantz and Owsley, 2001; Powell, 2005). Therefore, there is currently a consensus that the entire continent was occupied by human groups sharing a common morphological pattern by the end of the Holocene.

Cranial morphology is largely defined by stochastic evolutionary processes (for example, Harvati and Weaver, 2006a, b; Relethford, 1994; Roseman, 2004), with selective adaptation being restricted to extreme regions or localised anatomical regions in the skull (for example, González-José et al., 2005; Harvati and Weaver, 2006a,b; Hubbe et al., 2009). Consequently, cranial morphology has been used widely to reconstruct phylogenetic histories between human populations. Recently, a study compared the cranial morphology of Early Americans with Late Pleistocene individuals from East Asia and Europe (Hubbe et al., 2011), with the objective of testing whether Palaeoamerican morphology is a unique process to the New World or if it is related to the evolutionary processes that were shaping modern human morphology worldwide. The comparison is based on linear measurements of the skulls that together represent the morphology of the individuals included in the analyses. The Late Pleistocene and Early American groups were analysed within the frame of modern human cranial morphological variation, by comparing them to the reference series measured by Howells (Howells, 1973, 1989). Figure 2, adapted from Hubbe et al. (2011), shows the comparison between early Americans and Late Pleistocene Asians and Upper Palaeolithic Europeans, when compared to the worldwide morphological variation. The graph shows how similar series are to each other in two ways: the distribution of the samples along axes represents their morphological affinities according to the first two canonical variates, for instance, the closer the dots on the graph, the more alike their skulls. The lines connecting the series represent the Minimum Spanning Tree of the biological distance matrix and represent, according to this statistic, the shortest path connecting all series (see Hubbe et al., 2011 for details on the methods applied). In other words, series connected by lines are more similar to each other. The two approaches complement each other, giving a more reliable representation of the morphological affinities between series (see Hubbe et al., 2011, for justifications of the methods). When only the canonical variate information (position of the dots on the graph) is taken into account, all early samples appear closer to each other on the central region of the graph, in proximity to the Sub-Saharan African series, while the recent samples present a general geographic logic, with series from the same region appearing closer to each other. As expected, late and recent Native American groups appear to be associated with East Asian populations in the first canonical variate, as do some of the European samples (Norse and Zalavar). Furthermore, the MST connects all early samples to each other and to Sub-Saharan Africa. No connection between the early series and modern samples from their respective geographic regions can be observed, with the exception of European Upper Palaeolithic and Norse. Therefore, this analysis strongly supports that early Americans are more similar from a cranial morphology point of view to other Late Pleistocene groups on the planet than to recent populations from the same continent.

In the last decades, there has been a growing consensus that all modern human groups shared a late common ancestor in Sub-Saharan Africa and, as a consequence, all Late Pleistocene/Early Holocene groups derive from a single dispersion out of that continent. This idea is based on the fact that early modern humans, dating to the time period of the late modern human expansion (60-30 kyr BP), tend to be more similar to each other than to later populations from the same region (for example, Stringer and Andrews, 1988; Bräuer, 1992a, b; Stringer, 1992, 2002; Grine et al., 2007, Harvati et al., 2007; Harvati, 2009).

In this context, the origin of early American morphology is a relevant question, especially given that it also differs from the morphology that is seen in contemporary east Asia, the region from which these groups most likely dispersed into the New World. The analysis presented in Figure 2 favours the idea that this morphology might be a retention of the morphological pattern seen in the first modern humans leaving Africa (Neves et al., 2003), between 70 and 50 thousand years ago (Harpending et al., 1998; Macaulay et al., 2005; Mellars, 2006; Takasaka et al., 2006) and would thus precede the morphological differentiation in east Asian populations that likely occurred during the early Holocene. In this case, the first modern human expansion out of Africa into Asia, which likely followed a coastal route along south Asia (Lahr, 1995; Mellars, 2006), separated after reaching South-East Asia, with one branch expanding south into Australia and the other expanding north, towards Beringia, and subsequently into the Americas (Figure 3).

Retention of ancestral traits has also been observed in Late Pleistocene specimens from Africa (Grine et al., 2007), Europe (Harvati et al., 2007), East Asia (Neves and Pucciarelli, 1998; Harvati, 2009) and Australia (Schillacci, 2008). A common undifferentiated morphological pattern across Eurasia in the Late Pleistocene is consistent with the predictions of the Single Origin Model of modern humans, favouring a common recent ancestor for Late Pleistocene groups around the Old World (Stringer and Andrews, 1988). Therefore, these studies broadly support the idea that the morphological diversity seen among modern human groups today is a process of late differentiation that probably took place during the Holocene. In this scenario, the closer morphological affinities observed between Early Americans, European Upper Palaeolithic and Upper Cave samples presented here suggest that the largely undifferentiated Late Pleistocene modern human morphology also dispersed into the New World.

The fact that Palaeoamerican morphology might reflect a retention of the ancestral modern human morphology observed in the late Pleistocene Old World has implications for the settlement of the New World, especially if adaptation to cold climate is one of the forces responsible for the morphological differentiation in modern humans, even if only of specific anatomical regions (Roseman, 2004; Harvati and Weaver, 2006a,b: Hubbe et al., 2009; von Cramon-Taubadel, 2009). Since crossing the Bering Strait is believed to be the best route for early groups getting into the New World (Dixon, 2001; Goebel et al., 2008; Dillehay, 2009), this crossing through a harsh, cold environment must have been a relatively quick process, otherwise these populations would show evidence of cranial morphological adaptation to a cold climate. The speed of this process, however, is hard to evaluate at the moment given that the duration of the processes of morphological adaptation and response to environmental factors is poorly understood.

This suggestion goes against molecular evidence, which has recently proposed a period of biological isolation of proto-American groups, possibly in Beringia, between 35 and 25 kyr BP (Tamm et al., 2007; Gonzalez-José et al., 2008; Kitchen et al., 2008; Mulligan et al., 2008), although no major environmental or geographic barrier between Beringia and east Siberia existed to explain this isolation. Also, the idea of rapid migration following a coastal route has been proposed in recent years to explain the settlement of the New World (Dixon, 2001; Fagundes et al., 2008; Dillehay, 2009). It is reasonable to assume that the same pattern of dispersal was also adopted by earlier human groups prior to their arrival in the Americas (Mellars, 2006). Therefore, it is possible that rapid coastal migration had already been adopted in Asia by Late Pleistocene humans groups for a relatively rapid crossing of the Bering Strait. In this context, coastal environments could represent quick range expansion pathways, providing a relatively homogeneous ecological system for groups to spread without the necessity of significant technological innovations (but see Westley and Dix, 2006, for a critique of the diachronic stability of coastal environments).

Origins of morphological diversity during the Holocene

While the view on the origin of Palaeoamerican morphology described above has not been contested or contradicted by new analyses, the same cannot be said for the discussion about the origins of the morphology that characterizes most of the recent Native American groups. The increase of morphological diversity during the Holocene and the appearance of a new morphological pattern in the continent, closely resembling the morphology seen in modern east Asian groups, has been explained by either multiple dispersion waves into the continent (Neves and Hubbe, 2005; Neves et al., 2007a,b; Hubbe et al., 2010), a result of local microevolutionary processes (Powell, 2005; Perez et al., 2007, 2010) or the result of a continuous gene flow with north-east Asia during the Holocene (González-José et al. 2008; de Azevedo et al., 2011). Defendants of the first scenario argue that the differences between early and late morphological patterns are so large that they cannot be explained only by local microevolutionary forces. Under this scenario, the morphological pattern of Early Americans represents the morphology present on the planet by the end of the Pleistocene and was brought into the New World by the initial settlers crossing the Bering Strait. A new morphological pattern, similar to the one seen among recent east Asian groups, was brought into the Americas by a second wave of dispersion (but not necessarily only one discrete migration), which largely replaced the early pattern, although groups sharing a similar morphology with the early groups have been reported during the mid-Holocene in Colombia (Neves et al., 2007b) and Late Holocene in Baja California (González-José et al., 2003), Patagonia (Lahr, 1995) and central Brazil (Atui, 2005).

The second scenario developed to explain the morphological diversity observed across time in the Americas assumes that the morphological changes can be explained by local changes in time. This scenario has received some support from dental morphological studies (Powell, 2005) and studies in Argentina comparing cranial shape to molecular data (Perez et al., 2010), but has been considered less parsimonious than multiple migrations from or continuous gene flow with Asia in studies that tested which scenario fitted best the morphological diversity in the continent as a whole (Hubbe et al., 2010; de Azevedo et al., 2011).

The third and most recent scenario proposed to explain morphological diversity in the continent assumes that the early populations that entered the continent showed already high levels of morphological diversity and that the continuous gene flow between American and north-east Asian groups shaped the morphological diversity of American groups across time (Gonzaléz-José et al., 2008; de Azevedo et al., 2011). This proposal overlaps with the dual dispersion model by assuming that the diversity observed in the continent depends on the influx of extra diversity from outside the continent. The difference between these scenarios, thus, is the nature by which this influx occurred, with the first scenario defending more discrete migrations and the second maintaining that gene-flow was constant and continuous between Asia and America throughout the duration of the Holocene.

This lack of consensus in the process of human occupation of the continent is also observed among studies of the genetic variation of Native American groups. Largely restricted to recent populations, molecular studies in the past 25 years have defended between one and three discrete migrations into the continent (Bonatto and Salzano, 1997; Zegura et al., 2004; Tamm et al., 2007; Wang et al., 2007; Fagundes et al., 2008; Perego et al., 2009; Reich et al., 2012), sometimes defending continuous gene flow with north-east Asia (Tamm et al., 2007; González-José et al., 2008) or even a period of isolation of Proto-Americans (Tamm et al., 2007; Kitchen et al., 2008) from Asia before the dispersion into the New World. This lack of consensus among molecular data has hindered attempts to conciliate the morphological with genetic evidence (for example, Greenberg et al., 1986; González-José et al., 2008) difficult and prone to criticism.

Consequently, although the increased morphological diversity in time and the shift in morphological pattern across time in the Americas suggests an influx of further diversity into the continent, at present it is impossible to offer a more definite opinion on whether this was a product of multiple discrete migrations into the continent or a result of gradual influx as a result of continuous contact and gene flow between north-east Asia and North America.

Finally, although authors tend to extrapolate their conclusion to the entire American continent, it has to be noted that the early American series available to date all come from South America. Morphological analyses can be seen to favour the notion that all early North, Central and South American groups shared a common morphology, since Lagoa Santa and Early Colombian groups show the same morphological pattern seen in other parts of the planet by the end of the Pleistocene. Consequently, the increase in morphological diversity and the late appearance of a new morphological pattern in the continent was probably a continent-wide event. However, it is possible and reasonable to assume that the processes by which this influx of morphological diversity occurred in the continent might have been different between North and South America. As argued extensively in the literature (for example, Dillehay, 2008), there is enough archaeological evidence to show that the early South American groups do not culturally resemble early North American groups. Therefore, the same might be true of the biological characteristics of early populations in each continent. For instance, it is possible that in North America this influx was a result of a continuous influx with Asia, whereas in South America this same event could have taken place through more discrete waves of dispersion. This scenario has some support from recent molecular studies that suggest that continuous gene flow with north-east Asia was probably restricted to the northern regions of North America (Tamm et al., 2007; Reich et al., 2012). Also, discrete dispersion waves in South America has received some support by molecular studies, who suggested two discrete dispersion waves inside the continent, based on rare mtDNA lineages (Perego et al., 2009) and a much higher degree of between populations diversity in non-Andean native South Americans (Tamm et al., 2007).

Yet, many other molecular studies would refute this idea and defend one single wave of dispersion into South America (Greenberg et al., 1986; Tamm et al., 2007; Reich et al., 2012) or even the Americas as a whole (for example, Zegura et al., 2004; Wang et al., 2007). At present, it is hard to corroborate or refute a particular scenario of how populations dispersed across the continent, which highlights the fact that our data about early American groups is biased by being restricted to

South America and that any model to explain the origins of the first South Americans does not necessarily apply to North America.

Conclusions and future research directions

The importance of the Lagoa Santa region, with its dozens of late Pleistocene/early Holocene sites and hundreds of human burials, to the studies of the characteristics of early human groups in South America cannot be highlighted enough. The human presence in the region during the final millennia of the Pleistocene and early Holocene shows a series of groups adapted to the local environment, with lifestyle and burial practices remarkably different from that seen in other regions of South and North America. By itself, this shows that the early Holocene populations in the New World presented significant cultural diversity between themselves, being one more distinct piece of the mosaic of cultures that were present in the continent (for example, Dillehay, 2000, 2008; Dixon 2001; Arriaza et al., 2008; Goebel et al., 2008). This cultural diversity shows a quick process of differentiation in the initial periods of the human presence in the continent, showing that no matter who came into the Americas or how fast the colonization wave dispersed through the landscape, by 10,000 cal yr BP the continent shows signs of people adapting to their own landscape and developing clear local traditions that are defined by more than their technological background.

Yet, the same cannot be said from their biological characteristics, since as far as cranial morphology is concerned, the early Holocene populations of the continent show low levels of variation and a morphological pattern that is not the one most widespread among Late Holocene Native American populations. This strongly suggests a significant influx of extra morphological (and biological) diversity into the continent during the Holocene, either by a continuous gene flow with Asia or by multiple discrete dispersion waves into the continent during this time. Consequently, from the perspective of cranial morphology, the actual biological diversity of Native Americans does not derive exclusively from the early Palaeoamerican populations that settled the continent, and a linear causal connection between early and late populations on the continent should be established only when empiric data strongly supports it. In other words, our analyses of the Lagoa Santa remains in the past decades (Neves and Hubbe 2005; Neves et al., 2007b, 2013; Hubbe et al., 2010, 2011) as well as the ones presented here add to the growing body of evidence that the processes associated with the settlement and dispersion of human groups across the Americas were neither simple nor straightforward, and involved the complex interaction between different cultures and possibly biologically distinct populations during the entire period that humans occupied the continent.

Consequently, although the increased morphological diversity in time and the possible shift in morphological patterns across time in the Americas favours an influx of further diversity into the continent, at present it is impossible to offer a more definite opinion on whether this was the product of multiple discrete migrations into the continent or the result of gradual influx as a result of continuous contact and gene flow between north-east Asia and North America. This difficulty derives from the lack of good comparative data sets, with series that represent accurately the continent's past morphological diversity. Most studies of morphological diversity in South America do not incorporate the biological diversity seen during the Middle Holocene, including only representatives of early and late Holocene populations (for example, Hubbe et al., 2010; de Azevedo et al., 2011, but see Perez et al., 2010 for an exception), where in theory the Middle Holocene (between 7 and 4 kyr BP) must have been a period of intense morphological differentiation, either due to population replacement (dual-dispersion scenario), continuous influx of extra diversity from Asia via North America, morphological adaptation to new environmental factors (changes in life-style or climate) or any combination of these processes.

With this framework in mind, it is imperative that future work focuses on Middle Holocene populations in order to test the biological origin(s) of early South Americans and how the initial occupation(s) of the continent gave rise to the actual continental biological and cultural diversity. If the question about the origin of the morphological diversity seen in the Americas in the past is ever to be solved, more international collaborative initiatives must be established, focusing both on the analysis of larger datasets and on the creation of public and virtual databases that house information about the collection currently curated in the many archaeological and natural history museums of the continent.

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Human Dispersal and Late Quaternary Megafaunal Extinctions: the Role of the Americas in the Global Puzzle

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Abstract

As Alfred Russell Wallace once wrote, we live in a zoologically impoverished world, from which most of the largest, strangest and most spectacular animals disappeared quite recently. About two thirds of all animal species larger than 50 kg (the so-called megafauna) were extinct from the late Pleistocene onwards, starting in Australia at about fifty thousand years ago and following humans' footsteps is their expansion throughout Eurasia and the Americas. The extinctions went on through the Holocene, reaching islands all around the globe, that can be seen as 'time machines' where megafauna survived for millennia after the continental extinctions, such as the Caribbean, the islands off Alaska, and Wrangel Island in the Arctic Ocean. In Madagascar and New Zealand, extinctions are but a few centuries old. These late Quaternary extinctions were a global phenomenon that begs for a global explanation. Climatic hypotheses fail to explain these patterns for several reasons, for example, there were dozens of other glacial cycles throughout the Pleistocene, without associated mass extinctions; extinctions in Australia and the islands did not coincide with glacial peaks; and climate changes cannot explain why extinctions were systematically more recent on islands. However, the pieces of the puzzle immediately fit together when we observe the clear correspondence between the dates of humans' arrival and of megafaunal extinction in each landmass. Bernardo Araujo recently analysed the chronology of extinctions of megafaunal genera around the world. He found that extinctions took place closer than expected by chance to periods of high climatic variation alone in only two of the analysed cases, to dates of human arrival alone in seventy-four cases, and to both in eight cases, with 40 cases unexplained. Thus, anthropogenic impact is the most plausible and parsimonious main cause of the late Quaternary extinctions. In a modern view, the extinctions were a long process that took several millennia to occur in most continents, with a few stragglers like the Irish elk and the North American mastodons. Low reproductive potential was the main determinant of the extinct species; the apparent selection by size is an artefact of the inverse correlation between the two variables. The absence of evolved instincts against newly arrived humans, the difficulty of conserving meat and the lack of perception of the world's finitude must have contributed to the outcome. Thus, human-megafauna interactions are an important and undervalued part of human history that merits being represented on the UNESCO World Heritage List. Furthermore, learning from the extinctions of the past is crucial to allow us to minimise extinctions in the future. Candidate sites in the Americas might include those that show consumption of megafauna (such as Monte Verde), remarkable rock paintings (such as Serra da Capivara, Brazil) and the latest American megafauna (such as Las Breas de San Felipe, Cuba).

Introduction - the late Quaternary extinction sequence

In 1876, Alfred Russel Wallace wrote: 'we live in a biologically impoverished world, from which all the hugest, and the fiercest, and the strangest forms have recently disappeared' (Wallace, 1876, p. 150; quoted in Grayson, 1984). The sense of incompleteness felt by Wallace, at a time when palaeontology was still a young science, is well justified. In the last 50,000 years - the blink of an eye in geological times - the planet has lost an impressive array of large animals, including mammoths, mastodons, woolly rhinos, sabertooth tigers, giant ground sloths, gliptodonts, moas, elephant birds, marsupial lions and many others. These recently lost beasts represented about two thirds of all the world's megafauna - here defined as animals with adult body weight above 50 kg. For example, at least 97 of 150 genera of large mammals were lost between 50 thousand years ago (henceforth ky) and 500 years ago (Turvey and Fritz, 2011). When trying to understand the causes of this huge 'prehistoric revolution' (Martin and Klein, 1984), it is crucial to note that these extinctions were not an event well-defined in time, but rather a process: the megafauna disappeared at markedly different times in different parts of the planet. We will briefly review this dramatic sequence.

The extinctions first reached Australia, around 50 ky. By that time, the spectacular Australian fauna included the diprotodonts (genus *Diprotodon*), giant marsupial browsers that could weigh almost three tons; *Palorchestes*, ecological equivalents to tapirs; *Thylacoleo carnifex*, the 'marsupial lion' (actually a leopard-sized large carnivore) and a whole family of giant short-nosed kangaroos, the Sthenurinae (Murray, 1984; Johnson, 2006). Aside from the mammals, there were gigantic reptiles such as *Megalania prisca* that resembled an oversized Komodo dragon, *Wonambi naracoortensis*, similar to a large anaconda, plus some huge terrestrial birds, *Genyornis newtoni*. The Tasmanian 'wolf' or thylacine, *Thylacinus cynocephalus*, often considered endemic of Tasmania (where it survived until 1936), was also found throughout Australia at that time. In continental Australia, the extinctions took place during an 'extinction window' that went from 50 to 40 ky, with a peak at around 46 ky (Roberts et al., 2001). A recent claim by Wroe et al. (2013) that the extinctions in Australia were spread in time since the Middle Pleistocene does not seem consistent, because the species at that time were nearly all from the same genera as the ones that disappeared during the 'extinction window', and thus they are likely to represent taxonomical splitting rather than a truly different species set. An interesting point is that in Tasmania the extinctions happened distinctly later than in continental Australia, around 41 to 40 ky (Turney et al., 2008).

In Eurasia, the extinctions were quite spread out in time, roughly presenting two pulses (Turvey and Fritz, 2011). In the southern latitudes, around the Mediterranean Basin, most species vanished between 45 and 20 ky. The extinctions in the northern latitudes came much later, from 14 to about 9 ky. Some stragglers survived even later, such as the 'Irish elk' (*Megaloceros*) in the Ural Mountains until some 7,700 years ago (Stuart et al., 2004). Among the main losses suffered in Eurasia were the Eurasian mammoths (*Mammuthus primigenius*), woolly rhinoceros (*Coelodonta antiquitatis*) and cave bears (*Ursus spelaeus*). The coexistence of humans with this striking fauna, including the hunting activity, is richly documented in the superb Cro-Magnon rock paintings, in sites such as Altamira, Lascaux and El Pindal. This coexistence lasted until the big animals became extinct, soon followed by their artistic representations.

In North America, the extinction process was comparatively 'quick', as it took place mostly between 13.5 ky and approximately 11 ky. Again, some stragglers survived until more recent times, such as the mastodons (*Mammut americanum*), whose last records, in the region of the Great Lakes, are dated to 9,900 years ago (Woodman and Athfield, 2012). The North American megafauna at this time was very rich and much more similar to Africa's present fauna than we could imagine, based on the remaining species there (Anderson, 1984). Among others, there were North American mammoths (*Mammuthus columbi*), mastodons, giant ground sloths (see next paragraph) and also camels (*Camelops hesternus*), horses and bison, including the huge long-horned bison (*Bison latifrons*). Furthermore, North America was home to an exceptionally rich carnivore fauna, including the giant bear (*Arctodus simus*), the sabertooth tiger (*Smilodon fatalis*), the only slightly smaller scimitar cat (*Homotherium serum*), lions (*Panthera leo atrox*), oversized wolves (the dire wolf, *Canis dirus*) and cheetahs (*Miracinonyx trumani*) (Flannery, 2001).

In South America, the extinctions were spread along a longer period of time than in North America, from about 13 ky to 7.8 ky (Barnosky and Lindsey, 2010). This means that, although there is a considerable overlap in time between the continents, many of the South American extinctions took place after the process was mostly completed in North America. The South American megafauna, like their North American counterparts, also included at least two species of elephants (from the genera *Haplomastodon* and *Cuvieronius*), sabertooth tigers (*Smilodon populator*) and a rich diversity of ground sloths (families Megatheridae, Megalonychidae, Milodontidae and Nothotheridae). The largest ground sloths (genera *Megatherium* and *Eremotherium*) were huge, slow animals that could weigh more than five tons. Besides, there were large native grazers similar to hippos called toxodonts (*Toxodon platensis*), many gigantic armadillo-like gliptodonts and a rich diversity of roofed beasts including highly peculiar animals like *Macrauchenia* as well as more familiar horses (*Equus*). Although today South America is relatively poor in megafauna - the tapirs, jaguars and marsh deer are the few remaining large mammals - this was not by any means true about 15 thousand years ago.

The extinctions were not limited, by any means, to the Pleistocene-Holocene boundary - on the contrary, they went on through the Holocene. That is why it is more correct to talk about 'late Quaternary extinctions' rather than using the misleading expressions 'Pleistocene extinctions' or 'Pleistocene-Holocene extinctions', the latter seeming to imply that they happened in the boundary between the two epochs. It was indeed well into the Holocene that the extinctions finally reached some 'time machines' where some last members of the vanished megafauna still survived. These time machines –places were intact Pleistocene ecosystems could still be found well into the Holocene - were the islands.

In the Caribbean, all several dwarf giant ground sloths became extinct from about 6 ky to 4.7 ky, at least some 4,500 years later than anywhere in the mainlands of either North or South America (Barnosky et al., 2004; Steadman et al., 2005). The most recent records are from Cuba, the largest island in the Caribbean. In Beringia, mammoths (*Mammuthus primigenius*) survived on the island of St Paul (near Alaska) (Guthrie, 2004) and Wrangel (to the north of Siberia) until some 5 ky and 4 ky respectively. The last date (Vartanyan et al., 1993) is more than seven thousand years after the Younger Dryas, the last cold event of the last glacial cycle. In the Mediterranean, at least five species of dwarf elephants of the genera *Elephas* (*Palaeoloxodon*) and

Mammuthus became extinct over twenty islands. Most of these findings are not dated; the few existing dates are not quite reliable but if correct they would point to the survival of elephants until as recently as 4 ky in the Aegean islands (Theodorou et al., 2007 in Liscaljet 2012). A dwarf elephant is also present in Egyptian wall paintings of the eighteenth dynasty (near 3.5 ky), suggesting that the Egyptians coexisted with these now extinct animals in historical times (Masseti, 2001). Other quite recent - possibly Holocene - losses in the Mediterranean islands included several species of dwarf hippopotamus (genus *Hippopotamus*) from Crete, Sicily, Malta and Cyprus (Petronio, 1995).

Two of the most spectacular cases, however, were Madagascar and New Zealand -where the disappearance of the megafauna was most recent. In Madagascar, a dozen species of spectacular giant lemurs became extinct between 2,000 and less than 400 years ago, when the last of them, the man-sized *Megaladapis edwardsi*, was seen by the French governor, Etienne de Flacourt (Flacourt, 1658). Flacourt may also have seen the last of the half-ton elephant birds (*Aepyornis maximus*). When the European colonizers arrived, huge elephant bird eggshells still littered the beaches of the island's south and south-eastern coasts, pointing to a very recent extinction indeed. Furthermore, Madagascar also lost pigmy hippos and giant fossas (Dewar, 1984). In New Zealand, there was an equally spectacular fauna of a dozen species of moas, large terrestrial birds up to three metres tall, plus the gigantic Haast's eagle *Harpagornis moorei*. All these huge animals went extinct as recently as between 900 and 500 years ago (Trotter and McCulloch, 1984).

Unlike any other extinction wave in the geological past, this one appeared to be size-selective: only the largest animals were extinct (Lyons et al., 2004). The Quaternary extinctions deprived the planet of most of its large animals, but had little effect on the small ones.

The aim of this article is to briefly discuss how the late Quaternary extinctions relate to human dispersal across the planet, how this affects our views of human history, and the role of American sites in conserving this memory.

Pitfalls of the climatic explanations for the late Quaternary extinctions

Ever since Wallace, there has been much controversy on what caused the Quaternary extinctions, a dramatic revolution in the history of life so close to our time. The hypothesis that the demise of the big animals had been caused by climate changes was a favourite for near a century after Wallace (Grayson, 1984); it is still popular and has been proposed in many regional studies to explain the disappearance of Pleistocene faunas (review in Koch and Barnovsky, 2006). From a global perspective, however, the climatic hypothesis fails to explain too many of the extinction patterns; six of its main pitfalls are briefly pointed out below.

Firstly, climatic hypotheses do not explain the regional asynchrony of the extinctions. Climatic events linked to the last glacial cycles were planetary events that affected the whole planet at the same time, for example, cold peaks were also linked to dry periods in tropical regions. Nevertheless, as we saw, the extinctions took place at completely different times in different places around the world.

Secondly, the chronology of the last glacial cycle does not explain the timing of extinctions in several parts of the world. For instance, in Australia the extinctions occurred mostly within a relatively mild period about twenty thousand years before the Last Glacial Maximum that lasted from about 23 to 18 ky. On the other extreme of the time scale, the insular extinctions all occurred several thousand years after the end of the Younger Dryas, the last cold event of the glacial cycle, at about 13 to 11.5 ky (Burney and Flannery, 2005).

Thirdly, in the Pleistocene there were at least 31 other glaciations before the last, without any wave of extinctions associated to them (Cione et al., 2003; Barnosky et al., 2004; Johnson, 2006). The recent suggestion by Wroe et al. (2013) that the last glacial cycle was notably more intense than the previous ones, at least in the Sahul, is not convincing because intensification can be observed only in the warm (interglacial) phases that which are not implied in the extinctions in the climatic hypothesis. On the other hand, there is little difference where it matters, that is, among the cold extremes of the last cycles (see Wroe *et al.*'s own figure 5).

Fourthly, climatic hypotheses cannot explain why the extinctions on islands all over the world, independent of their latitudes and longitudes, were systematically more recent than in the continents - all of them in the Holocene, a period of relatively stable climate.

Fifthly, climatic hypothesis would predict many extinctions among plants that are usually more affected by climate changes than animals, but this prediction conspicuously fails: there was no wave of floristic extinctions in the Quaternary.

Sixthly, the climatic hypothesis predicts that small warm-blooded animals would be more affected than large ones, because the former have higher surface/volume ratios and thus less efficient homeothermy (Thompson, 1917). But what happened was exactly the opposite: the large animals were the ones that disappeared.

The Quaternary extinctions are a global phenomenon that begs for a global explanation. Arguably, a major reason why the subject still seems puzzling is that many studies have tried to explain the extinctions using regional approaches, thus losing sight of the immense explanatory power of a comparative, global analysis. The pieces of the puzzle indeed immediately fit together when we observe the close similarity between the dates of human arrival and the extinctions in each land mass. A quick review of modern man's spread across the globe may be useful here. I make no claim to present a detailed appraisal of the complex process of colonization of our planet; rather, I intend to provide only a brief sketch of the main events.

Man's dispersal across the planet

Modern humans originated in eastern Africa and had most of their existence restricted to a relatively small part of the world. The oldest dates for our species are at least 160 ky and the oldest ones out of Africa - in the Middle East - are about 120 ky. From the Middle East, modern humans dispersed to Tropical Asia and remained restricted to these regions until about 50 ky (Stringer and Andrew, 2005).

From there, the first new land mass to be colonized was Australia, reached by humans at about 50 ky. As the colonizers came from the north, the last part of Australia to be reached was the southern tip, where Tasmania lies. At the time, Tasmania was connected to Australia, New Guinea and smaller islands forming a single landmass, Sahul.

The expansion of humans towards the temperate parts of Eurasia started at a roughly similar time, at over 40 ky, but this was a much longer process as humans seemed to have reached the cold areas of the gigantic Eurasian continent, such as northern Siberia, by less than 20 ky. It was the first time humans had to colonize a continent against a temperature gradient - from warm to cold - and possibly this factor helps to explain why it took so long (Araujo, 2013).

However, once reaching the eastern tip of Eurasia, humans had free access to the Americas, as Eurasia and North America were then connected through Beringia. North America was reached around 15 ky or a little before this. At the time, northern North America was still covered by a thick ice cover, because the deglaciation following had still not finished. Progression through this part of the continent seems to have been slow, but at about 13.5 ky is the first evidence that humans had reached North America's central plains.

Within the Americas, and especially in South America, the colonization frontier seems to have expanded at quite different speeds in different directions. The oldest reliable archaeological dates in South America are from Monte Verde, near Puerto Monte, in southern Chile, at over 14 ky. This striking date seems consistent with the hypothesis of a faster colonization route along South America's Pacific coast. For pre-technological people, the Andes were surely an imposing geographical barrier and this may have conditioned a 'fast' (lasting a few hundred years) movement southwards through the narrow land strip between the Pacific and the gigantic mountain chain. To the east of the Andes, with a more complex geography and dense forests, human expansion seems to have been much slower than on the west coast.

The last places to be reached by humans were the islands, all around the world, for the obvious reason that reaching them only became possible after the invention of efficient watercrafts, capable of traversing extensions of saltwater (with the exception of land-bridge islands such as Tasmania, which were connected to the continents at times of low sea levels during the late Pleistocene). The first important oceanic islands in the Americas that were reached by humans were the Caribbean islands, at nearly 6 ky. The Mediterranean islands seem to have been reached slightly later, and Wrangel, the home to the last mammoths, was occupied at about 4 ky. Madagascar, one of the world's largest islands, was first reached by humans only about 2,300 years ago and surprisingly, the first colonizers came from south Asia rather than Africa. Finally, New Zealand was the world's last large landmass to be reached by humans, just about 900 years ago.

A quantitative, global analysis making use of improved dating

The striking similarity between these dates of human arrival and the dates of the extinctions at the different landmasses across the world has been pointed out by many authors, including Martin (1984, 2005), Fernandez (2000), Lyons et al. (2004), Burney and Flannery (2005), Johnson (2006) and Gillespie (2008). However, Bernardo Araujo (2013) provided the first global

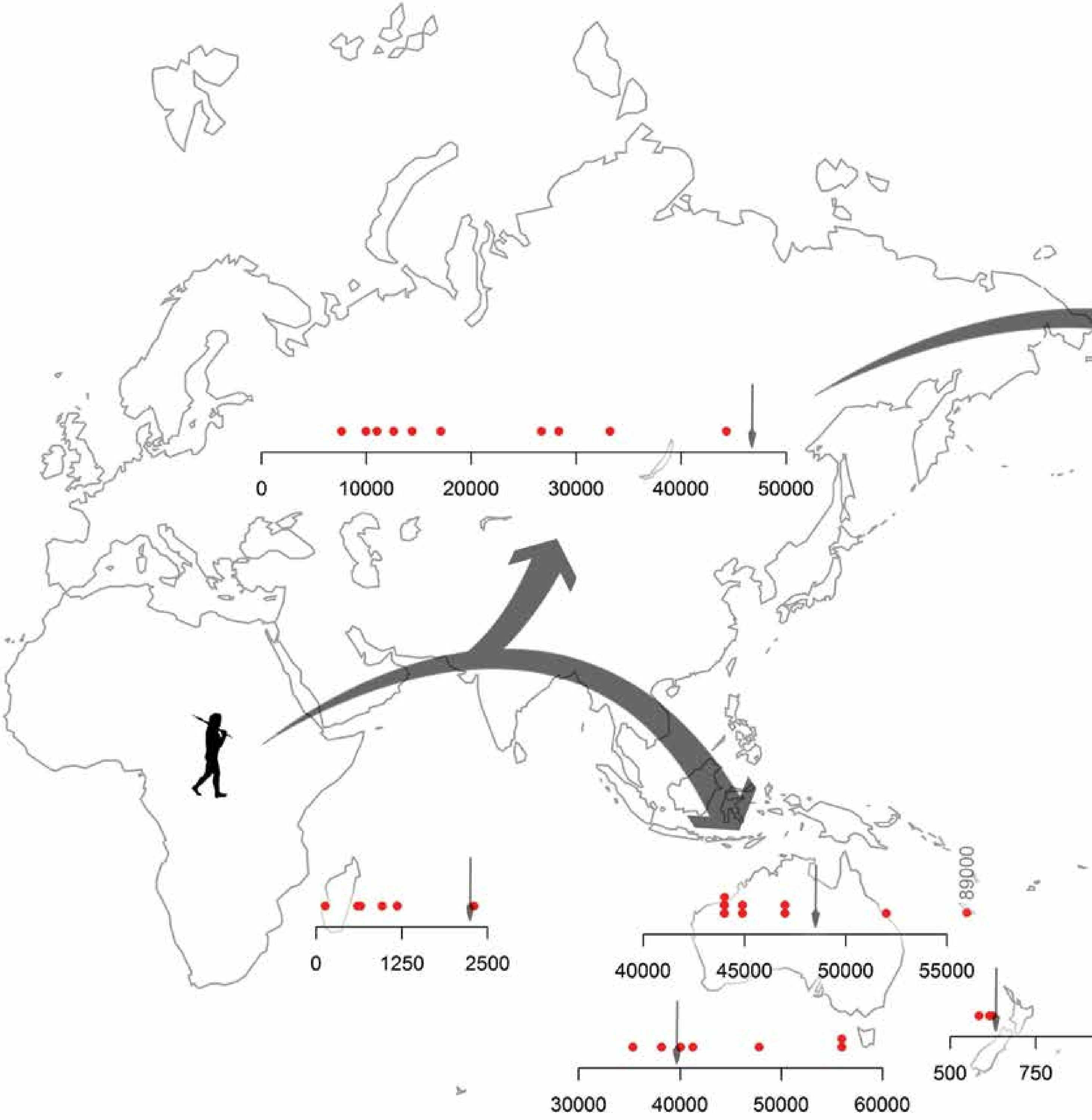
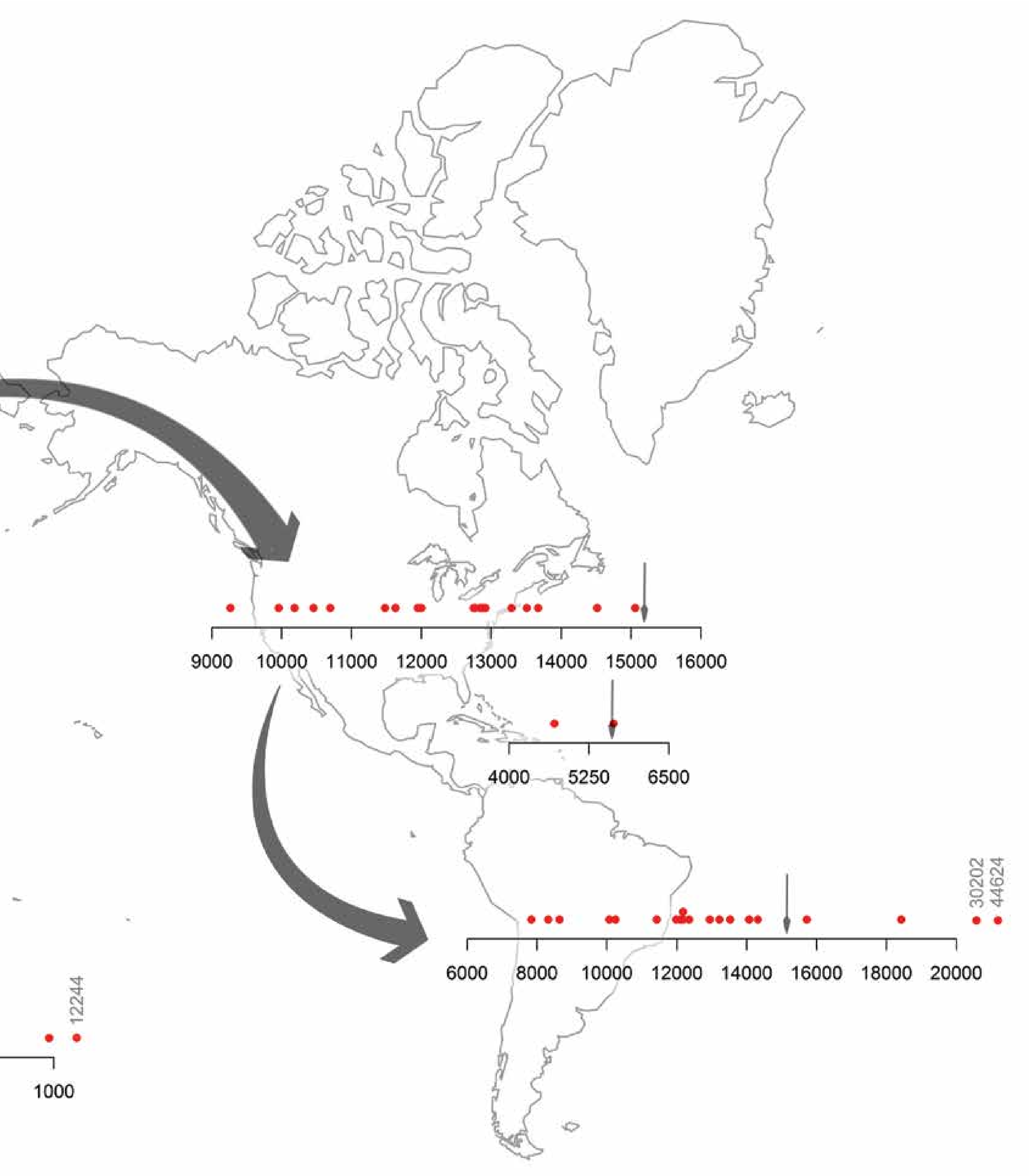


Figure 1. The timing of human arrival and megafaunal genera extinction across the world in the late Pleistocene and Holocene, as analyzed by Bernardo Araujo (2013). The displayed quantitative axes show the last known dates of occurrence at each landmass (calibrated dates, in years before past) of megafaunal genera (red dots). Grey spears point to the time of first known dates of human presence at each landmass. The large grey arrows show the main routes of human dispersal across the globe. © Bernardo Araujo.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quantitative analysis of the relations between the timing of the megafaunal extinctions, climatic changes and human arrivals to each of the world's land masses, taking advantage of the massive recent progress in dating methods. Using inaccurate time frames in quantitative analyses (for example, as in Prescott et al., 2012, for human arrival), it would be difficult to disentangle the effects of different putative causes for the extinctions (Lima-Ribeiro et al., 2012).

In Araujo's (2013) analysis, the intensity of climatic variation in the late Pleistocene and Holocene was assessed through the North Greenland Ice Core Project data on oxygen isotopic composition on ice cores (Andersen et al., 2004). This database comprises $\delta^{18}O$ data (a temperature proxy) for the last 122 ky. Megafaunal dates and human dates were obtained from literature for nineteen regions of the world where these events took place at markedly different times. The regions considered in the analysis were Australia, the Caribbean, Japan, Madagascar, New Zealand, Tasmania, Wrangel Island, Beringia (north-westernmost North America and north-easternmost Eurasia), central North America, eastern North America, western North America, northern Europe, southern Europe, west Siberia, central Russia, northern South America, central South America, Patagonia and the Andean region (the Andes and South America's western coast). Only calibrated dates, regarded as reliable according to the Mead-Melzer modified scale (Barnosky and Lindsey, 2010) were used. The database included 2,088 megafaunal dates (for 67 genera) and 762 archaeological dates.

Araujo's (2013) main results are summarised in Figure 1. The dates shown are the last known occurrences of each megafaunal genus and the first known human presence in each landmass. For sampling reasons, the last known date of a fossil genus tends to overestimate how long ago the extinction occurred and the first known human date tends to underestimate how old is the arrival (Signor and Lipps, 1982; Buck and Bard, 2007). Taking this in account, the clustering of the extinctions dates around the times of human arrival can be clearly seen. Comparing the two variables (human arrival and climate variation), the extinction times were nearer than expected by chance only to the time of human arrival in 76 cases (each case being the extinction of a genus in one of the 19 regions). On the other hand, the time of the extinction was closer than expected by chance only to the times of intense climate change in just 2 cases (a value close to the expected by a random placement of the extinctions along time). Extinctions were closer than expected by chance to both human arrival and times of intense climatic variation in 8 cases, and to neither of these variables in 40 cases, out of a total of 126 cases. These findings provide clear support for the hypothesis that anthropogenic impacts, rather than climate variation, were the main driver of the late Quaternary extinctions.

The eight cases where the extinctions were close in time both to human arrival and to climatic variation were mostly in the Americas. In these continents, human arrival approximately coincided in time with the events linked to the Younger Dryas, the last cold phase of the last glacial cycle. This finding is consistent with the view that climate changes actually played a role in the late Quaternary extinctions. But what role was this? Several authors have interpreted this kind of result as a 'synergy', for the Americas (Barnosky et al., 2004; Lima-Ribeiro and Diniz Filho, 2013) and elsewhere (for example, Nogués-Bravo et al., 2008, Lorenzen et al., 2011). However, this terminology can be misleading, by seeming to attribute similar roles to both factors: climate and humans. Synergy refers to an interaction between two or more factors that, when acting together, produce an effect that is larger than or different from the sum of their individual effects. However, the global approach provides 'natural experiments' in time and space that allow us to separate the factors: the megafauna survived through many other intense glacial cycles throughout the whole Pleistocene and it also persisted well into the Holocene in islands not yet reached by people. Both lines of evidence show that if it were not for the anthropogenic impacts, it is unlikely that the megafauna would have become extinct. Thus, climate changes seemed to have acted mostly as intensifiers, when they coincided with humans' arrival in a given landmass. In the context of logic, one could say that human arrival was the necessary cause of the extinctions - without it, the megafauna would not have disappeared - while climate change was just a contributory cause - by itself it would have little effect, but once present it played a role as well.

The associational critique and why it does not refute the anthropogenic hypothesis

Within archaeological contexts, a question often raised regarding the anthropogenic hypothesis is, if it is correct, then why there are relatively few sites showing associations between humans and megafauna? This has been called the 'associational critique' (Meltzer, 1986). Is this pattern incompatible with the hypothesis of anthropogenic impacts?

To answer this question, let's suppose just for a moment, that the anthropogenic hypothesis is correct. If so, using the mammoths as an example, in which proportion of mammoth sites would we expect to find associated archaeological remains? First, we must keep in mind that the time of coexistence of mammoth and humans, until mammoths became extinct, was a tiny part of the geological time range of mammoth records (Lister and Bahn, 2009). But this is still not the point. About twenty centuries in North America was the time of coexistence of mammoths and humans in the same continent, but *in any one locality the coexistence was much shorter still.* Thus, one would have to be very lucky indeed to find an archaeological site from precisely the few decades or so when mammoths and humans coexisted in *that given locality*. In any other case, he (she) would find only mammoths without humans (before coexistence) or humans without mammoths (after coexistence). The expected pattern would be that a small fraction of megafaunal sites would have archaeological remains, and that is what is found.

Recently, Surovell and Grund (2012) presented another, complementary, refutation of the associational critique. They compared the relative temporal depths of coexistence (time spans between human arrival and megafaunal extinction, in proportion of the whole length of the archaeological record) among Australia, North America and New Zealand. Furthermore, they modelled taphonomic biases and also human demography to estimate how long it would take for humans to become abundant in a given landmass after their first arrival. Their results show that kill sites would be expected to be very common in New Zealand, to have intermediate frequency in North America and to be extremely rare or absent in Australia. This order of frequency of kill sites again is similar to the patterns we observe in the real world.

A modern view of the anthropogenic hypothesis

It is interesting to think about the process that resulted in these patterns. The hypothesis that the late Quaternary extinctions were caused by anthropogenic impacts has been considerably improved, in light of more recent knowledge, since it was put forward by Paul Martin (1967, 1984). A modern view of the anthropogenic extinctions as part of our early history would be as follows.

Except where megafauna co-evolved with early hominids (in Africa and south Asia, where there were few extinctions, and northern Eurasia, where they were quite spread across time), there is no reason to expect that big animals would have evolved instincts to avoid man. This is the phenomenon of ‘island naivety’, well known from many historical examples (Diamond, 1984). In the most plausible scenario, big beasts in the newly-colonized lands were quite unaware that humans could be dangerous hunters - to their downfall.

Putting the extinctions in the perspective of the time in which they happened, at least in three aspects, helps us understand that crucial period of human history. First, there was neither agriculture nor livestock - probably not a coincidence, as they were invented only after the megafauna disappeared. Thus, consumption of meat from large animals was probably indispensable for feeding a growing human population and if humans had any access to this resource - and technologically they had - one would hardly expect that they would not have used it. Second, once a large beast was killed, there was no efficient way to conserve vast amounts of meat. There were some valiant attempts such as underwater meat caching, first discovered in the Heisler site in Michigan (Fisher, 1995), and possibly the use of salt as well - but this was hardly enough. Therefore, a highly efficient use of megafaunal meat is unlikely. Third, people living at the time of our species’ dispersal did not even know that the world had an end. They went on finding virgin hunting fields, until one day - in the Americas, probably the day when the southernmost tip of Tierra del Fuego was reached - there were no more. Given these three points, if we put ourselves in the shoes of a Clovis or any other people of the time, how could we expect them to use the megafauna in a cautious, sparing way? What for, not knowing that the world had an end? Such restraint may make sense from our perspective, but not from theirs.

Although in its original modern formulation (for example, Martin, 1967, 1973), the hypothesis of anthropogenic impacts puts much emphasis on hunting as the main extinction mechanism (hence its common label the ‘overkill hypothesis’), more modern views have highlighted a diversity of anthropic impacts, all of which must have affected megafauna to different extents. Among these factors are introduced diseases (MacPhee and Marx, 1997) and fire. The later process is well documented, especially in Australia (Flannery, 1994; Johnson, 2006; Rule et al., 2012) and in North America (Flannery, 2001; Kerr, 2003; Gill et al., 2009). Increased frequency of fire actually seems to have been a consequence of the decline of plant-eating beasts, but it may have further affected the megafauna through habitat changes. Besides, some of the extinctions must have been caused indirectly through cascading ecological effects, especially the demise of large carnivores and scavengers. It is unlikely that the Clovis extinguished sabertooth tigers through hunting them for meat; there must have been easier sources of protein around. However, after all their big prey species were gone, sabertooths were doomed as well. The same must have applied to the huge North American teratorn birds and other large scavengers that depended on megafauna. The California condor’s habit of scavenging on stranded marine mammals must have emerged as a much-needed ecological niche shift after its usual food sources had all but disappeared.

Another point is that it was not a ‘quick’ extinction at all, as had been proposed by Martin’s ‘blitzkrieg’ version of his hypothesis (Martin, 1973). The extinctions were a long historical process that lasted several thousand years in each continent, with a few stragglers left even after that, as expected - the last on the islands. A comment here about the time scale involved in the events here described could be useful. Palaeontologists work with so-called ‘geological time’, which comprises very long time scales, often in the order of millions or billions of years. Besides, the farther away we look to a given time span in the past, the shorter it seems. There seems to be little difference between 40,500 to 40,000 years ago, but from Columbus to us it seems a long time. This trap of our perception and Martin’s unfortunate expression help to explain many misunderstandings about the anthropogenic hypothesis. ‘Blitzkrieg’ means lightning war, but it was not a war at all, nor was it quick. As far as we know, the animals were hunted not because of our species' urge for killing, but because they provided valuable resources for which there were no substitutes at the time. It was a very long process that took several millennia in continents and centuries in large islands.

The Quaternary extinctions do not imply that humans were terrible hunters. Big, slow-breeding animals are the most vulnerable to hunting. The species that became extinct had low fecundity, usually approximately less than one young per female per year (Johnson, 2002). Wallace's first impression - that the extinctions affected preferentially large animals - is an artefact of the negative correlation in nature between body size and breeding rates. Big animals might not have even been a major component of the diet and even so, they would be expected to become extinct. For example, Johnson (2006) estimated that a group of ten Australian aborigines needed to kill only about two diprotodonts per year to extinguish a population of these huge marsupials. The point with the late Quaternary extinctions was not the intensity of the hunting - it was the fragility of the hunted.

Altogether, from an ecologist's point of view, it is not surprising that humans' arrival in the new continents would have extinguished megafauna - it would be surprising if it had not.

The conservation of the memory of the human-megafauna interactions and the south-central American sites

In light of the evidence now available, without the anthropogenic impacts following human dispersal, nobody would be talking of 'Quaternary extinctions' today. It remains quite plausible that anthropogenic impacts were magnified by climatic events in some places, but climate change does not seem to be a major cause. However, regardless of whether anthropogenic impacts were the main cause or 'just' one of the major causes, what we know today is more than enough to show that these extinctions were one of the main events in the history of man's interactions with natural environments, as our species dispersed across the planet. Yet, perhaps because of the relative recency of Martin's hypothesis, or perhaps because the extent of humans' role is still debated, these are undervalued pages of our history. The late Quaternary extinctions are a fascinating subject that have seldom received the attention they deserve in education or in the media. The UNESCO World Heritage Convention can have an important role in changing this scenario.

The Americas must play a special role in the effort for changing this scenario. After all, the Americas were the New World, not just in the familiar, Eurocentric, cultural way - they were also the biological New World. The Americas were the last continents to be reached by modern humans and therefore the continents where megafaunal extinctions as a whole were the most recent. They therefore a have a crucial role in preserving the memory of our interactions with the extinct large animals. Herein, we would like to tentatively propose three American sites which can be particularly valuable for this goal.

The first is Monte Verde in southern Chile. With its very old dating, Monte Verde is of course a key site in understanding human dispersal into the continent. But there is more to it; Monte Verde also illustrates particularly well the use of megafauna by humans, with a chunk of gomphothere meat found in an archaeological context. As Monte Verde is likely to reflect the oldest colonization of the continent, this finding may well represent a snapshot of the early utilisation of the just discovered South American megafauna.

The second site is Serra da Capivara, within Serra da Capivara National Park, in Piauí state in north-eastern Brazil. This is also a highly valuable site, not because of its unreliable claims to greater antiquity, but for its richness in rock paintings, many of which represent extinct species and their interactions with the early settlers. To our knowledge, there is no other site which represents so well human-megafauna interactions in Brazil. Besides, these paintings unfortunately are threatened by vandalism, which increases the urgency of efforts to conserve them.

The third site proposed is Las Breas de San Felipe, in Cuba. It would be important to represent the last of the American extinct megafauna and its interactions with humans. Hence, Cuba was home to the last surviving megafauna in the Americas. The most recent records are from the sites of Las Breas de San Felipe and Solapa de Silex, with human artefacts associated to dwarf giant ground sloths (genera *Parocnus* and *Megalocnus* respectively), dated to 5.7 and 4.7 ky respectively (reliable calibrated dates). Las Breas de San Felipe is a tar pit, a kind of miniature Rancho Las Breas, the famous Californian tar pit site (Iturralde-Vinent et al., 2000). Among Cuban sites, Las Breas de San Felipe is the richest, with easiest access and thus the one that presents more potential to be nominated to the UNESCO World Heritage List, despite the slightly younger dating of Solapa de Silex's ground sloths (MacPhee et al., 2007).

Conserving evidence of human-megafauna interactions is important for us to learn from our history - about when our impacts on nature were severe, when they were not, and what caused the different outcomes. It is also a useful reminder of the fragility of nature – especially of the big animals – to our actions, in a time when so many people still deny the full magnitude of our impacts on the natural systems. Now that we are extinguishing species at unprecedented rates, more than ever we need to learn from the past. As Paulinho da Viola (1972) sang in *'Dança da Solidão', 'Meu pai sempre me dizia / Meu filho tome* *cuidado / Quando eu penso no futuro / Não me esqueço do passado'* ('My father always told me / My son, be careful / When I think about the future / I don't forget the past').

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The Last Continent: Prehistoric America in Comparative Perspective

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The prehistory of the Americas was never lost to view: the shell middens, ceremonial mounds, rock art and less conspicuous traces were parts of the landscape long before Europeans arrived in the fifteenth and sixteenth centuries. The 'rediscovery' of the continent is hence a questionable concept. Yet the long separation of the Americas from the rest of the world has given it a special status in the understanding of human social development. For whereas early historians, antiquarians and archaeologists might well question whether parallels between distant ends of the Old World might not, despite their separation, be the result of direct or indirect contact, the likelihood of contact between the Old World and the Americas, while never entirely discounted, has generally been dismissed as unlikely. Thus, the development of human society in the Americas, since the first settlement of the continent in the latter part of the last Ice Age, has been an independent and indigenous process: 'from approximately 15,000 BC, when ancient peoples first entered the Americas, until roughly AD 1500, to speak in round numbers, there were two entirely separate populations on earth, one in the New World, one in the Old, each unaware of the other' (Watson, 2012).

Some earlier scholars considered the Americas a 'laboratory' for the study of evolutionary processes, because of its separate yet in many senses parallel development. This curious perspective bestows apparent primacy on the Old World and treats the Americas as a kind of test bed for anthropological theories that compare and contrast it with the former. The practice goes back to the sixteenth century, when artists such as Jacques Le Moyne de Morgues and John White produced images of ancient Picts and Britons that drew directly upon their own paintings of Native North Americans. Le Moyne had accompanied a French expedition to Florida in 1564, while John White travelled on Sir Walter Raleigh's 1585 expedition to Virginia (Moser, 1998, pp. 71-76). The idea that Native American societies were in some way equivalent to those of earlier periods in Europe was deeply judgmental but persisted into later centuries. It is exemplified for example in the opening chapter of Ancient Society by American anthropologist, Lewis Henry Morgan, writing in 1877:

> So essentially identical are the arts, institutions and mode of life in the same status upon all the continents, that the archaic form of the principal domestic institutions of the Greeks and Romans must even now be sought in the corresponding institutions of the American aborigines, as will be shown, in the course of this volume. This fact forms a part of the accumulating evidence tending to show that the principal institutions of mankind have been developed from a few primary germs of thought; and that the course and manner of their development was predetermined, as well as restricted within narrow limits of divergence, by the natural logic of the human mind and the necessary limitations of its powers. Progress has been found to be substantially the same in kind in tribes and nations inhabiting different and even disconnected continents, while in the same status, with deviations from uniformity in particular instances produced by special causes. The argument when extended tends to establish the unity of origin of mankind. (Morgan, 1877, pp. 17-18)

Morgan's 'essential unity of mankind' was predicated upon the notion of European and American social development as essentially separate phenomena. Other European settlers maintained alternative theories of cultural contact to explain the pre-Columbian monuments that they believed were beyond the capacity of Native American peoples to create. The most famous of these was the myth of the 'Mound builders', that the large ceremonial mounds built by Hopewell and Mississippian groups in the eastern USA had been the work of a vanished pre-Indian population. It was only towards the end of the nineteenth century that this was decisively disproved (Feder, 1996, pp. 119-40).

The same period saw the rise of diffusionist theories that disregarded the possibility of independent development and argued that the prehistoric and early historic world had been linked by long-distance maritime voyages that had carried Mediterranean and Near Eastern innovations to distant lands. A key proponent was British surgeon, Sir Grafton Elliot Smith, who argued that features as diverse as artificial head deformation and the boomerang had been carried to the New World by maritime voyagers, and that knowledge of Greek art (transmitted by these same interconnections) underpinned the development of Maya art. Egyptian civilization had a primary role within this process (Smith, 1933).

The theory of connectedness has found little support in archaeological thought during the twentieth century, although it has continued to be a focus of interest (for example, Riley et al., 1971; Jones et al., 2011). Ventures such as Thor Heyerdahl's famous Kon-tiki expedition of 1947 that endeavoured to show how South American navigators could have sailed to Easter Island have not generally been found convincing. What the twentieth century has witnessed, however, is a new and improved understanding of global patterns of prehistory. This has been the result of a dramatic increase in the amount and dispersion of archaeological fieldwork, bringing some regions into perspective for the very first time; and to the development of scientific techniques, notably in the realm of dating, that allow global chronologies to be constructed reaching far back into the prehistoric past. Thus, comparisons between the prehistory of the Americas and other regions, or between different regions within the Americas, can now be assessed in their own terms. It also means that timescales of change can be evaluated and compared.

The parallels between the prehistories of the Americas and Eurasia are well-known and striking. They include general processes such as domestication, urbanism and state formation as well as more specific features such as irrigation, metallurgy and writing. Since all the evidence (as we shall see) suggests that the two hemispheres were isolated from each other, these convergent developments must be explained in terms of common underlying features such as the response of human societies to similar environmental opportunities (the availability of particular plant and animal species, or mineral resources, coupled with climate, soils and topography). Demography is a key factor: growing population sizes in both the America and the Old World encouraged the development of novel strategies in subsistence, settlement and social organisation. Each society was of course unique: the many parallel outcomes in the two hemispheres are nonetheless remarkable.

The first Americans

The date of first settlement of the Americas remains controversial, although the majority view envisages initial colonization some 17,000 years ago, with groups of hunter-fisher-foragers reaching the southern tip of South America by 15,000 years ago (Méndez Melgar, 2013).

The settlement of a land area of 42.5 million km2 appears to have been achieved relatively rapidly by comparison with the colonization by modern humans of other parts of the habitable world. Recent research suggests, for example, the first movement of modern humans from Africa into the Arabian peninsula during Marine Isotope Stage 5, possibly before 100,000 years ago, reaching south Asia by c. 80,000 years ago, but crossing to Australia no earlier than 60,000 years ago and probably only 45,000 years ago (Boivin et al., 2013). A similar prolonged process of range expansion took modern humans to north-east Siberia and thence across the Bering Straits into North America. Alternative scenarios of a transatlantic colonization across the edge of the Arctic sea-ice have not commanded broad support (Stanford and Bradley, 2012; cf. O'Brien et al., 2014), and are inconsistent with recent aDNA analysis of the Clovis skeleton from Anzick in Montana that indicates a Siberian ancestry for the first North Americans (Rasmussen et al., 2014). The skeleton from Hoyo Negro in Mexico (*c.* 12,910-11,750 BP) has also been shown by aDNA analysis to represent an early population expansion out of Beringia, not an earlier migration from elsewhere in Eurasia (Chatters et al., 2014; see also Chatters, this volume).

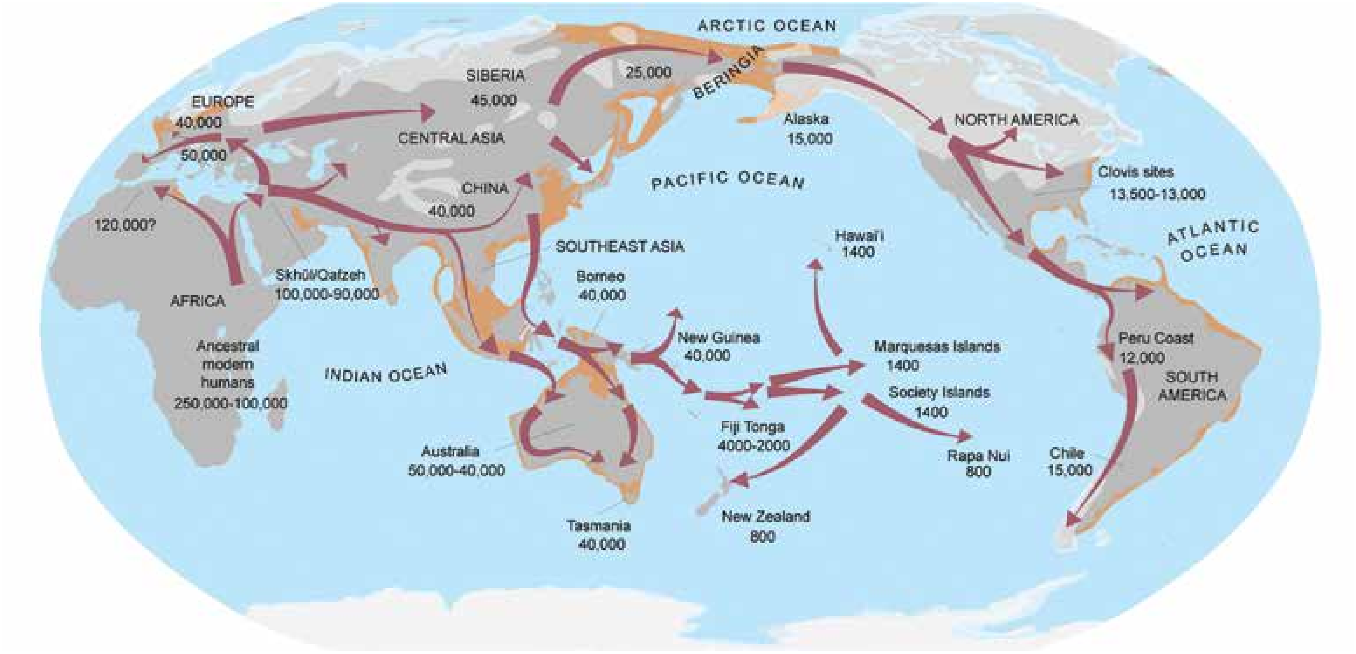

Figure 1. The expansion of anatomically modern humans from their African origins to Europe, Asia, Australasia and the Americas. The colonization of Australasia before 40,000 years ago would have required maritime technology capable of crossing open sea; the colonisation of Polynesia within the last 2000 years required sophisticated maritime technology and navigational skill, though whether Polynesian seafarers reached the coast of South America is still uncertain. Illustrator: ML Design.

Once they had penetrated south of the Laurentide and Cordilleran ice sheets, the human settlers encountered a land of warming climate and abundant resources. In contrast to most of the areas previously colonized by modern humans (with the notable exception of Australasia) there were no established hominid communities (cf. Neanderthal in Europe and western Asia, Homo erectus in east Asia); in hominid terms this was pristine terrain. The rapid expansion of settlement was accompanied by the extinction of many of the larger terrestrial mammals that had populated the Americas during the Pleistocene. Recent research concludes that this megafaunal extinction may partly have been a response to climate and habitat change but it was exacerbated and perhaps largely driven by human predation (Prescott et al., 2012; Johnson et al., 2013), even though in specific cases the connection with human action may be unproven (for example, Campos et al., 2010). The fact that the pattern is repeated across several continents is strongly consistent with some measure of human responsibility, and is supported by the impact of more recent human colonization on the flightless moa of New Zealand or the elephant birds of Madagascar.

Both the Americas and Australasia might be considered 'New Worlds': the last continents settled by modern humans, long after Africa, Asia and Europe. But while together they share that distinction, their subsequent social, cultural and demographic development differ in striking respects.

In large measure this can be explained by geography and environment. Nearly 70% of the land area of Australia (3 million km2) is desert (Smith, 2013, pp. 1-6), while only limited areas of the north, west and south coasts have more than 100 days of rain per year. The tropical north of Cape York and Arnhem Land give way to subtropical and then temperate zones as one moves south along the east coast, but inland extensive areas of desert are fringed by extensive areas of grassland.

In terms of biomass, Australia is hence much smaller than the Americas than their respective land areas would suggest and pre-contact population levels were much lower. Most estimates suggest fewer than 1 million people (Williams, 2013), as compared with 53.9 million in the Americas (Denevan, 1992). Indeed, populations in the desert areas of Australia may have numbered only 60,000-100,000 (Smith, 2013, p. 10). Despite specific adaptations to plant use and management, cultivation was never adopted, even in the relatively benign and fertile regions of the east coast or the Murray-Darling drainage.

It is striking nonetheless to note the evidence for population increase in Australia and the Americas from the period of first settlement up to European contact. Johnson and Brook (2011) argue from modelling taphonomic processes and abandonment rates at rock shelter sites that Australian population size was broadly stable during the first half of the Holocene but grew significantly from 5,000 years ago up to European contact. Williams (2013) has extended the curve back into the Pleistocene and, with a larger dataset of radiocarbon dates, has largely confirmed the mid-Holocene population growth posited by Johnson and Brook, with pronounced population growth from approximately 4,000 years ago, peaking 1,600 years ago with an estimated population of 1.2 million.

Despite the relatively small population size the clustering of communities in the more habitable areas of the continent and the growing numbers of people during the later Holocene might have been expected to lead to sociocultural complexity. There were indeed innovations in technology, economy and social interaction (Hiscock, 2009). The arrival of the dog and the presence in northern Australia of wild populations of bananas, taro and greater yam, three important food plants of New Guinea, may suggest contact across the Torres Strait and limited or experimental cultivation during the later Holocene, but if so it was a practice that did not spread or become firmly established (Denham et al., 2009).

All that is in sharp contrast to the pattern of development in the Americas. A similar methodology to that employed for Australia has used changing overall frequencies of radiocarbon dates from a hypothesised colonization date of 13,000 BC to the present to construct a proxy demographic curve for prehistoric North America. This concludes that population levels grew slowly at first, increasing pace after 6,000 BC, with a still further rate of increase after 200 BC. Maximum population density was reached around AD 1150, when the North American population may have numbered some 2.5 million people (Peros et al., 2010). Other recent estimates, based on historical and archaeological sources, suggest an even higher figure of between 1.2 and 6.1 million (Milner and Chaplin, 2010). The increased rate of growth after 200 BC relates to the impact of agriculture. In the south USA, for example, where maize cultivation was introduced around 2,000 BC, the development of more productive landraces and the addition of beans, squash and turkey led to significance population increase around the middle of the first millennium BC (Kohler et al., 2008). Still higher densities of population may have been present in the tropical zone. Total population in the heavily settled Maya lowlands alone during the Late Classic period must have numbered in the millions (Demarest, 2004, p. 294).

These population estimates are far larger than those for pre-contact Australia, but modest by comparison with heavily settled regions of the Old World. The Roman Empire, for example, is estimated to have numbered between 60 and 70 million people in the first century AD (Scheidel, 2007, p. 47); and census returns from the Han Empire of China in AD 2 record over 12 million households and 57.7 million people (Twitchett and Loewe, 1986, p. 206). In the Americas, such high densities of population may only have been encountered in Mexico, where some estimates have suggested a population of over 25 million people for the Aztec realm at the time of Spanish contact (Cook and Borah, 1948). Against such high figures, however, others have calculated that the total population of the Americas in 1492 may have numbered only 53.9 million people. This would imply that in the late fifteenth century, the Americas held only one seventh of the global human population (Denevan, 1992; Thornton, 1987, p. 37). Nevertheless it is clear that at European contact the Americas were heavily settled: perhaps more so than has sometimes been appreciated given the impact of the European diseases that preceded the first European settlers in some regions.

First cultivation in the Americas

When the Spanish conquistadores arrived in the New World they found a land populated by farming communities. The crops were different from those grown in the Old World, and there were few of the domestic animals that made such an important contribution in Europe and Asia, but the fundamental subsistence economy that they encountered was based on the cultivation and management of plants. That was not true of the entire continent, and hunting and gathering persisted in areas unsuitable for agriculture, such as the Arctic north, but the bulk of the indigenous American population relied on farming for their food.

Agricultural origins on a global canvas have often been envisaged in terms of core areas, where the wild ancestors of important domesticated species had their origins. The number of core areas has been disputed, and the concept itself has been challenged (for example, Harlan, 1971; Piperno, 2011; Fuller, et al., 2011a). It is clear that early human foraging communities not just in ‘core areas’ but in many other parts of the world entered into close relationships with the plant and animal species on which they depended. Nonetheless, certain specific plants or groups of plants, sometimes accompanied by animals, assumed a considerable importance in particular regions over the long term, and provided the basis on which settled communities of larger populations could be supported.

A number of key areas can be identified in the Americas: south-western Mexico, central Pacific and western Panama, premontane Colombia, the Colombian Amazon, south-western Ecuador, and northern Peru, and eastern North America (Piperno, 2011; Smith, 2011). At the time of European contact, maize was the key staple in three of those areas, and manioc in the fourth. It is misleading, however, to focus on the origins of these staples, since the earliest cultigens appear to have been the squash Cucurbita moschata and the bottle gourd Lagenaria siceraria. Remains of both have been found at several sites in northern South America and Panama dated between 8200 and 5600 BC (Piperno, 2011). Cucurbita squash yields edible seeds, but it is possible that both it and the bottle gourd were cultivated largely for their use as containers. Hence agricultural origins in the Americas may have been propelled by the need of mobile hunter-gatherer communities for means of carrying things, notably water, which would have been a vital resource in this arid landscape.

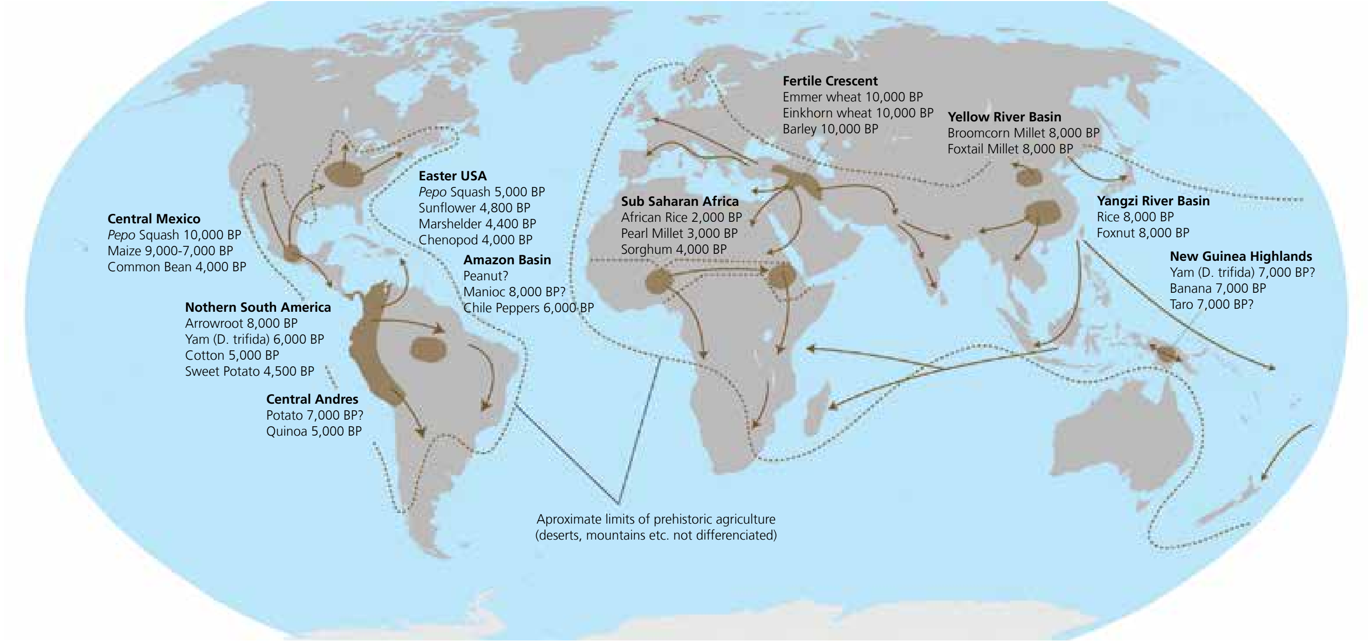

Figure 2. Principal centers of plant cultivation. Note how these are confined to tropical and middle latitudes between 20°S and 40°N, and consist predominantly of large-seeded grasses and tubers. Illustrator: ML Design.

The date of first domestication of the Mesoamerican staple crop, maize, has been much disputed. Excavation in the dry cave deposits of the Tehuacán Valley in the 1960s yielded remains of maize cobs at various stages of domestication and coupled with early C14 dates suggested that the transition from hunting and foraging to farming had been a very gradual process, extending over several thousand years. The first domestic maize, it was claimed, dated to 6,000 BC, and at first played only a minor part in the overall diet, becoming a key staple only in the third millennium BC (MacNeish, 1964).

This early field research in the Tehuacán Valley challenged the prevailing orthodoxy of Old World agricultural origins which since Gordon Childe (1936) had interpreted the beginnings of farming as a 'Neolithic revolution', a radical and relatively sudden shift in human subsistence. The focus in the Old World explanations was on the staple cereals wheat and barley (in south-west Asia) coupled with domestic livestock: sheep, goat, cattle and pig. The Tehuacán evidence poses two separate challenges to this conventional view: first, in demonstrating that the earliest cultigens were not necessarily staple food crops; and second that the path to fully farming communities was not necessarily a sudden shift.

New World farming differs from Old World farming in one other signal respect: the much smaller role accorded to domestic animals. Old World farming communities could call upon a variety of domestic animals, not only as food sources but for dairy products, transport and traction. There was nothing strictly comparable in Mesoamerica and North America, and the camelids domesticated in Andean South America were not exploited extensively for their meat, nor as plough animals, but for transport and wool. Cultivation remained the back-breaking work of human labour.

With the exception of the dog (brought across the Bering Straits by the first settlers: Thalmann et al., 2013) and the bottle gourd (carried from Africa by accidental drifting on South Atlantic Ocean currents during the late Pleistocene: Kistler et al., 2014), all the plants and animals domesticated in the pre-Columbian New World were indigenous to the Americas. The process is testimony to the inherent embeddedness of domestication within human behaviour, at least since the emergence of modern humans. It has been argued, indeed, that under the relatively stable climatic conditions of the Holocene, agriculture was, in the long run, inevitable (Richerson et al., 2001; Bettinger et al., 2009). Such a perspective places New World agriculture alongside that of the Old World regions as parallel processes, driven essentially by (a) the availability of suitable species, capable of thriving under domestication and providing high returns (such as the large seeded grasses: rice, wheat and barley, maize), and (b) demographic growth, encouraging closer interactions between societies and their wild food sources, leading eventually to domestication. Humans were conscious actors in this process, but it might also be envisaged as a form of co-evolution, with people adapting to domesticates just as domesticates adapted to human needs (Rindos, 1984).

In south-west Asia, close relationships between humans and their food sources led to an early exploitation of wild emmer wheat, barley and oats in the Levant. The key site of Ohalo II on the Sea of Galilee has evidence of the systematic exploitation of these resources 23,000 years ago (Nadel et al., 2012). This preceded by over 10,000 years the transition to agriculture. That may be contrasted with the process of subsistence change in the Americas. The settlement history of the Americas was much shorter than that of the Near East. If we assume first colonization of the continent no earlier than 17,000 years ago, and relatively rapid expansion of human communities implied by the available dating evidence from South America, then the period for adjustment of human societies to the regional suites of plant and animal resources had a much later start.

Once again, however, the advent of stable and more benign climatic conditions at the advent of the Holocene appears to have a major role. In South America, a range of Neotropical plant species appear to have been domesticated at the very beginning of the Holocene in Colombia, Ecuador and Peru. In the millennia that followed, human manipulation of gourd, arrowroot, manioc, yam and perhaps maize led to their domestication in this same region. In the Andean zone, there is evidence for the adoption of cultigens in certain upland valleys in the terminal Pleistocene and intensified use in the early to middle Holocene (Dillehay, 2012, p. 43). Yet the impact on communities of these increasingly intertwined plant-human relations appears to have been more gradual than in key regions of the Old World. In the Levant, the size of the largest settlements expanded massively during the early and middle Holocene, from 0.2 hectares in the tenth millennium BC (Late Natufian) to over 10 hectares in the seventh millennium BC (Late PPNB) (Kuijt, 2000). The large settlement of Çatalhöyük in central southern Turkey, founded c. 7100 BC, covered 13 hectares. Within a millennium, furthermore, substantial farming settlements had been established in south-eastern Europe, and by the end of the sixth millennium settlements of large timber longhouses had spread along the river valleys of central Europe to reach the shores of the English Channel. In China, too, the first domesticates quickly became established in the context of large nucleated villages in river valleys. That was not the case in the American Neotropics (Piperno, 2011, S461).

The contrast between the Americas and western Eurasia raises a series of fundamental questions. Why were they so different? One important feature that stands out is the focus in the latter region on the systematic gathering of large-seeded wild grasses – the ancestors of the domestic cereals – for several thousand years. These provided an effective staple foodstuff that could support large sedentary populations, in combination with pulses and domestic livestock. Many of the early New World cultigens did not have the potential to serve as staples in this way. But others clearly did – notably maize, manioc and potato, and it was those ultimately that provided the means for sociocultural complexity and the development of urban state societies in Andean and Pacific South America, in highland and lowland Mesoamerica and in the Mississippi Valley.

Settling the land

As human populations grew in numbers during the Postglacial, human impact on the landscape also increased. This was witnessed in growing levels of deforestation, both in the Americas and Eurasia. Much of that was associated with the clearance of land for agriculture, although hunter-gatherer impacts through burning to encourage new growth may have had unintended and irreversible effects in some areas. In coastal California, for example, the establishment of more sedentary communities of hunter-fisher-gatherers around 1500 BC was associated with increased burning of the local vegetation (Anderson et al., 2013). A general relationship between population size and forest clearance for farming has been documented at both the continental and global scale, and may have contributed to slowly rising levels of atmospheric CO2 recorded in the Atlantic ice cores (Kaplan et al., 2011).

Human impact was also marked in more symbolic ways. The most widespread took the form of rock art. Palaeolithic rock art (in the form of engraved or painted motifs) is present on every settled continent, including Australia. Evidence from North America suggests that petroglyphs were being carved at Winnemucca Lake, Nevada, as early as 10,000 years ago (Benson et al., 2013). Of similar or slightly earlier age is an engraved anthropomorphic motif from the Lapo do Santo rockshelter in central Brazil (Neves et al., 2012). It is not only the practice of rock painting or carving, but the motifs themselves that find broad international resonance. Images of humans and animals, whether naturalistic or schematic, are widespread on all continents. Still more striking are the middle Holocene hand stencils, present for example at the Cueva de las Manos in Patagonia, inscribed on the World Heritage List in 1999. Hand stencils are also known from North America, North Africa, Australia and Borneo, and from Upper Palaeolithic caves in France and northern Spain, where they constitute some of the earliest dated rock art in the world (Pike et al., 2012; Pettitt et al., 2014). Recent studies of hand stencils in Sulawesi have shown they are of comparable antiquity to the oldest European examples (Aubert et al., 2014). Both the practice of rock art and the individual motifs place the Americas once again within a global context of human behaviour, in this case one where symbolic expression, and the marking of special places within the landscape, occasionally takes very similar forms.

Postglacial societies modified their landscapes in other ways, too. Monuments of earth and stone are a feature of many regions within and outside the Americas. The manipulation of large stones to create pillars, colossal statues or burial chambers (frequently in the form of 'megalithic' monuments) draws upon the need to impress, as power relations became more complex and societies more unequal. Monuments also provided the settings for ceremonial and cult. At Nanchoc in the Andes, platform mounds were built as early as the sixth millennium BC, with steep stone-faced sides (Moseley and Heckenberger, 2013, p. 646). They mark the beginning of a tradition that became widespread in the 3rd millennium BC, as represented by sites such as Aspero on the Pacific coast or La Galgada in the interior. Watson Brake in the Mississippi Valley, a fourth millennium complex consisting of eleven mounds around an oval plaza, provides a North American parallel (Saunders et al., 2005). They invite comparison with west European ceremonial structures of comparable date such as Silbury Hill or Avebury, but such comparisons fail at the detailed level, in terms of form and function. It is the creation of ceremonial settings at monumental scale that is the connecting characteristic.

As communities grew in size and complexity other parallels arose between American and Old World societies. The construction of irrigation canals to bring water to crops, or to natural stands of vegetation (Smith, 2001) is a feature of both hemispheres from at least the sixth millennium BC, although the most elaborate irrigation systems belong to more recent periods. It was only state-level societies that could command the skill and resources to construct such extensive irrigation works as the Nahrwan canal in sixth century AD Mesopotamia (Adams, 2006) or the inter-valley Andean canal systems of the Chimú (Ortloff, 1995). Control of water was a feature of many early and historical societies and once again, there are striking parallels between distant lands and places. The same extends to terracing of mountainous landscapes to create cultivable fields, a feature of Mesoamerica and Andean South America at the time of European contact, as well as in many parts of Asia and southern Europe.

Intensification, in terms of population numbers, settlement density, social inequality and food production, led ultimately to urbanism and state formation in both hemispheres, through a series of separate but parallel processes. The global chronological patterning is very uneven, with the first cities in Mesopotamia during the fourth millennium BC, in the Indus Valley region of South Asia a millennium later and in northern China by the end of the second millennium BC. They are marked by monumental structures, pronounced social hierarchies represented in iconography and burial, and intensified food production. In the Americas, cities form during the late first millennium BC and AD in highland Mesoamerica

(Teotihuacán and Monte Albán) and in the early first millennium in the Maya lowlands. Once again there are striking interregional parallels, between, for example, the low intensity tropical urbanism of the Maya lowlands and the Angkor complex in South-East Asia, or Anuradhapura in Sri Lanka (Isendahl and Smith, 2013; Fletcher, 2012). By the time of European contact, sophisticated urban societies were present, as independent developments, in highland and lowland Mesoamerica and Andean and Pacific South America, just as throughout much of Eurasia and North Africa. Millennia of demographic growth, subsistence change and social inequality had produced a global pattern whose common origin lies in the first settlement of the Americas during the final stages of the last Ice Age, and little or nothing to subsequent contacts.

The New World in isolation: maritime contact before Columbus

In the context of global prehistory, the Americas present a paradox of early connection followed by later apparent isolation. Modern humans arrived in North America around 15,000 years ago, if not before. There may have been as many as three separate immigrations, probably crossing the Beringian land-bridge from Siberia into Alaska (Greenberg et al., 1986). The alternative, of coastal or maritime migration using boats, opens the alternative possibility of colonization from Europe across the southern edge of the Arctic sea-ice (Stanford and Bradley, 2012), although as we have seen, a north-western point of entry is still generally preferred.

Whichever the point of arrival, the general belief backed by overwhelming evidence (or more accurately absence of evidence) is that the Americas, once settled, were thereafter isolated for over 10,000 years. It is that isolation that gives the parallel nature of many social, cultural and economic developments in Eurasia and the Americas its special significance. Cities, agriculture, metallurgy and writing are among the many key developments that find parallels in both hemispheres, suggesting that in a certain perspective human societies may be considered self-organising systems, tending to find the same solutions, technologies or traditions when faced with similar circumstances and opportunities.

There are, nonetheless, tantalising hints of external connections between the Americas and the Old World over the lengthy period from first settlement to the Spanish conquest. As we saw earlier, domestic dogs were probably brought from Asia by the first settlers, even though the earliest evidence of their presence in the New World is several years later than the presumed period of colonization.

Two specific pieces of archaeological evidence suggest later contact, although they may have been of a relatively ephemeral nature. The first of these is the sweet potato Ipomoea batatas. Sweet potato is a domestic plant of tropical America origin, yet it appears in archaeological contexts on a number of Polynesian islands several centuries before European contact (Horrocks and Rechtman, 2009; Montenegro et al., 2008). Recent genetic analysis confirms their pre-Columbian dispersal from the Americas to Polynesia (Roullier et al., 2013). How this came about has been the subject of considerable controversy. The maritime capabilities of Polynesia seafarers are well-established. The settlement of Rapa Nui (Easter Island) involved an open sea crossing of over 2,000 km, its nearest inhabited neighbour being Pitcairn Island, 2250 km to the north-west. Beyond Rapa Nui, the coast of South America lies 3747 km distant (Bahn and Flenley, 1992, p. 22). The possibility that Polynesian voyagers reached South America, whether by accident or design, is entirely plausible. The presence of sweet potato in Polynesia, however, indicates not only landfall in South America but a successful return journey. Westward flowing currents from Guayaquil in Ecuador would have made that possible, if nonetheless challenging (Scaglion, 2005; Scaglion and Cordero, 2011). Other evidence for Polynesian contact has been proposed (Jones et al., 2011), although sweet potato remains the most convincing.

The alternative scenario, that South American coastal peoples themselves undertook maritime voyages in the Pacific, was championed by Thor Heyerdahl in his 1947 Kon-tiki expedition. However, although ceramics found on the Galapagos islands, 926 km from the coast of Ecuador, may indicate maritime contact with South America, earlier claims for their pre-Columbian age have been discounted (Flett and Haberle, 2008; Froyd et al., 2010). There is no other evidence of distant South American seafaring, in contrast to the extensive record of Polynesian voyaging. Alleged parallels between monumental architecture in Polynesia and South America are imprecise and unconvincing, and testify merely to independent regional manifestations of a globally dispersed pattern of ceremonial platforms and standing stones. Accidental drift voyaging from South America to Polynesia remains nonetheless a possibility (Montenegro et al., 2008).

The second is the presence of wheeled toys in Pre-Columbian Mesoamerica. Several terracotta models of wheeled vehicles, with disc-like wheels mounted on wooden axles supporting a terracotta frame sometimes in the form of an animal, have been found mainly in Olmec contexts in the coastal Veracruz region (Ekholm, 1946). It has been suggested that these are evidence of trans-Atlantic contact, perhaps involuntary and spasmodic (e.g., shipwrecked mariners). While that possibility cannot be excluded, an indigenous derivation from spindle whorls offers a more plausible origin (Ekholm, 1946, p. 225).

The absence of any South American domesticates other than sweet potato from Polynesia suggests that such contact as may have existed were ephemeral. Nor is the evidence any stronger for Central or North America. This stands in stark contrast to the movements of crops between different regions of the Old World during the middle and late Holocene. There was active transmission across the Indian Ocean, with Chinese millet reaching Africa, and no fewer than five African crops reaching India soon after 2000 BC (Fuller et al., 2011b). Even the relative isolation of Australia was broken by the introduction of the dingo some 4500 years ago, and already noted, domestic crops may briefly have been introduced from New Guinea to Arnhem Land two millennia or more before European contact (Hiscock, 2009, p. 146; Denham et al., 2009). Given the relatively short sea crossings separating north-east and north-west North America from Europe and Asia respectively, its sustained isolation is all the more remarkable.

The first documented external contact can be dated to around AD 1000 and offers a foretaste of things to come. The Norse (Viking) settlement found at L'Anse aux Meadows on Newfoundland consists of a group of Icelandic-style halls radiocarbon dated to the period AD 980-1020. It is identified as a short-lived exploratory base established by Leif Eriksson in around the year AD 1000 and documented in the later Vinland Sagas. The attempted colony (if such it was) failed, however, owing to the hostility of the local populations and the sheer distance (3200 km) from the small Viking settlements of Greenland (Wallace, 2000). A scatter of Norse artefacts among the Dorset peoples of Arctic Canada testifies to only limited contact between the Greenland Vikings and indigenous North Americas in the two or three centuries that followed (Sutherland, 2000).

Hence by the beginning of the second millennium AD, the isolation of the Americas was under threat from two directions: the Polynesian maritime expansion from island South-East Asia to the west, and the Viking maritime expansion from north-west Europe to the east. The latter succeeded in making landfall, for at least a few short years; the former may also have done so but left no definite trace. In neither case were there long-term impacts. Neither Vikings nor Polynesians reached the Americas in sufficient numbers to pass on the deadly Old World diseases that ravaged indigenous populations following the Spanish conquests of the sixteenth century.

Epilogue: European conquest and colonialism

The arrival of Spanish and other European adventurers and colonists brutally truncated the indigenous development of Native American societies that had been unfolding since the first settlers crossed the Bering Straits some 15,000 or more years before. In the centuries that followed European contact, warfare, displacement, maltreatment and disease reduced the indigenous population to perhaps 10% or on one estimate as little as 6%, of its original size (Thornton, 1987, p. 42). That cultural dislocation has coloured the subsequent investigation of pre-Columbian societies, as scholars and antiquarians in the western tradition have sought to apply the methods of archaeology to an understanding of American prehistory. European collections of Aztec and Maya antiquities began to be formed during the nineteenth century, but these could not be incorporated into the narrative of the rise of western civilization in the same way as those of Greece and Rome, or Mesopotamia and Egypt (Díaz-Andreu, 2007, p. 172). It was only in the middle decades of the twentieth century that accounts of world prehistory began to be developed in which the early societies of the Americas were accorded a proper and more appropriate standing in the global picture of the human past.

Many of the features of those early societies are widely represented in the Americas and beyond, as we have seen. The underlying trend, of human population increase and adjustment to resources, environments and opportunities, has produced striking parallels which in some respects take us back to Lewis Henry Morgan's 'unity of the origin of mankind' (Morgan, 1877, p. 18). In World Heritage perspective, they have intrinsic value as reminders of the complex patterns of the past that preceded European expansion.

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Peopling of the Americas: Potential Insights from Modelling

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Introduction

This paper offers a comment on the value of modelling, as an aid to explanation of the archaeological record of the first peopling of the Americas. Models are simplifications of reality that enable us to explore alternative processes that may have given rise to the patterns we observe today. They may initially be formulated in qualitative terms as narrative representations of some system of interest (where the axioms – assumptions that are taken as given, to enable hypotheses to be formulated - often remain implicit). But, we suggest, models are more useful if their premises are made explicit, and if their assumptions about the dynamics of the system of interest are formalised as a set of rules or mathematical relationships. In this way the input variables can be quantified, the assumptions about dynamics can be checked, and the archaeological consequences of alternative scenarios can be properly explored.

Models are fundamental to scientific explanation: at one extreme, science can be defined as

> a process of constructing predictive conceptual models. Within this framework, the purpose of research is to produce models which represent consistent, predictive relationships. These models are representations of 'target' systems existing in the ambient world. They are the systems of words, numbers, pictures, programs, actions, and concrete images that constitute scientific communications (Gilbert, 1991: 73).

Fifty years ago, Levins (1966) pointed out that all models involve trade-offs between realism, generality and precision, and that the trade-offs we make in any single instance reflect not just our scientific priorities, but also our own mental limits in grasping cause-effect relationships in complex multicomponent systems and the limitations of the technology we use to model those systems. These observations remain true today. Levins also pointed out that

> The validation of a model is not that it is 'true' but that it generates good testable hypotheses relevant to important problems. A model may be discarded in favor of a more powerful one, but it usually is simply outgrown when the live issues are not any longer those for which it was designed' (Levins, 1966, p. 430).

Unless we make model-building part of our plan of scientific activity from the outset, archaeological research is reduced to a process of empirical observation and description in which broader interpretation is constrained by an implicit (and often outdated) conceptual frame of reference. Our predictive conceptual models and their assumptions and frames of reference must therefore always be kept under review.

In this paper, as an illustration of the value of the approach, we will firstly summarise a recent body of work on early Palaeoindian archaeology by one group of archaeological modellers based in the USA. This work focuses on the Early Palaeoindian food economy, and in particular, on the role of proboscideans (mammoth, mastodon) in the subsistence strategies of those early hunter-gatherers who used Clovis spear point technology. We will then, secondly, review the current stage of development of a longer history of modelling the spread of the earliest hunter-gatherer colonists of the Americas (or rather, the spread of the populations that became successfully established; we will not consider the possibility of earlier entries by small populations that subsequently went extinct, although this is an interesting avenue to explore). This second focus of our paper involves work done during the past fifty years by multiple authors, with a variety of modelling techniques and problem focuses. Finally, we will comment on the issue of shelf-life raised by Levins – do existing models of early Palaeoindian subsistence and dispersal adequately address the 'live' issues which we might want to prioritise for investigation today?

An example of a modelling approach: Surovell, Waguespack *et al.*'s models of a specialized Palaeoindian large game economy

A familiar, but contested, scenario for the economy of early Palaeoindians in North America in the Clovis era associates their spear point technology with specialized hunting of megafauna, including proboscideans (mammoth, mastodon). The arguments in support of this include the co-occurrence of Clovis points with proboscidean remains at many archaeological sites and the chronological coincidence of the Clovis tool horizon with the extinction of these (and other) putative prey species.

However, counterclaims have been made that the early Palaeoindian economy in North America was in fact a generalised foraging adaptation, and that human predation was unlikely to have been a factor in the extinction of these megafaunal species. The arguments in support of this alternative scenario include the relative paucity of sites with Clovis points and proboscidean remains, and the weakness of the chronological association between radiocarbon dates for early Palaeoindians and for the last observed occurrences of the now-extinct species.

Resolving this debate rests on a solid understanding of what patterns we should *expect* to observe in the archaeological record, under one or other scenario. This requires us to construct predictive models both of the original ecological system and of the factors affecting its archaeological visibility today.

A good start at this has been made by Surovell, Waguespack and collaborators. In a series of papers, they have shown (using simple predictive models) that the archaeological record as we know it today is indeed compatible with a hypothesis of Clovis-era economic specialization. In a paper that addresses the record of precursor communities in Siberia, Surovell et al. (2009) model the rate at which archaeological sites disappear from the record after deposition, reflecting a range of physical processes of attrition. They point out that that radiocarbon-dated occurrences of proboscidean remains in Siberia ought to increase with recency (at least, prior to the extinction cut-off) and that the fact that they do not implies that the underlying animal populations were in decline during the period of co-existence with Upper Palaeolithic human groups. Their model of the expected increase in survivorship of archaeological remains as a function of recency is an empirically estimated function, derived by analogy with the fall-off in frequency of volcanic events with age in the global archaeological and geological record during the same period (which must reflect taphonomic processes of attrition, since ice core records suggest that the true underlying frequency was uniform).

Elsewhere, Surovell and Waguespack (2008) compare observed frequencies of archaeological sites containing proboscidean remains from Clovis-era North America with those in various periods and regions of the Palaeolithic Old World; they show that after adjusting for time depth and spatial extent, the early Palaeoindian record is indeed characterized by a relatively high density of such sites. Their model consists of a formula for predicting the expected rate of deposition of archaeological sites per unit space and unit time, under different foraging regimes.

In a third paper (Surovell and Waguespack, 2009; cf. Waguespack and Surovell, 2003), the same authors analyse the relative abundance of remains of animals of different size classes in the Clovis-era archaeological record and compare it with the profile of relative abundances of captured animals of these differing size classes in the ethnographic records both of generalists and of large game specialists. Their model describes the expected prey abundance profiles of these two strategies, under the (ecologically valid) assumption that smaller-bodied species can typically be found living at higher densities; in such a world of prey availability, the archaeological sites of generalists should show a preponderance of game of smaller body sizes, while those of large game specialists should show the reverse pattern. It is the latter that is found in the Clovis-era archaeological record.

Models of early Palaeoindian population increase and spatial range expansion

Surovell, Waguespack and collaborators have been careful to separate their detailed models of an early Palaeoindian big game economy from the larger question of the timing of arrival of the first peoples of the Americas. Nevertheless, they do address this issue. In another recent paper, Surovell and Grund (2012) consider the limited likelihood of finding archaeological sites with remains of extinct fauna, if the period of overlap of humans and their potential prey was short and restricted to an initial phase of human population growth (when total numbers of people and thus their cumulative archaeological impact were low when compared with their successors). Surovell (2003) had earlier modelled the potential population growth rates of hunter-gatherer bands with high rates of relocation of their base camps (high 'residential mobility'), showing that women in such societies – perhaps counterintuitively – would have been capable of high levels of fertility, because such a strategy reduces the distances of daily foraging movements (and therefore their energetic cost). Waguespack (2005), meanwhile, had argued from ethnographic analogy that in such economies with a heavy meat-dependence, women could be predicted to have taken on a larger share of the non-subsistence tasks.

In a related body of work, several other authors have modelled the spread of an invading population of hunter-gatherers into North America and their possible impact on native prey species. Whereas models of the kind developed by Surovell and collaborators focus on prey choice and on the preservational biases of the archaeological record, this related body of work focuses instead on population expansion (and predator-prey interactions) as a geographically-structured process. Here, a major focus is on the time required to colonize the Americas from an entry point in the north-west, subject to the constraint that groups must multiply by growing and budding off within some neighbourhood; typically, it is not considered realistic to model a new group appearing thousands of kilometres from its parent group, without some intervening chain of links forged by shorter-distance migration and group splitting – a process that is modelled as unfolding over a multi-generational timescale.

An influential early exponent of such models was Paul Martin, who argued in 1973 that the Americas could have been colonized in 1,000 years. He estimated game densities based on modern analogies and analysed a model of an expanding, densely-populated migrating front of hunters who were capable of doubling their number every 20 years and who migrated an average annual distance of up to 30 km per year. If they hunted large game at a rate consistent with the needs of their modelled population densities in the front, but with wasteful use of carcass resources, then the large game species would have been depleted faster than their potential reproductive rates of replacement, leading to local and ultimately species-level extinction. In an extended version of this work, Mosimann and Martin (1975) considered a more detailed predator-prey model, obtaining essentially similar results for the likelihood of extinction of large game species in North America. These results were further confirmed by simulations in a new analysis of the Mosimann and Martin model by Whittington and Dyke (1984).

Alroy (2001) reported a more recent and more detailed exploration of the same issues. He modelled the expansion of an initial hunter-gatherer population entering North America from the north-west and expanding (in number and in space) at a rate determined by ethnographically plausible values for fertility and for mobility. His early Palaeoindian population was modelled as subsisting partly by hunting animal prey, whose distribution, densities and life history strategies were modelled – species by species - from empirical palaeontological data and from modern ecological analogy. Alroy analysed the likely trajectories towards extinction for different prey species under different assumptions about hunting pressure, finding that hunting efficiency (and thus human population density) was the most sensitive predictor of prey extinction rates. His models also predicted a boom-and-bust cycle in initial human population numbers, with a crash following prey extirpation.

Other models have also considered the fact that prey densities vary in space and how this may have affected demography and economic strategy. These models have usually, however, made an additional assumption that early Palaeoindian hunter-gatherers were locally adapted to primary and secondary biomass resource profiles. Thus Belovsky's (1988) optimal foraging models refuted the 'overkill' hypothesis, but only by assuming that human hunters varied their focus on hunted game versus collected plant foods as a function of local net primary productivity, that human population growth rates were sensitive to local food availability, and that prey species recovered from background predation pressure at a constant rate independently of their individual life history characteristics. Steele, Adams and Sluckin (1998) considered the evolution of the population distribution on the North American late glacial landscape as a function of regional variation in ecosystems, but again making unreasonable equilibrium assumptions about the stability of founding populations at carrying capacities that reflect a high degree of local economic adaptation. These assumptions of local cultural and economic adaptation are precisely what the proponents of 'overkill' and of a Clovis-era large game specialization would dispute, arguing instead that a large game focus was an efficient adaptation for an expanding colonizing population (for example, Kelly and Todd, 1988): it would have enabled them to expand into diverse environments where the local resource structure was poorly understood, but the behaviour of the large prey animals could be readily generalised from previous experience elsewhere.

A separate approach to modelling early Palaeoindian demography for the whole of the Americas has been taken by Anderson and Gillam (2000; see also Anderson and Faught, 2000; Banks et al., 2006). Their models explore possible geographical corridors of dispersal (based on GIS least cost path analyses of late glacial topography), with an associated 'leap-frogging' demographic model in which the velocity at which populations expand along a corridor is determined by the dimensions of the typical band's territory, its doubling rate and the distance which a new group is prepared to migrate after fissioning. Other than this tethering to resource corridors (and the assumption that leap-frog migration is an efficient way to colonize a continent of widely-dispersed but food-rich 'megapatches'), their models do not consider predator-prey dynamics or the validity of any associated equilibrium assumptions; but they highlight the possible importance of coastal, riverine and ecotone corridors in channelling movement as the colonizing population expanded.

Modelling early Palaeoindian range expansion: what are the 'live' issues today?

As we noted above, models are valuable when they generate useful predictions about important, 'live' issues. The models reviewed above remain extremely useful, but they are also - to greater or lesser degrees – linked to the broader assumptions of the 'Clovis first' and 'overkill' scenarios for the peopling in the Americas. We now review some respects in which the live issues have changed in recent times and the implications of these changes for how we should build our models in the future.

Coastal versus inland dispersal routes. Most examples from the earlier generation of models of the peopling of the Americas have assumed that the lands south of the ice sheets were reached through an 'ice-free corridor', which opened up between the receding Cordilleran and Laurentide ice sheets some time in the late last glacial. However, recent work suggests that this corridor may not have opened up until well after the Clovis era (Gowan, 2013). If that is the case, then late glacial colonization models should focus instead on the possibility of an initial coastal migration route (for example, Surovell, 2003; Anderson et al., 2010, 2013; Misarti et al., 2012; Clark et al., 2014).

Origins of Clovis technology. Recent fieldwork suggests (albeit controversially) that Clovis spear point technology may have originated in North America south of the ice sheets (Waters et al., 2011a), implying both an *in situ* precursor population (cf. Gilbert et al., 2008; Walters et al., 2011b) and the rapid diffusion of an advantageous cultural innovation. This scenario therefore now needs to be modelled at the continental scale. One focus for modelling is the demography and spatial expansion of a precursor population: what are the chronological and other empirical constraints? For Anderson and Gillam (2000, p. 60), 'The fluted point distribution […] probably better represents the process of population in-filling and the spread of a specific adaptation, than the locations where the first peoples settled […] Clovis could still be a founding population in some areas, although it no longer appears to be the founding population across the hemisphere'; but this does not affect their topographic modelling of possible dispersal corridors, only its timing. Meanwhile, older Clovis-first models can probably be adapted fairly easily to model the spread of Clovis technology (if that innovation was associated with increased hunting efficiency and increased hunter-gatherer population densities). The results might not look that different to those from models of 'Clovis first'. Mosimann and Martin (1975, p. 308), for instance, commented that in their models 'the hunters move south through the region of radiocarbon-dated kill sites in 60 years. It would be very difficult to detect so slight an age difference by radiocarbon dating'; but the same problem arises if the predation wave started from elsewhere within the continent and if the direction of innovation diffusion was reversed.

Climate change and faunal turnover. Most earlier models of 'overkill' did not take adequate account of processes of climate change and associated habitat fragmentation and loss, although these were occurring contemporaneously with initial human settlement and with human predation. More recent models suggest that megafaunal extinctions were at least partly driven by such changes in the natural environment, with human hunting simply adding further pressure, although there is still disagreement on the relative importance of the human factor (for example, Lorenzen et al., 2011; MacDonald et al., 2012; Johnson et al., 2013; Lima-Ribeiro et al., 2013a,b; Sandom et al., 2014). New models of predator-prey interactions and the early Palaeoindian archaeological record must therefore take this external, climatically-drive instability into account as well.

Latin America: radiocarbon chronologies for human occupation and megafaunal extinctions. In recent years the radiocarbon timescale of early human occupation of the different countries and ecoregions of Latin America has become much more clearly demarcated, due not just to new discoveries, but also to new availability of large-scale archaeological databases and syntheses (for example, papers in Bueno et al., 2013) and of the results of programs of redating of previously excavated archaeological material (for example, Steele and Politis, 2009; Gonzalez et al., 2015). Systematic reviews of the evidence for human involvement in, and for the timing of, South American megafaunal extinctions are also now more widely available (for example, Borrero, 2009; Barnosky and Lindsey, 2010; Prado et al., 2012). New models of human dispersals, prey choice and megafaunal extinctions should therefore be explicitly constrained by (and seek to explain patterns in) these bodies of evidence alongside those from further north.

Genetic and cultural evolution (and landscape learning). At a more theoretical level, it is surely now time for archaeologists to address the issue of congruence between their data and models, and the colonization models inferred from ancient and modern human DNA. Archaeology seems to be able to provide more precise chronologies than can archaeogenetics, but has not yet taken its demographic models and used them to predict genetic patterns (even as a by-product of what must remain, for archaeologists, an archaeological record-focused endeavour). But if, for example, our models and observations predict large-scale late glacial booms and busts in Palaeoindian populations, then it must be worth asking whether such fluctuations might be expected also to yield some modern or ancient DNA diversity signature. Meanwhile, it is surely also time for us to address more rigorously the modelling of rates of cultural evolution (and of local or regional ecological adaptation). Different schools of thought in evolutionary anthropology lead to differing expectations for the trade-off between optimisation of economic strategies in changing environments and the persistence of social traditions (for example, Smith, 2000; Winterhalder and Smith, 2000). These expectations have implications for our understanding of the rate of cultural evolution of local variation in population densities (carrying capacities), as well as of the potential for adaptive responses to rapid climatic and environmental change. A programmatic overview of some of the issues in 'landscape learning' has been set out by Rockman (2003) and by Meltzer (2003), but such models have not yet been explored in a fully quantitative framework.

Finally, it is worth reiterating that models are not typically proposed as 'true' representations of what happened in the past. They articulate explicit assumptions about key aspects of that past reality according to alternative hypotheses, build schematic representations of the dynamics of such past systems, and use these to generate testable archaeological predictions. For this reason, model builders are constrained both by the willingness of others to articulate their speculative hunches explicitly enough to enable them to be formalised and also by the availability of empirical data on a scale and measured to an accuracy and precision sufficient to enable model predictions to be tested. Model-building is most useful, therefore, as part of a dialogue with those engaged most directly in empirical data gathering.

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Social Evolutionary Dynamics and Property Relations in Primitive Societies

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This paper looks at social evolutionary dynamics and property relations in primitive societies. It is divided into seven sections that explore different theories posited over time which identify various 'motors' of social evolution and eventually gives way to an articulation of the forces and the social relations of production in the evolutionary dynamic of societies without social classes. To accomplish this, Sahlins's Domestic Mode of Production is analysed and then framed to produce a four-stage model for the development of property relations over the course of prehistory.

1.

Sixty years ago, when Childe (1951), Steward (1955) and White (1949) were practically the only Western scholars in the anthropological disciplines committed to an evolutionist perspective, they adopted a straightforward technological determinism. Human beings were assumed to be rational decision-makers. In the '*bricolage*' (Lévi-Strauss, 1962, p. 26) characteristic of their production, they would come upon useful innovations (ones that increased long-term net energy capture, in White's terms). These would tend to be retained and communicated to other producers, would form the basis for further useful innovations and so forth. Given a few rudimentary assumptions about human nature, the logical unfolding of technology would be the driving force of evolutionary change in human prehistory. Particular ecological circumstances might accelerate the adoption of certain innovations (as in Childe's [1951] 'oasis theory' of domestication), but, as Braidwood (1952) recognized, such circumstances are not necessary to the general theory.

The idea that technological development was the prime mover of human social evolution has come under attack from two quarters. From the cultural ecological perspective of the New Archaeology, the supposed autonomy of technology's development depended on assumptions about a corresponding development of human capabilities and, as such, constituted an unscientific explanation. 'Vitalism ... is unacceptable as an explanation. Trends which are observed in cultural evolution require explanation; they certainly are not explained by postulating emergent human traits which are said to account for the trends' (Binford, 1968, p. 322).

Technological development invokes, furthermore, the conscious decision-making of the producers as a causal force and is, accordingly, an explanation of change that is: 'needlessly teleological (since) many system states and adaptive responses in societies are not conscious to many or most of the people involved -- they are in no useful sense goal oriented' (Hill, 1977, pp. 66-67).

2.

What general cause for social evolution does the New Archaeology offer us to replace technological development? Given the New Archaeology's postulate that human cultures are homeostatic regulatory systems, changes in those cultures must come from the outside. Since environmental changes are not directional (while human social evolution has been), the preferred choice for causation external to the system has been population pressure. First put forward in a limited form by Binford (1968), then generalised (following Boserup [1965]) by Cohen (1977), population pressure has become accepted in most overviews of social evolution as its primary motor. For example: 'Over the long course of human cultural development, the archaeological and historical record shows a consistent ... increase in population worldwide. ... As a result of this population increase their subsistence economy must be intensified' (Johnson and Earle, 1987, p. 16). 'Population pressure introduces an element of instability into all human cultures. This instability often interacts with natural sources of instability (called 'perturbations') ... to bring about large scale shifts in modes of production' (Harris, 1991, p. 91).

Now, the difficulties with this approach are well known (Cowgill, 1975). It is a general Darwinian principle, for human households as for any other group of organisms, that reproduction can outstrip production. A universally present cause cannot explain any particular consequence, however. Even if one were to establish that a particularly grave imbalance exists between a population and its resource base (almost always, 'population pressure arguments assume what they should demonstrate' [Chapman, 1990, p. 147]), there is no reason to suppose that adjustment would be with respect to production (and not reproduction). As Flannery (1986, p. 15) points out, 'in zoology, population increase is generally taken as the sign of a successful adaptation or as evidence that a favourable evolutionary advance has already been made, rather than as a cause for further evolution.' Those who espouse the notion that population pressure is the motor of evolutionary change seek perhaps to escape the optimistic connotations of technological 'progress'. Scholars living at the beginning of a millennium in which interrelated social and technological changes have brought the human species to the verge of extinction have, however, little reason to reject their causal force.

3.

The other main alternative to old-fashioned technological determinism has come from the neo-Marxists (Johnson and Earle's [1987, p. 9] 'effete materialists'). Just as capitalism is the cause of industrialism (and not vice versa), just so in the evolution of non-class societies the social arrangements governing production would control technological development. As Godelier (1973, p. 122) puts it:

> 'Si l'anthropologie moderne a confirmé la thèse que le rapport entre développement des forces productives et développement des inégalités sociales n'était pas mécanique, elle a dans l'ensemble démontré que la compétition sociale dans les sociétés primitives comme dans les sociétés de classe fournit l'incitation majeure à la production de surplus et, dans le long terme, entraîne indirectement un progrès des forces productives'. ('Just as modern anthropology has confirmed the thesis that there is no mechanical relation between the development of the forces of production and the development of social inequalities, it has generally shown that in primitive as in class societies social competition constitutes the most important spur to the generation of surplus and, in the long run, indirectly brings about progress in the forces of production'. [Translation: author])

Arguments along these lines have been deployed by Bender to account for the development of simple farming from foraging: '... social hierarchization ... may have preceded the change in subsistence base' (Bender, 1978, p. 215), a change orientated to providing leaders with commodities they could control. Such views originate in a certain conception of historical materialism and are (as we shall see below) not incompatible with a Childean evolutionary perspective, but the tendency of those who espouse such positions has been to reject materialism altogether:

> 'The explanation of social phenomena, be it the division of labour, age-sets or potential inequalities in both gatherer-hunter and early farming societies, have (sic) tended to be naturalised and made law-like by stressing the dominance of techno-environmental/alias subsistence forces. We legitimise the divisions and inequalities in our own societies by making them the inevitable outcome of inevitable forces' (Bender, 1989, p. 87).

Bender's particular intellectual trajectory is typical of post-processual archaeology in general: a neo-Marxism that wishes to give greater weight to the social relations of production develops into a neo-Hegelian rejection of materialism in any form (cf. Hodder, 1986).

To be sure, one can give due weight to the importance of the social relations governing production without abandoning materialism altogether. To avoid a position which reduces social organization to homeostatic mechanisms regulating human ecology one does not have to support the idea that social organization is entirely independent of human ecology. Hayden (1990) provides a useful concrete example of how positions such as Bender's (that animal and plant domestication arose in the context of competition associated with incipient social ranking) can be articulated to the antecedent development of foraging techniques. My intention in what follows is to sketch out in general terms the articulation of the forces and the social relations of production in the evolutionary dynamic of societies without social classes.

4.

Sahlins's (1972) model of the 'Domestic Mode of Production' provides the definitive account of these relations. The fundamental characteristics of the Domestic Mode of Production are:

1. The dominant division of labour is by age and sex: 'the normal activities of any adult man, taken in conjunction with the normal activities of an adult woman, practically exhaust the customary works of society' (ibid., p. 79).

2. Production and exchange 'are oriented for livelihood, not profits' (ibid., p. 83), so that Chayanov's Rule ('intensity of labor in a system of domestic production for use varies inversely with the relative working capacity of the producing unit' [ibid., p. 91]) applies.

3. The system of land tenure provides to all households equally the resources they need for their autonomous production: 'where these resources are undivided, the domestic group has unimpeded access; where the land is allotted, it has claim to an appropriate share' (ibid., p. 93).

4. What the household produces is pooled among its members.

Necessarily correlated with these features is a simple technology: 'the basic apparatus can usually be handled by household groups; much of it can be wielded autonomously by individuals' (ibid., p. 79). This simplicity makes 'labor ... more significant than tools, the intelligent efforts of the producer more decisive than his simple equipment' (ibid., p. 81). The social relations of the Domestic Mode of Production and their technological correlates may be assumed to be present in all earlier prehistoric societies from the Palaeolithic to the Neolithic, that is to say until the time arrives when social inequalities are so strong that the production of some households is effectively at the command of others.

Now, as Sahlins makes clear (in spite of his somewhat perverse arguments in favour of an 'original affluent society'), it is characteristic of the Domestic Mode of Production that households sooner or later fail in their autonomous production (cf. Colson, 1979). Partly because of the inherently limited goals of domestic production for use (as reflected in Chayanov's Rule), partly because of the vagaries of environmental and other external circumstances, households are always actually or potentially in trouble. The intelligent efforts of the producers must, therefore, be devoted to counteracting potential failure, to reducing the variance in mean subsistence income. Reducing subsistence risk lies, after all, at the very heart of the logic of production for use. This is a point which the proponents of population pressure miss. For Cohen (1977, p. 39), 'the various techniques that constitute agriculture ... provide only one economic benefit: the ability to grow and harvest more food from a unit of space in a unit of time.' The main goal of autonomous domestic units, be they foragers or food producers, is not to maximise but to satisfice, however. (That, after all, is the thrust of Sahlins's notion of primitive affluence.) Rather, it is the potential contribution of food production to expanded storage strategies that should be stressed. A granary or a herd of animals reduces the short- and middle-term production risks associated with most foraging strategies.

Households reduce subsistence risk by a variety of social expedients. Thus, households mitigate their risks by participating in webs of alliance. By sharing (pooling their risks) with others in good times, families can accumulate obligations that may help them in times of shortage (for example, Wiessner, 1982b). Alternatively, households can engage in 'negative risk transfers' (Wiessner, 1982a, p. 173); that is to say, they can organize themselves to expropriate what they need from others (for example, see Sahlins, 1961). Households also reduce subsistence risk by a variety of techno-environmental expedients. Over the course of the Stone Ages, humans were able to develop techniques that broadened the range of resources that they exploited, that preserved resources over longer terms by developing means of storage, that improved control over the exploitation of particular resources (ranging from controlled burning to eventual domestication) and that stabilised resource yields (for example, by developing hydraulic farming). In the ethnographic present, all human societies incorporated some of these risk-reducing practices in their behavioural repertoire.

It is important to note, however, that social and techno-environmental approaches to risk reduction have different potentials for further development. *Ceteris paribus*, households are limited in their capability to expand the scope of their positive risk pooling: their ability to attract sharing partners will be constrained by the amount of surplus they themselves can produce. Likewise, a household's efforts to increase negative risk transfers will be checked by the increasing numbers of enemies its depredations will generate. Techno-environmental approaches to risk reduction are not so immediately limited. In their intelligent, ongoing, autonomous *bricolage*, households can little by little expand their commitment to r-selected species such as wild grasses, develop storage facilities to accommodate the increased harvests, cultivate the grasses so as to control their availability, water their crops so as to stabilise their supply and so on. Given the social relations of the Domestic Mode of Production (the autonomy of the household), risk-reducing technological development is, then, an independent variable that unfolds following its own logic (subject, of course, to environmental opportunities and limitations). To recapitulate, households are in control of their production; they can be assumed (on Darwinian grounds) to have an interest in more secure production strategies; their opportunities for increasing their security by social means are inherently limited; therefore, they will, if they can, take practical steps to increase their security, what steps they can take being constrained by the antecedent nature of their technology and by their natural setting.

5.

Within the general framework of the Domestic Mode of Production (that encompasses, in terms of traditional social evolutionary typologies, social formations covering the broad range of bands and tribes), the development of the forces of production carries with it social changes, which in turn stimulate further technological change. Thus, the development of more effective foraging techniques leads over the course of the Upper Palaeolithic to the closing of networks of mutual assistance (to increased territoriality and inter-group competition) (Gilman, 1984). Increased social competition promotes the development of social storage (Ingold, 1986, p. 207) and of production technologies (domestication) that can be oriented to the development of such storage (Hayden, 1990). Farming involves delayed-return production strategies (Woodburn, 1980) and the transformation of land from the 'subject' to the 'instrument' of labour (Meillassoux, 1972; Vicent, 1998). This transformation stimulates long-term investments in the land, diminishing the possibilities of social fission to the point that, eventually, exacerbated social competition results in the permanent subordination of some households to others (Gilman, 1981). With the emergence of class stratification comes what Mann (1986) aptly terms the 'end of general social evolution'.

Throughout the evolutionary cycle which begins in the Palaeolithic and ends with the Bronze Age, household producers were essentially independent. They had access to resources and possessed the skills necessary for production. Their production strategies were sufficiently unintensive to free them to arrange social alliances as they might prefer (that is, to break off unwanted ties). Under these circumstances social and technological decisions concerning household security would be for the household to make. Decisions to improve security through technological means would complicate the achievement of security by social means, however. The development of storage facilities (practical storage, in Ingold's terms), for example, would attract requests for assistance at the same time that it would diminish the need for assistance from others; to enjoy the benefits of practical storage, households would have to exercise exclusive claims over it (transform their practical storage into social storage), undermining sharing (Testart, 1982) and thus increasing competition between households. 'In short, technological improvements in the security of production would lead to potential decreases in social security' (Gilman, 1984, p. 124), decreases to which further technological intensifications would be the most directly available response. Within this cycle, technology appears to unfold logically as an independent variable causing social change, but this appearance is the result of a social organization of production in which the ability of 'thoughtful' foragers (Mithen, 1990, cf. Flannery, 1986, p. 4), farmers, producers of whatever kind to develop or adopt new technologies is not constrained by powerful superiors. In other words, both the forces and the social relations of production constitute the dynamic force behind human cultural evolution. The dynamic of change suggested here is what Stark would term a 'pull model', in which the 'minimal role for population growth is that of a 'gatekeeper' preventing reversal to less productive strategies' (1986, p. 303).

The broad range of times and settings in which transitions from foraging to farming have now been demonstrated to have taken place obviously makes it difficult to accept any single proximate cause, such as population pressure or climate change, as sufficient. As a result, in recent years scholars of the transition to food production have been reluctant to suggest an underlying common process that might account for this nearly universal re-orientation of human production strategies. Thus, according to Bruce Smith: 'agricultural origins' is a convenient umbrella term for what is, in fact, an extensive and complex mosaic of many different and distinct developmental puzzles [2001, p. 202]).' Or according to Graeme Barker: 'the extraordinary diversity of the evidence ... sits uncomfortably with any attempt to build a grand cross-cultural theory of universal applicability for why foragers became farmers (2006, p. 411).' I believe it may be helpful to take a step backward so as to bring into focus a broader explanatory dynamic along the lines sketched out above.

6.

Be that as it may, I now want to consider how the dialectical development of forces and social relations of production plays out in terms of property relations. The starting point for a social evolutionist analysis of property is Locke's (1960 [1690], pp. 19-20) definition of the term: 'Whatsoever ... [man] removes out of the state that nature hath provided and left it in, he hath mixed his labour with it, and joined to it something that is his own, and thereby makes it his property. It being by him removed from the common state nature placed it in, it hath by this labour something annexed to it that excludes the common right of other men'.

This definition has the virtue that it permits us systematically to link a juridical concept to forms of production. As Robert Netting (1990, p. 47) notes, 'when land is brought into regular use by invested labor (as in heavy, specialized fertilization, terracing, levelling, or irrigation) or when it can produce consistent crops of grain, fruit, nuts, or hay because of special conditions of soil or moisture, there will be a system of enduring claims [to that land] by households or individuals'.

Thus, the material evidence developed by archaeologists for such intensified agricultural production can by extension be used to argue for the existence of demand-rights and/or duties with respect to some tracts of land between members of the society that generated that evidence. To put it another way, two generalisations with systematic implications for property relations can be drawn with reasonable confidence from our historical and ethnographic experience: first, that individuals or groups who have access to or have created a resource that yields a stable income will seek to retain that resource for their own use; second, that individuals or groups committed to the exploitation of such a resource can in turn be exploited (for instance, serve as a source of income for other individuals or groups). The principle of 'sweat equity' permits one to link systems of property (a juridical concept whose reading in the archaeological record is obviously problematic) to systems of production (material facts whose archaeological interpretation is less problematical).

7.

Based on this line of thinking one can, I think, develop a four-stage model for the development of property relations over the course of prehistory:

Stage 1. Towards the end of the Middle Pleistocene populations of large-brained hominins had successfully occupied a broad range of tropical to temperate environments in the Old World. These populations were committed to mutual provisioning and, given their as yet rudimentary forces of production, they would have had extremely low population densities. The limited foraging proficiency of each of the widely dispersed groups would require them to help one another, a requirement presumably reinforced by an exogamic kinship system rooted in the prohibition of incest. Under such circumstances the self-interest of all these groups would not permit any exclusive property claims whatsoever.

Stage 2. Over the course of the Later Pleistocene the gradual development of foraging technologies would permit the capture of a broader range of resources on a more stable basis over the long term. As a result, population densities would rise to the point that a group large enough to reproduce itself could do so within a delimited territory. At this point it would be in a group's self-interest to claim exclusive possession of that territory. The households composing the group would continue to have equal access to resources and to pool their risks by sharing, but collectively they would seek to limit the access of outsiders to their collectively held territory. This initial emergence of ethnicity would, of course, require rituals and paraphernalia to represent and reinforce each group's exclusive identity.

Stage 3. The further development of foraging would eventually lead to the exploitation of resources susceptible to storage and encourage the adoption of delayed-return productive practices (such as animal and plant domestication) that would promote such accumulation. At this point, the Lockean notion of property becomes directly relevant. In Ingold's terms, households would seek to convert their practical storage into social storage, that is, to establish exclusive ownership of the fruits of their labour. A storage-oriented production system makes negative risk transfers increasingly feasible. This and the potential for differential accumulation of surplus would stimulate the development of within- and between-group competition and promote the development of social ranking.

Stage 4. Households engaged in the internal and external competition inherent in a storage-based economy would have reason to increase and/or stabilise their production. Innovations that produce such increases would often involve investments of labour to create durable facilities (terracing, irrigation, tree crops and so on) that permit greater production on a more stable basis. This primitive accumulation of 'landesque capital' is built up over generations and increases yields over periods much longer than the annual production cycle. Social units that have sunk their labour into such long-term investments will seek to establish trans-generational, inherited ownership of them. Such investments also diminish the possibilities of social fission to the point that, eventually, exacerbated social competition results in the permanent subordination of some households to others. With the emergence of class stratification comes what Michael Mann (1986) aptly terms the end of general social evolution.

Such a model finds broad support in both the ethnological and archaeological records, I believe, but demonstrating that support falls beyond the limits of this article.

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The Neolithisation Process in the Americas

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Abstract

All over the world, the Neolithisation process - the shift toward food-producing life-ways - was kicked off at the end of the Late Glacial Maximum and was amplified at different paces in different places during the Holocene. The almost simultaneity of these transformations begs an explanation. The Early Holocene global warming triggered profound environmental changes that offered new resources and subsistence opportunities to the post-Pleistocene hunters-gatherers. Plant and animal domestication took place in different parts of the world resulting from the exploitation and manipulation of selected range of species. Different hypotheses have been formulated to understand the driving forces and mechanisms sustaining these processes. In the Americas, the shift to food-production occurred in three large areas of the continent: in eastern North America in the north, in Mesoamerica in the middle, and in the Andes and part of Amazon basin in South America. The cohorts of domesticates, including maize, squash, manioc, yam, beans, turkey, llama and alpaca, spread through contact and exchange. Population pressure or tipping carrying capacity do not account for the Neolithisation processes in the Americas.

Introduction

As is the case for the onset of symbolic behaviour and self-awareness, the production of visual art, pottery making, metallurgy and urbanism, the emergence of food-producing economies is a critical milestone that paved the way for the construction of modern humanity. The driving forces behind each of these milestones are fiercely debated by researchers. The issue is both scientific and philosophical in nature and cannot be addressed exclusively from the empirical side of the equation. Empirical data are, however, essential. Facts matter and are crucial even if the same body of empirical data can lend itself to a wide range of interpretations. In general, the rationales adopted to frame a coherent view on any of the important issues mentioned earlier are strongly constrained by the worldviews and academic traditions that shaped the minds of the scientists involved in the debate (Kuhn, 1962).

The debate on the best explanation for the emergence of food-producing economies at the end of the Pleistocene - the Neolithic Revolution or the Neolithisation process as it applies to the American situations – is discussed in this paper, and is an important issue. Two direct and blunt questions can be framed at this juncture; and these simple questions are: Why the shift from foraging to food - production in the first place? And, where did that happen?

I - Neolithisation processes: review of hypotheses

The Neolithisation process resulted in the shift from hunting and gathering to an increasing reliance on food-production. As such, human selective pressures operated on plants and animals, leading to the formation of subsistence-cultural systems based on agriculture, livestock husbandry and/or a varying combination of both.

The attempts at a general theory of the Neolithisation processes can be arranged into three successive and partially overlapping generations. Gordon Childe (1929, 1951) was the first archaeologist to craft a comprehensive theory of the shift from hunting-gathering to food-production, dubbed ‘the Neolithic Revolution’, in analogy to the ‘Industrial Revolution’. Much has been written about the ‘Childean’ use of the concept of revolution in this regards, but Gordon Childe was clearly referring to the consequences of this change in subsistence systems; a change that laid the foundations for ‘modern’ settled village life and the ‘Urban Revolution’.

The ‘Oasis’ or ‘propinquity theory’ posited climate change as the prime-mover for the dramatic shift from hunting-gathering to food production at the end of the Pleistocene. According to the drafted scenario, the general warming of the earth´s climate resulted in the extension of arid lands and deserts at the end of the Pleistocene/Early Holocene. Plants, animals and humans were confined to a few restricted and favourable oasis-like areas, and in this case along the major rivers of the Fertile Crescent, the Tigris, Euphrates and in a certain sense, the Nile. Humans took advantage of the situation to start the cultivation of some of their favourite plant foods - wheat, barley, emmer, lentils. They also allowed wild herds of animals to feed on their fields after the harvests and from there, initiated livestock husbandry. These initial stages in the practice of agriculture and livestock husbandry led to sedentary villages and the invention of pottery (Demoule, 2009; Price and Bar-Yosef, 2011). Childean theory was unrivalled for several decades up to the late 1950s and early 1960s.

The first systematic objections to Childe´s, 'Neolithic Revolution' narrative were raised by Robert Braidwood (Braidwood and Howe, 1960). He questioned Childe's suggestion of the general onset of aridity all over the Near Eastern Fertile Crescent and launched the first coherent multi-disciplinary field research project at Jarmo, in the Zagros Mountains in Iraq. The research team included soil scientists, fauna and plant analysts, as well as experts in different domains of material culture archaeology. The starting point of Braidwood´s reasoning was anchored on the environmental diversity of the Fertile Crescent, which includes coastal plains along the Mediterranean, hills, plateaus, mountain ranges, hilly flanks and valleys. This diversity had significant implications for the natural distribution of wild plants and animals, and their pattern of change through time. The record from the Early Neolithic site of Jarmo did not show any evidence of a sustained shift toward increasing aridity at the end of Pleistocene. Small mammals like goats where hunted and later domesticated in that area. A comparative analysis of the material from other sites points to significant regional variation in the shift toward food-production. For Braidwood, this was the indication that each area had its own specific evolutionary trajectory, derived from its peculiarities. He drew on the plant geneticist Nicolai Vavilov´s concept of a 'nuclear zone' and dubbed his hypothesis the 'Nuclear Zone Theory'. In contrast to Childe, Braidwood did not address the 'why' question. Instead, he explained the shift to food-producing economies as a timely change in the long-term socio-cultural evolution. In his 'vitalist' approach, that change took place because human societies were ready for this to happen.

These two approaches to the Neolithisation process feature environmental change and its impact on human subsistence and social systems on the one hand (Childe) and human agency on the other (Braidwood). These major dimensions, with different dosages, are included in each of the theories that came to be crafted later, in the second and third generation.

The second generation of explanatory theories is characterized by more elaborate scenarios combining environmental change and population dynamics. There are interesting nuances between authors. Cohen´s 'food crisis' hypothesis (1977) and Binford´s (1968) 'marginal zone theory' provide a good sample. For Cohen (1977), relying on the number and elaboration of Levantine Epi-palaeolithic sites - or Mesolithic ones elsewhere -, there was a sustained population growth during that period. This dynamic demography threatened the subsistence sustainability of Late Pleistocene hunting-gathering societies. Consequently, they adjusted to the new situation through selective and intensive gathering of a narrow range of plants and animals, triggering their domestication.

Binford's (1968) marginal zone theory is also anchored on population growth, but with a more systematic focus on the spatial - or territorial - dimensions. Accordingly, Late Pleistocene hunter-gatherers´ intensification - as indicated by the Natufian case for example - took place in cores of the delineated 'nuclear zone', with the development of bulkier dwelling features, storage facilities, as well as systematic burials within and between habitation units. According to Binford's (1968) model, sustained population growth triggered out-migration from the core areas, along moving-frontiers. It is in this context that the new settlers tried to preserve their original food-ways and initiated what later became the domestication of a range of selected plant and animal species. In other words, the Neolithisation process that resulted in the emergence of agriculture and livestock husbandry took place in the margins of the core-areas instead of their centres.

The third generation theorists were critical about what they saw as an 'environmental deterministic' approach to the Neolithisation process. They pointed to the neglect of the sociocultural mechanisms that may have been part of the process. They consequently suggested alternative approaches with more systematic integration of sociocultural processes with long-term consequences.

Barbara Bender (1975) formulated the 'exchange theory', which was anchored environmentally with a focus on social dynamics and patterns of foraging groups' mobility. There were a series of intriguing archaeological finds, such as sea shells from the Mediterranean found several hundred kilometres in the hinterland, that remained unexplained and were left floating. Bender suggested that they may have been part of exchange systems linking connected late Pleistocene circum-Mediterranean foraging groups. According to Bender's (1975) theory, the intensification and 'routinization' of these social links led to the selection of a narrow range of resources to fuel the round of exchanges. Coastal groups may have selected a certain range of goods including peculiar and colourful sea-shells, while the hinterland groups may have brought cereals and baby mammals. Seasonal gatherings of these foraging groups in their overlapping territorial ranges were a crucial mechanism of their biological and social reproduction. The Neolithisation process was therefore the consequence of the linkage loops outlined above.

Brian Hayden (1995) aims to explain the puzzling early domestication of pepper, tomatoes and guinea-pigs in South America. These domesticates were clearly not a response to a food-crisis. For Hayden, large social gatherings were part of the social organization of some Late Pleistocene/Early Holocene foragers. Whatever the purposes of these gatherings, the assembled people had to be given food and beverages. In competitive feasting contexts, special food items were distinctive enough to set one group apart relative to the other. The feasting theory (Hayden, 1995) accounts for the selection of special plants and animals that may have been important elements of feasting in which elaborate items of material culture were used and displayed. The domestication of some plants and animal species was consequently an unintended consequence of the generalisation of large social gatherings and feasts.

1 - The Neolithic Revolution as a revolution of symbols

Jacques Cauvin's (2000) radical approach to the Neolithisation process deserves special treatment. In his book *The Birth of the Gods and the Origins of Agriculture*, Cauvin (2000) puts a significant distance from all materialistic explanations for the emergence of sedentary village life, the practice of agriculture and livestock husbandry that took place in Southwest Asia from 10,000 to 7,000 BC. Relying on the 'mentalités' rationale, he argues that the onset of Neolithic life-ways was derived, not from population growth, climatic change and forced adaptation of human communities at the end of the Pleistocene, but from a 'revolution of symbols', the invention of deities, that generated new religions and worldviews. Cauvin (2000) relied on a series of zoomorphic and anthropomorphic figurines and statues from different southwest Asian Late Pleistocene and Early Holocene sites interpreted as staging the new religious beliefs. The Mother Goddess, sitting on a leopard throne in a Çatalhöyuk Early Neolithic sanctuary, is claimed to document a radical shift in human symbolic behaviour. The presence of a number of female figurines, interpreted as emphasising fertility, is relied upon as additional supporting evidence. According to Cauvin's rendering of the developmental sequence, a new religion articulated on a Mother Goddess and Bulls took shape in the western flank of the Fertile Crescent during the Pre-Pottery Neolithic A (PPNA) and led to the adoption of Neolithic life-ways.

In the introductory part of his book, *Naissance des divinités, naissance de l'agriculture*, Cauvin (1997: 40) asserts that art is the 'main path to access the collective psyche of ancient societies without writing' *['notre principale voie d'accès au psychisme collectif des sociétés anciennes sans écriture'*]. This position is predicated on the fact that the representational part of art expression of these remote societies can be preserved in the archaeological record, accessible through archaeological research and analysable through conjecture and refutation. For Cauvin, who rejects all naturalist attempts at explanation of long-term culture change, '*l'imaginaire*', the capacity to construct binding symbols, is the driving force of social evolution. In his perspective, the shift to food-production was the consequence of transformational relationships between humanity and divine entities: the Revolution of symbols came first and the Neolithic Revolution followed.

For Cauvin (1997), the first evidence of the new revolution of symbols can be traced back to the post-Natufian El-Khiam period, around 10,000 - 9,500 BC, prior to the onset of the PPNA. The Natufian art repertoire included representations of gazelle, deer, birds and dogs as shown by finds from Wadi Hammeh and Nahal Oren. The art repertoire from El-Khiam period consists essentially of female figurines, pointing to a radical shift from zoomorphic to anthropomorphic representations. The selection of the woman's body as an icon is claimed to emphasise fertility, and was a conception that led to the later emergence of a Mother Goddess figure. Such figurines were already known and widespread during the Upper Palaeolithic period but for Cauvin they were part of an above all zoomorphic and relatively anarchic system of representation because "most of these animal representations are clustered, without any evidence (…) of a dominant animal that can be considered as a supreme being figure" *["on ne met nulle part en* évidence *(…) un personnage animal dominant les autres et pouvant faire figure d'être supreme"*] (Cauvin, 1997, p.101).

The new religious symbols, especially the carved or painted representations of the Goddess, spread widely in southwest Asia from the end of the El-Khiam period to 7,000 BC. The Early Neolithic site of Çatalhöyuk in Anatolia is considered to have provided the most extensive evidence of this new worldview. The representation of the Mother Goddess figure is associated with that of a bull. These images are found in different places, frescoes and sanctuaries, and also as smaller lightly fired portable clay figurines. Accordingly and beside its frequent representation, it is the specific place in which this figure of the Mother Goddess is set at Çatalhöyuk that points to its divine character. According to Cauvin, she is 'dominant on the northern and western wall of the domestic sanctuaries', represented in the process of giving birth to bulls. The numerous female figurines from Tell Mureybet, Hacilar and Çatalhöyuk point to an overemphasis on fecundity through the exaggeration of the proportions of waists and breasts. The control and domination over leopards is added to motherhood and fecundity symbols. For Cauvin, this symbolic system persisted during the whole Neolithic period and the Bronze Age up to the emergence of Jewish monotheism.

Despite local variations, the duo 'Goddess Mother/Bull' which emphasised complementarity, but subordination of the latter to the former, points to the secularisation of a new 'worldview', conveying new relationships between humans and nature (Cauvin, 2000). How is the genesis of this new worldview connected to the shift from hunting-gathering to food-production and village life remained unfortunately unaddressed.

Ian Hodder (2006: 195) presents a different view on the art from Çatalhöyuk: 'It can be argued that the 9,000 year-old art at Catalhüyük is closer to science than it is to some contemporary art, in the sense that it aims to intervene in the world, to understand how it works, to change it'. This position points to a more dialectic relationship between mind and matter, society and nature. Alain Testart (1998, 2010, 2012) pointed to serious weaknesses of the reasoning crafted in Cauvin's '*Révolution des Symboles, Naissance des Divinités*' and carried out a convincing refutation of the religious assumptions embedded in that model. The Revolution of Symbols thesis ignores all environmental circumstances that are strong constraining forces on human social systems. Cauvin's failure to link human behaviour to processes operating independently in the biosphere is a serious weakness. Paradoxically, and very surprisingly, Testart's vigorous refutation of Cauvin's theses is significantly weakened by his own unwillingness to take seriously into account the biological component of the domestication process (Testart, 2012).

Humans are part of the biosphere that supports and enhance their lives and social reproduction. Plant cultivation and livestock husbandry are clearly predicated on the existence of biological entities that allowed this co-evolutionary conundrum to take place in human history. The emergence of food-producing economies and settled life ways are the result of contingent interaction between independent variables with mutually re-enforcing consequences. Depending on circumstances - it is obvious that many equally interesting attempts have failed - some of these interaction loops became co-evolutionary nodes, shifting the system into a 'directed variation' mode.

II - Toward a new synthesis: coevolutionary landscape dynamics

The Neolithic Revolution debate is clearly much more subtle and fine-grained today. The two 'explanatory lineages' outlined above are still alive and well (Cauvin, 1997; Rindos, 1984; Zeder, 2009). They are both derived from a gradualist approach to cultural evolution. Punctuated equilibrium models are very likely much more relevant for the understanding of accelerated change that would seem to have popped up all of the sudden (Endersby, 2009; Elredge and Gould, 1972; Gould, 1991). Naturalist-oriented researchers tend to consider the shift to food production that started at the end of the Pleistocene as a series of adaptive adjustments to a wide array of dynamic change. There are nuances between parallel approaches, essentially Human Behavioural Ecology (HBE) through its Optimal Foraging Strategies (OFS) and Diet-Breadth Model (DBM) (Piperno and Pearsall, 1998) and macro-evolutionary perspectives (Smith, 1994, 2011; Zeder, 2009). Seen from such perspectives, the adoption of agriculture and sedentary life-ways as well as livestock husbandry and pastoral nomadism are the results of co-evolving dynamic systems. The driving forces that triggered these contextual adaptive shifts can accordingly be pinned down, analysed and 'falsified' (Popper, 1963). The key variables under scrutiny include landscape, wild life, climate and humans, or more precisely the complex interaction loops between these variables. Some researchers favour climate change as prime-mover. Others single out demography or patterns of social interaction like exchanges, or feasting. For all these researchers, it is important to construct bridging arguments for the explanation to be coherent and testable.

There are different nested levels involved in the 'construction of food ways', all resulting from conscious or unconscious selection processes. The landscape, constantly impacted by humans offers a more or less wide assortment of resources, restricted in this case to plants and animals. Not all edible items are eaten, and the construction of standard cultural food – staple food - is in constant adjustment depending on circumstances. This core category of people's diets includes most of the desirable food items that are generally in large and reliable supply. Without going into the detail of past 'culinary' traditions in different parts of the world, the staple diets were made of key source of carbohydrate plants (wheat, barley, maize, millet, sorghum, rice, yams, bananas, manioc and so forth), plant and animal proteins (beans, lentils, cowpeas, soya, meat, fish, molluscs), and plant and animal fat (palm oil, olive oil, peanut oil, animal fat and so on). Staple food was generally supplemented by occasional food. This category consists of edible items that can be relied upon as substitute or in addition to the basic cultural foods. The third and last category is that of emergency food, made of all edible items that can be relied on in circumstances of food crises.

Knowledge of all these food categories is learned and transmitted from one generation to the next. Consequently, there is a certain inertia in the composition of staple diets that is nonetheless exposed to abrupt changes - punctuated equilibrium.

Cognition is thus crucial in modelling the shift from hunting-gathering to food-production (D'Andrade, 1995; Fauconnier, 1997; Renfrew, 2008). Human conceptual networks are intricately structured by analogical and metaphorical mappings. Mappings between different domains are the heart of the unique human cognitive faculty of producing, transferring and processing meaning. These mappings play a key role in the synchronic construction of meaning and its diachronic evolution (Fauconnier, 1997, p.18). The idea of mapping as a process of transfer from one domain to another is critical for a systematic investigation of past and present food ways as cultural phenomena and knowledge. In the most general mathematical sense, this process is a correspondence between two sets that assign to each element in the first set a counterpart in the second (Fauconnier, 1997). As is the case for art expression, food ways are probably another manifestation of the human ability to create and use symbols. It 'functions at a crucial intersection of mind and body, society and nature' (Hassan, 1993, p. 271). Food ways have to be regarded as cultural constructs embodying thought, communicating information and eliciting action. They involve human minds, motor skills and techniques. The cognitive operations that play a central role in the construction of everyday meaning are the same operations that apply to reasoning, thinking and understanding generally (Fauconnier, 1994, 1997). Food ways thus denote cognition; and cognition is the key parameter holding it all together.

'Human knowledge is much too precious a thing to be carelessly discarded each generation with the hope that it will be rediscovered in the next. Human knowledge is carefully preserved and passed from one generation to another. Most of what any human ever thinks has been thought before, and most of what any human ever thinks has been learned from other humans. Or to put it another way, most of what anyone knows is cultural knowledge … Knowledge which is embedded in words, in stories, and in artefacts, and which is learned from and shared with other humans' (D'Andrade, 1995, p. xiv).

The sudden bursts of completely novel patterns of behaviour were in all the cases followed by a period of stasis. It is axiomatic that cultural evolution is Lamarckian and epigenetic. Once established, the new behavioural patterns are learned and transmitted through habituation processes. This is generally done through 'parental care', learning, transmission from generation to generation, as well as enforcement of the psycho-behavioural schemes. 'The potential for directed change in cultural systems is greatly, perhaps even exponentially, enhanced over that found in biological systems by the human ability to evaluate outcomes of behaviour and to abandon, adjust, or perpetuate behaviours based on this evaluation'(Zeder, 2009, p. 10).

The Neolithic Revolution took place at different times and places, and within different environmental circumstances all over the world. In the co-evolutionary approach adopted in this paper, human agency is a crucial element of cultural adaptation. 'It allows cultures to respond to pressures more quickly and with greater degree of flexibility and directness' (Zeder, 2009, p. 1). In order to explain culture change, one has to unwrap the processes shaping different levels of the culture under investigation. Human societies are part of an inclusive trophic chain. They are inserted into a population ecology made of constantly interacting multi-components systems. The dynamics of food complexes is driven by selection pressures that are populational and cultural. The operations of all these complex adaptive systems preside over the construction of cultural landscapes, in a dialectic between the 'naturalization of the societies and the socialization of nature' (Chorin and Holl, 2013).

1 - Mapping the earliest 'Neolithic' complexes

The shift toward food production took place during the Holocene period, at different times and places (Demoule, 2009). The earliest manifestations are dated to 10,000 BP in the Fertile Crescent in western Asia where domesticated wheat and barley have been recorded. Sheep, goats, cattle and pigs were also domesticated in the same area in the first half of the Holocene (Figure 1). With variation from one area to the next, the western Asia complex consisted of mixed economies, combining mainly cereal agriculture and livestock husbandry (Bellwood, 2005; Cauvin, 1967, 1971; Demoule, 2009). This complex spread later around the Mediterranean and continental Europe (Jones et al., 2013).

Foxtail millet, rice and pigs were domesticated in eastern Asia around 8,000 BP (Li and Xingcan, 2012). Broomcorn millet, foxtail millet and pig remains were found in the Yellow River basin in northern China. Rice, foxnut and pig remains are documented in the Yangtse River basin in central/southern China (fig. 1). Both complexes spread all over eastern Asia to reach Korea, Japan, southwest China and the Himalayas (D'Alpoim Guedes et al., 2013).

The Kuk Swamp in New Guinea provides evidence for the domestication of bananas, plantain and yam (*Dioscorea alata*) around 7,000 BP (Bellwood, 2005) (Figure 1). This complex spread later throughout the Indian Ocean to reach Africa.

The practice of agriculture emerged comparatively late in Africa (Harlan et al., 1979). The remains of cultivated pearl millet (*Pennisetum glaucum*), sorghum (*Sorghum bicolor*) and African rice (*Oryza glaberrima*) are dated to 4,000 - 3,000 BP in the

Figure 1. Main Neolithisation zones worldwide.

Sudano-Sahelian belt of the African northern hemisphere (Figure 1). Cultivated non-domesticated sorghum dated to 10,000 - 9,000 BP was found in large quantities in several storage pits from the early Holocene village site of Nabta Playa (Wendorf and Schild, 1998). In contrast, livestock husbandry through the domestication of cattle took place around 10,000 - 9,000 BP in the eastern Sahara and spread from there to the mountain ranges of the central Sahara (Barich, 1998; Cremaschi and Di Lernia, 1999; Di Lernia and Cremaschi, 1996; Holl, 1989, 1994, 1998, 2004).

III - The Neolithisation processes in the Americas

As is the case for the rest of the world, the shift toward food producing life ways occurred during the Holocene. The end of the Late Glacial Maximum, around 11,600 BP worldwide, set the stage for far-reaching environmental changes that impacted late Pleistocene hunter-gatherers communities (Smith, 2011; Piperno, 2011; Price and Bar-Yosef, 2011). The significant increase in atmospheric CO_2 that was 30% higher than at the height of the Last Glacial Maximum (LGM) ca. 21,000 BP (Ridgewell et al., 2003), higher temperatures and increased rainfall made the shift toward plant cultivation possible. In fact, the key issue is more about the cultivation of plants than the 'origins of agriculture' *stricto sensu*.

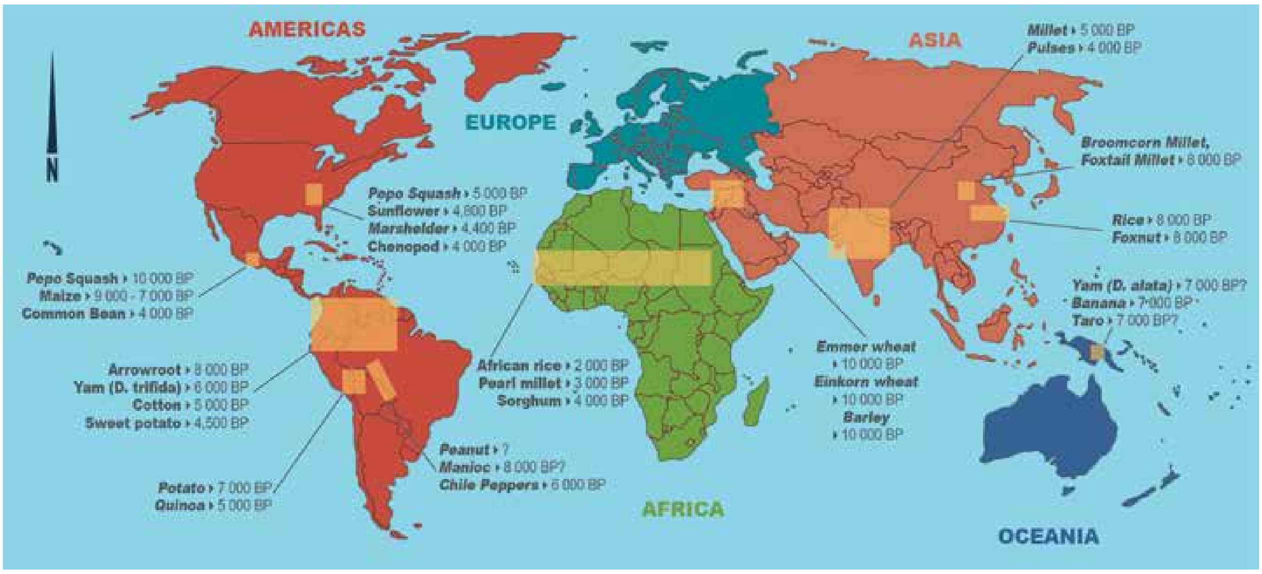

Figure 2. Distribution of initial areas of plant domestication.

The Neolithisation processes began more or less independently in three large geographic areas in the Americas, the south-central Andes in the south, Central America in the middle and eastern North America in the north. Central America and the south-central Andes have many features in common and are part of the Neotropics (Piperno and Pearsall, 1998; Piperno, 2011). In all these large geographic zones, 'external environmental stress, population growth, landscape packing, constricted resources zones, carrying capacity imbalance or resource scarcity' (Smith, 2011, p. 482) do not account for the shift towards food production. As far as the Americas are concerned, this shift occurred within the context of small scattered late Pleistocene mobile hunter-gatherer groups alternating the occupation of rich river valleys and more or less elevated caves and rock shelters. Different plant and animal cohorts were collected and exploited one way or the other, with some relied upon more heavily than others, triggering their shift to the status of domesticates (Larson, 2011).

1 - Place and time of earliest domesticates

The significant improvement and increased precision of research methods allow us to track the presence of domesticated plants species, their area of distribution and the chronology of their appearance in human cultural contexts (Larson, 2011; Price and Bar-Yosef, 2011; Smith, 1994, 2006; Zeder et al., 2006).

The Neotropical zone

The earliest human settlements of the Neotropical forest recorded from Belize to eastern Brazil are dated to 13,000 BP. After 11,400 BP, these hunter-gatherers 'settled into' their landscapes, staying for longer and/or more frequently returning to specific locations, and they frequently manipulated and altered their environments by creating clearings in forest and/or burning them' (Piperno, 2011, pp. 456-7).

In the northern half of the Neotropics, a number of sites and regions like Guila Naquitz Cave (Flannery, 1986), Tehuacan Valley (McNeish, 1975), San Andres, Xihuatoxtla shelter, Rio Balsas, western and central Panama contain evidence of domesticated maize, squash, chile pepper, cotton, sieve bean and jicama. In Mexico, at Xihuatoxtla Shelter in Guerrero state and San Andres in Tabasco state, domesticated maize and cucurbita - squash - are dated to 8,960 - 8,940/8,780 - 8,630 cal. BP and 7,204 – 6,904 cal BP. (Piperno, 2011).

Beside the dog, the turkey is the only animal species domesticated in Mesoamerica and North America. Turkeys were sought after for their feathers and probably their roles in different rituals, and may have as such been targeted by ancient Mesoamerican communities (Thornton et al., 2012). The precise timing and location of American turkey (*Meleagris gallopavo*) domestication are still unknown (Thornton et al., 2012, p. 1). Turkey domestication may have taken place independently in two distinct areas, one in the American south-west and the other in central Mexico. 'In central Mexico, archaeological *M. gallopavo* bones have been identified at sites dating to 800 - 100 BC….. It is [however] unclear whether these early specimens represent wild or domestic individuals, but domestic turkeys were likely established in central Mexico by the first half of the Classic Period (*c.* AD 200-1,000)' (Thornton et al., 2012, pp. 1-2). The recent discovery of domesticated turkeys in the Late Preclassic context (cal 327 BC-AD 54) at El Mirador in the Yucatan province opens the way to a reconsideration of turkey domestication and dispersal in Mesoamerica and American south-west.

Five interesting sites are found in Panama, three in the central Pacific region and two in the western region. Aguadulce rockshelter, Cueva de los Ladrones and Cerro Mangote in the central Pacific region have evidence of squash, leren, bottle gourd and arrowroot dated to 8,600 cal BP; maize and manioc to 7,922 – 7,734 and 7,740 – 7,640 cal BP; and yam (*Disocorea trifida*), around 5,700 cal BP in the first site. Maize dated to cal 7,804 – 7,584 BP is recorded at the second and third site. Arrowroot, maize and manioc are recorded at Chiriqui rockshelters and Hornito in western Panama, dated to 7,779 – 7,584/ 7,534 - 7,381 cal BP for the first two plants and 5,600 cal BP for the third.

Colombian sites can be arranged into two subsets: the Andean sites on the one hand and the Amazonian ones on the other. The Andean sites stretched from the Middle Porce Valley in the north to the Upper Cauca Valley in the south and include the Porce Valley site, El Jasmin, El Recreo, hacienda Lusitania, Hacienda El Dorado and San Isidro. Maize is dated to 7,321-7,032 and 6,799-6,597 cal BP in the north, 8,000 - 6,000 cal BP at El Jasmin in the middle and finally, 6,138 - 5,721 cal BP and 7,771 - 7,349 cal BP in the Calima region of the Middle Cauca Valley. Yam, squash and bottle gourds are recorded at El Jasmin, dated to 8,493 - 8,313 cal BP, squash at El Recreo, dated to 9,001 - 8,508 cal BP, and finally bottle gourd at San Isidro, dated to 11,058 - 10,706 cal BP in the south. The Colombian Amazon sites, found in the Middle Caqueta region,

Figure 3. Distribution of domesticates from Central and South America.

include Pena Roja and Abeja. Squash, leren and bottle gourd dated to 9,107 - 8,884 cal BP are documented in the former, and maize and manioc dated to 5,539 - 5,351 cal BP attested in the latter.

Ecuadorian sites are found in the southern part of the country. They can also be subdivided into Andean and Amazonian sites. The Andean group is made of four sites, OGSE-80 and OGSE-67 (Las Vegas sites) and Real Alto and Loma Alta (Valdivia sites). The Amazon group includes a single site, Ayauchi. Maize is dated to 6,000 cal BP at Ayauchi in the Amazon, 8,015 - 7,945 and 6,850 - 6,810 cal BP in Las Vegas sites and finally, 5,260 - 5,000 and 5,000 cal BP in Validivia sites. Squash, leren and bottle gourd are dated to 11,750 - 10,220 cal BP in Las Vegas sites. Leren, achira, arrowroot manioc and jack beans occurred much later in Valdivia sites where they are dated between 6,500 and 5,000 cal BP.

Further south in Peru, there are five sites distributed in two subsets, with two sites: Zana valley sites and Siches in the north, and three, Paloma, Chilca 1, and Quebrada Jaguay in the southern coastal region. Squash in its different varieties is dated to 11,015 - 10,885 / 10,402-10,253 cal BP at Siches and Zana Valley sites. Peanut (*Arachis* sp.) – 8,630 – 8,580 cal BP - manioc – 8,500 cal BP - and cotton – 6,301 – 6,133 cal BP - are confined to northern Peru. Sites from the southern coastal Peru present evidence of bottle gourd – 8,800 – 8,395 cal BP -, squash – 6,500 – 4,500 cal BP-, guava – 6,500-5,700 cal BP at Paloma and finally, achira, jicama (the edible tuberous root of a Mexican vine) and jack bean – 5,400 cal BP at Chilca 1.

Livestock husbandry through the rearing of alpaca (*Lama pacos*) and llama (*Lama glama*) also took place in the Peruvian Andes. As indicated by the faunal evidence of the long occupation sequence of Telarmachay rockshelter in the Puna region at an elevation of 4,000 - 4,900 m above sea level, the first groups of hunter-gatherers settled in the area around 9,000 cal BP. They relied on generalized hunting life-ways, and from 7,200 to 6,000 cal BP they focused on guanaco and vicuna as their main large prey. Domesticated camelids are attested in the archaeological record from 6,000-5,500 cal BP, with a fully-fledged herding economy established at Telarmachay around 5,500 cal BP. The larger guanaco is the wild progenitor of the llama, with the smaller vicuna, the wild progenitor of the alpaca (Barberena et al., 2009; Kadwell et al., 2001; Morales et al., 2009; Pollard and Drew, 1975).

There are two cases of documented cultivated plants in the eastern part of South America. One is found at Geral in eastern Amazon in Brazil and the other at Los Ajos in south-eastern Uruguay. Evidence of maize, dated to 3,800 cal BP, has been recorded at Geral as well as good indicators for the practice of slash and burn cultivation that existed around 6,662 - 6,464 cal BP. Maize, pulses and squash dated to 4,800 - 4,540 cal BP are attested at Los Ajos in Uruguay.

This short review of the chronology and geographic distribution of the earliest domesticated plants in the Americas Neotropics clearly shows that 'the earliest crop complexes were neither seed, tree, nor root crop based but rather mixtures of these different elements' (Piperno, 2011, p. 459). There is strong evidence for the diffusion of crop plants in different directions, probably using rivers as transfer corridors. Peanuts and manioc spread northwards. From the central Balsas River Valley of Mexico, maize spread both north- and southwards, to reach southeast Uruguay around 4,800 - 4,500 cal BP and eastern North America around 400 BC (Smith, 2011). Piperno (2011, p. 461) suggests that simple down-the-line forms of exchange, with cultivars cascading from one group to its nearest neighbour, without population relocation or significant transfers of material culture can well account for the diffusion of early crop plants in the Americas Neotropics. The first food producers of Central and South America were organized into small scattered mobile groups. It is only later, after the widespread adoption of plant cultivation and livestock husbandry of camelids in the Peruvian and Ecuadorian Andes that large permanent settlements developed in Central and southern America.

Eastern North America

Four seed-bearing plants, the pepo squash (*Cucurbita pepo* ssp.), the sunflower (*Helianthus annus*), marsh-elder (*Iva annua*) and the chenopod (*Chenopodium berlandieri*) were domesticated in eastern North America in the time interval, also called Late Archaic, ranging from 5,000 to 3,700 BP (Smith, 1994, 2006, 2011). Maize was added to this package later, around 200 BC. Evidence of these domesticates have been recorded at seven archaeological sites, all located in the relatively resource-rich oak-savannah and oak-hickory forest regions. They are scattered over five states, Arkansas and Tennessee in the south, Illinois in the north, with Missouri and Kentucky in between. Additional plant remains dated to the same Late Archaic period are recorded at Jernigan II, Peter Cave and Iddens. They belong either to bottle gourd, - a non-food item but an important container - or do not present significant morphological differences with wild varieties (Smith, 2011: 472).

The archaeological sites with undisputed evidence of Late Archaic domesticated plants are found in two main environmental settings: the rugged uplands and the river valleys.

Marble Bluff, Cloudsplitter and Newt Kash, at both the western and eastern ends of the geographic area under consideration, are rock shelters located next to streams. Marble Bluff above Mill Creek in Arkansas has a 1 m thick cultural deposit with a low density of material culture remains. The remains of domesticated pepo squash, chenopod, sunflower and marsh-elder were found in a well delineated charred storage context 'in a crevice against the back wall of the shelter and could not be easily associated with other cultural features or artefact assemblages' (Smith, 2011, p. 474).

The Cloudsplitter rockshelter, 55 m long and a maximum width of 15 m, is located some 100 m upslope from an intermittent stream in Kentucky. A Late Archaic occupation dated to 4,500 - 3,000 BP was recorded in a small area that may have been enclosed near the rear wall of the overhang. The samples of plant remains from Late Archaic occupation are dominated by nuts, with black walnut and hickory accounting for 90% of the recorded nuts. Domesticated plants are present but marginal. They include chenopod, pepo squash, bottle gourd, sunflower and marsh-elder.

Phillips Spring in the Pomme de Terre River Valley in Hickory County, Missouri, is located on an artesian spring. Six stratified occupation surfaces are documented. The unit K squash and gourd zone is the oldest part of the exposed sequence. It 'contained abundant plant remains (hickory, walnut, abundant acorns, grape, elderberry, ragweed). Bottle gourd rind fragment and 125 uncarbonized *C. pepo* seeds and seed fragments' (Smith, 2011, p. 474). A direct AMS dating of one of the seeds to 5,025 cal BP makes this relatively large sample the earliest indication for the domestication of pepo squash in the area.

Napoleon Hollow in western Illinois is a deeply stratified predominantly Middle-Woodland site with, however, a series of Middle and Late Archaic occupations. An excavated Late Archaic pit contained '*Cucurbita* rind fragments, … *Chenopodium berlandieri*, sunflower and ragweed seeds, along with 44 carbonized marshelder achenes' (Smith, 2011: 475). The recorded marsh-elder achenes, large in size and dated to 4,400 cal BP, are the earliest evidence for the domestication of this plant.

Riverton site, one of the Late Archaic localities of the 'Riverton Culture' is located on the shore of the Wabash River in south-eastern Illinois. It is a large deeply stratified midden, with, in Unit X, a series of Late Archaic rectangular clay house floors dated to 3,800 – 3,700 cal BP. Soil samples from the clay house floors revealed the presence of two varieties of domesticated chenopod and pepo squash, as well as a small number of wild species like persimmon, elderberry and *Polygonum*. Carbonised fragments of acorns, walnut and hickory nuts were also recorded (Smith, 1994, 2011).

Hayes site is a large multicomponent midden, in the valley of a tributary of the Tennessee River in central Tennessee. Soils samples from a Late Archaic deposit 'contained six complete domesticate-size sunflower seeds, one of which yielded an AMS radiocarbon date of 4840 cal BP' (Smith, 2011, p. 476). .

All the sites reviewed above were inhabited on a seasonal basis, with the length of individual occupation episodes more important in the river valley settlements. Upland rock shelters, Cloudsplitter and Marble Bluff were short-term seasonal camps, visited frequently and part of a subsistence-settlement system anchored on larger semi-permanent river valley sites. The latter were multi-family core settlements with virtually no inter-family unit differentiation. The river valleys appear to have been the areas of initial domestication of plants in eastern North America (Smith, 1994, 2006, 2011). The marsh-elder, pepo squash and *Chenopodium* are floodplain weeds. They are pioneer species thriving on 'disturbed and exposed soils… created on an annual basis by spring floods … Their abundant seeds are dispersed by floodwaters, and they colonize the sandy banks and backwater margins exposed each year .. in the shifting landscape of the river floodplains' (Smith, 2011, p. 477).

Concluding remarks

In the Americas, the Neolithisation processes were driven above all by relatively small fluid and mobile groups of forager-planters. A range of selected species were grown and spread in different ecological micro-zones in the seasonal/annual territorial ranges of these different groups, starting from the end of the Pleistocene. These processes were accelerated during the Middle Holocene and around 5,000 cal BP, the cultivation of selected plant species, and the practice of agriculture relying on slash and burn techniques, were fully adopted in the Neotropics and eastern North America. Crops spread down-the-line, along river systems, in opposite directions. Maize spread south to today's Uruguay and reached today's north to eastern North America around 200 BC.

Neither in the Neotropics nor in eastern North America was the Late Pleistocene population of above-all mobile foragers dense enough to trigger population pressure and resource depletion. With the significant exemption of the American Northwest with its dense population of sedentary hunter-gatherers, it is the generalized adoption of food producing life ways that allowed for the aggregation of a large population in the rest of the continent.

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Methodological Approach to the Study of Early Cultural Developments and Adaptations in Hunter-gatherer Communities: A Case Study from Keatley Creek on the Canadian Plateau

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Abstract

The emergence of socioeconomically complex hunter-gatherer communities has been identified as one of the most critical theoretical issues in the study of early cultural evolution. This issue has important implications for understanding the origins of our modern social systems and the relationship between early cultural developments, innovations and human adaptations to ecological changes.

In North America, one of the key geographical areas for studying the emergence of complex hunter-gatherer societies has been the Northwest Coast and Plateau. The village site of Keatley Creek in the Mid-Fraser Region of British Columbia is one of the largest sites of complex hunter-gatherers in western Canada. Ongoing research has been conducted at the site since 1986, representing one of the longest running research programmes for any site in Canada. Over the past three decades it has featured prominently in understanding the emergence and evolution of socioeconomically complex hunter-gatherer cultures. In terms of its size of over one kilometres long and well over 100 semi-subterranean pithouses, its location and impressive natural setting, its preservation of some of the largest corporate group structures in the region, and its early ritual structures with specialized floor deposits (unique to the region and to Canada), Keatley Creek is well positioned in regional and national archaeology to provide critical insights into early cultural developments in the Americas. Only half a dozen large pithouse village sites remain in the Mid-Fraser Region. Others have been fully or partially destroyed.

Models of population dynamics and the evolution of the village site are undergoing re-evaluation in the current research programme at Keatley Creek. Work to date suggests that the height of population and complexity at the site occurred roughly 1,000-2,500 years ago. Some archaeologists have tried to minimise the extent of inequality and complexity represented at this and other similar sites. Yet, given the size of the community, the magnitude of the effort expended in construction, the degree of sedentism displayed, the use of prestige items (including exotic imported materials from the coast, copper and jade), domestication and ritual use of dogs and the evidence of costly feasting and rituals, it is clear that this was a community of complex hunter-gatherers replete with important socioeconomic inequalities.

The *specific timing* and *conditions surrounding* the emergence, evolution and organization of these cultural developments have been the focus of some debate, which has generated further research at Keatley Creek. This has led to the integration of a new multi-dimensional and detailed methodological approach to advance the recording, documentation, analysis and interpretation of complex stratigraphic sequences that reflect the full occupation period of houses across the site, in addition to the management and analysis of data and collections. This involves a combination of a geospatial database, digital recording and analysis techniques, high definition video and photographic recording, micromorphology, palaeoethnobotanical and other detailed analyses. This paper discusses some key aspects of the updated methods as applied to specific complex and fine-grained stratigraphic contexts and how this is helping to advance understanding of the initial stages of village development including, the co-evolution of ritual structures and social complexity. The results are relevant for investigations of hunter-gatherer adaptations elsewhere in the world

Key words: Cultural evolution, emergent inequality, complex hunter-gatherers, ritual, resources, climate, GIS, digital methods

Introduction

Understanding the processes and conditions surrounding early cultural developments and emergent complexity is of central concern in studies of human and cultural evolution in the Americas and elsewhere. One of the major themes in research on this topic has involved understanding why transitions from more egalitarian organizations to non-egalitarian, hierarchical relations occur and under what conditions socioeconomically complex hunter-gatherer communities develop. This transition is one of the most important issues in hunter-gatherer adaptations on the world stage today since it represents a major threshold in cultural developments leading to contemporary types of societies with all their inequalities and complexities. Thus, understanding why inequalities developed, persisted or diminished has been identified as one of the most critical theoretical issues in the study of human cultural evolution (Price and Brown, 1985; Price and Feinman, 1995, 2010; Arnold, 1996; Boehm, 1999; Wiessner, 2002; Ames, 2010; Dubreuil, 2010; Hayden, 2011; Flannery and Marcus, 2012; Smith, 2012; Carballo et al., 2014; Kintigh et al., 2014). This issue has wider implications for understanding a broad range of issues in human evolution including: human cooperation and competition; the origins of our modern social and economic systems including resource ownership, the development of complex technologies and storage, the development of elaborate art and prestige items; the origins of agriculture; and the influence of environmental changes on cultural developments. Keatley Creek is one of the only sites in North America which has had an intensive research programme addressing such issues for nearly three decades (Hayden, 2000a, b, 2004; Villeneuve, 2010, 2014) encompassing site formation processes, social archaeology, political and ritual organization, economics dynamics and the processes underlying the emergence of inequalities and complexity.

Most prehistorians believe that small groups of simple hunter-gatherers, or foragers, undertook the initial peopling of the Americas and that these groups characterised human adaptations until sometime during the Archaic period. As simple foragers, these PalaeoIndian and possible pre-Clovis groups are generally thought to have consisted of highly mobile, low density, small egalitarian bands, probably with no more than 30 people and often only with 10 to 15 members. It is generally assumed that these groups did not rely on stored foods, they lacked any significant notions of private ownership, they had few or no prestige objects, they had no socioeconomic inequalities and no economically-based competition. This is a particularly apt description of the early occupational history of north-western North America (Matson and Coupland, 1995). The archaeological remains from elsewhere in the Americas for this initial period of occupation also seem to support these interpretations. However, at various times in different regions, fundamental changes began to occur in this simple forager system together with some new fundamental technological innovations (for example, grinding stones, mortars, fish hooks and leisters, weirs and stone boiling). Population densities increased, band sizes increased, some sites were repeatedly occupied or used by semi-sedentary groups, more permanent architecture became established, storage of food was adopted, prestige items began to appear (implying private ownership), cemeteries with notable grave goods occurred together with other evidence that makes it possible to begin thinking about emerging socioeconomic inequalities. Groups with these new adaptations are generally referred to as complex or transegalitarian hunter-gatherers.

There is considerable debate as to the nature, organization, internal dynamics and origin of these groups (for example, Thomas and Sanger, 2010). Earlier generations of archaeologists dealing with these theoretical issues relied extensively on social theories (for instance, the ideas of Jean-Jacques Rousseau, Thomas Malthus, Karl Marx, Émile Durkheim and Friedrich Engels) and anthropological theorists (such as Sahlins and Service, Carnerio and Harris) to establish their models. Early archaeologists tended to use simple prime movers such as ecological circumscription and demographic pressure to explain a wide range of processes involved in the evolution of social complexity (for example, Binford, 1968; Cohen, 1977). Since the 1980s, archaeologists have increasingly developed their own theories, relying on archaeological data and their own analyses of historical records and early ethnographies (for example, Flannery, 1977; Earle, 1989; McGuire and Paynter, 1991; Brumfiel and Fox, 1994; Arnold, 1996). Explanations for the development of complex or transegalitarian hunter-gatherers now frequently appeal to demographic pressures, climate changes, technological changes and ideological shifts. Thus, any study which can shed additional light on these factors is especially valuable in furthering our understanding of cultural evolution.

In the Americas, one of the key geographical areas for studying the emergence of complex hunter-gatherer societies has been the Northwest Coast and Plateau of North America (for example, Ames, 2004; Sassaman, 2004). On the Canadian Plateau, as in other regions of archaeological interest, debates have arisen over the timing and conditions surrounding the emergence of inequalities and whether they are represented by early developments of semi-sedentary large villages. Models focus on whether inequality emerged with early village developments under conditions of resource abundance and changes in procurement or storage technology (Burley, 1980; Matson, 1985; Hayden, 2001, 2005a) or whether inequalities occurred later in village development under resource and demographic pressures during periods of climate change (Prentiss et al., 2007). Research into these issues on the Canadian Plateau is of considerable importance since it has contributed to archaeological models used elsewhere in the world for understanding the adaptation patterns of early complex hunter-gatherers, and the pathways to more complex social and economic organizations including the initial stages of institutionalised inequalities which has been considered one of the 'dimmest,' least understood areas in the study of cultural evolution (Wiessner, 2002, p. 233).

These models are testable by examining the timing of cultural changes (the beginning of large villages and multi-family structures, specialized ritual structures and wealth-related artefacts reflecting inequality) in relation to coterminous environmental conditions or technological changes and their magnitude. Attempts have been made to use various types of analysis to monitor economic, social and climatic changes over time in Canadian Plateau large pithouse village sites (Hayden, 1997b, 2000a, b, 2004; Prentiss et al., 2003, 2007). However, a number of new techniques provide an improved means of monitoring changes over time, including the use of digital approaches discussed in this paper for the recording and analysis of deposits and artefact distributions, correlating micromorphology and detailed sampling for macro and micro-botanical remains combined with more traditional data such as fauna and lithic analysis and the sequential radiocarbon dating of strata. The research and methods are helping build a more comprehensive dataset and an improved approach to evaluating models (Villeneuve, 2014). This, in turn, is making theoretical progress possible in the discipline, especially for understanding processes surrounding early cultural developments and important adaptive changes of hunter-gatherers.

2. The Canadian Plateau

2.1. The Mid-Fraser region

The prehistoric pithouse villages of the Mid-Fraser Region on the Canadian Plateau are especially well suited for investigating adaptations and early cultural developments of complex hunter-gatherer communities. The pithouses (semi-subterranean structures) of these villages were occupied in the winter by domestic groups, involving multiple families organized into corporate groups, at least in the case of large houses (Hayden and Cannon, 1982). The structures at these sites are easy to identify and differentiate in comparison to the more heavily vegetated village sites in coastal regions of western North America. Sparse vegetation and semi-arid conditions provided excellent preservation conditions on the Canadian Plateau for archaeological sites. The fine-grained record preserved from the structures permit the study of change over time because of their highly stratified and organic rich refuse deposits on the perimeter of each structure, and the living floors (sometimes layers of floors) inside each structure that were buried by the collapse of soil-covered roofs after their abandonment.

Approximately 1,000 to 2,500 years ago about a dozen unusually large pithouse villages appear to have developed in the region around the modern town of Lillooet, British Columbia, at the confluence of the Seton and Fraser Rivers (Figure 1).

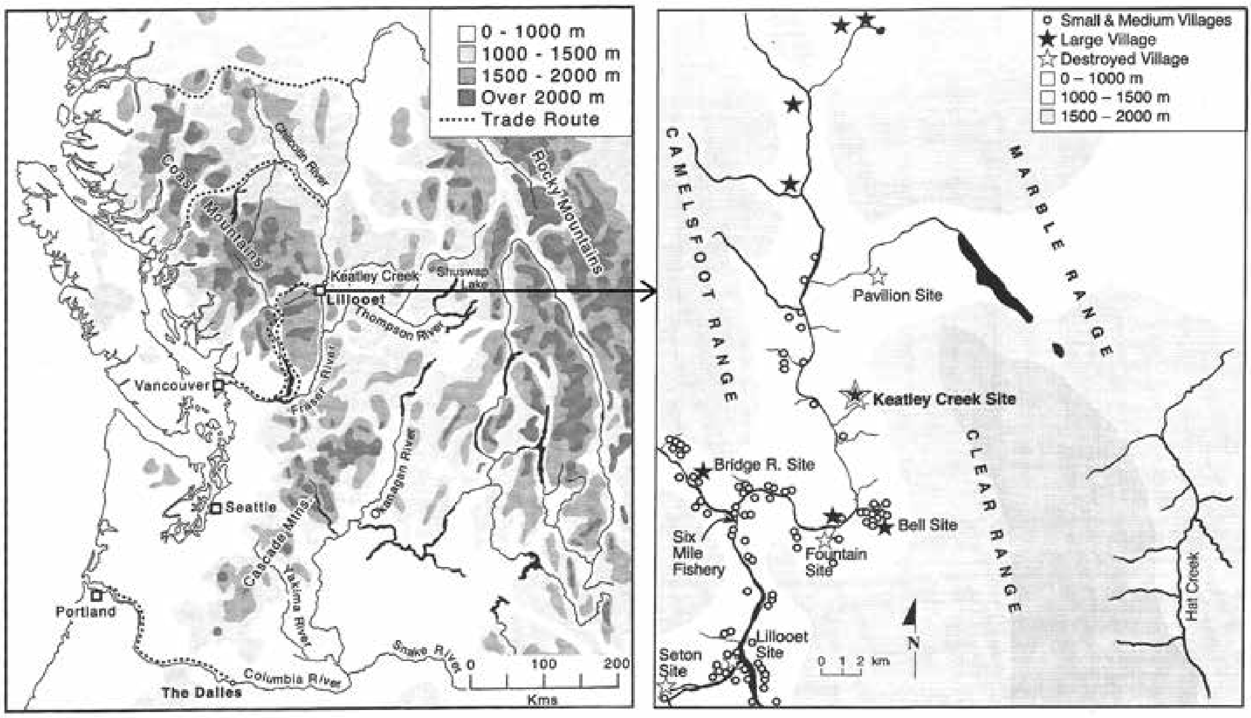


Figure 1. Map of the Mid-Fraser Region on the Canadian Plateau and locations of pithouse village sites including Keatley Creek.

Figure 2. Individuals fishing at the Six-Mile Fishery near Lillooet, along the Fraser River. This is the most productive fishery in the Fraser River drainage. (Photo taken with the permission of Xaxli'p First Nation community members).

At contact this area was inhabited by Interior Salishan speaking peoples, including the Stl'atl'imx (Upper Lillooet, Teit, 1906), Secwepemc (Shuswap) and Nlaka'pamux (Thompson) linguistic groups. The rich ethnographic accounts of these peoples (for example, Teit, 1900, 1906, 1909) and continuous archaeological culture traditions in the area provide an abundant record of information for developing direct historical approaches for archaeological interpretations. The continuing vibrant native cultures of the region also help to link traditional practices with the archaeological past.

Traditionally, and still today, the St'átimc peoples call this area a 'land of plenty' as food resources are abundant, especially salmon, deer, roots (geophytes), berries and other plants (Alexander, 1992; Turner, 1992; Pokotylo and Michell, 1998; Peacock and Lepofsky, 2004; Rousseau, 2004). Pithouse villages were primarily occupied in the winter and involved the intensive use of stored foods that were harvested in the warm season. The combination of rich resource conditions and the development of storage technology have been postulated to be key critical components underlying the shift to semi-sedentary adaptations of early hunter/gathers in this and similar regions (Hayden, 1992, 2000b). These resources could also be used to acquire goods (ornaments, foods, prestige items) from the coast or other adjacent regions (Hayden and Schulting, 1997).

The exceptionally productive salmon fisheries along the stretch of the Fraser River near Lillooet (Figure 2) plausibly underwrote the development of these large communities. The salmon from this region were especially prized since they had lost sufficient fat stores in their migration so as to preserve well, but still retained enough fat to make the dried fish very nutritious and tasty (not too lean and dry, nor too fat). The hot and dry climate of this region during the salmon runs also favoured the preservation of dried salmon. When properly dried, salmon could last in storage for up to two years or more (Kennedy and Bouchard, 1992; Kew, 1992). Isotopic analysis suggests that salmon constituted a large percentage of human protein diets, as much as 60 to 70% in adults (Chisholm, 1986; Lovell et al., 1986).

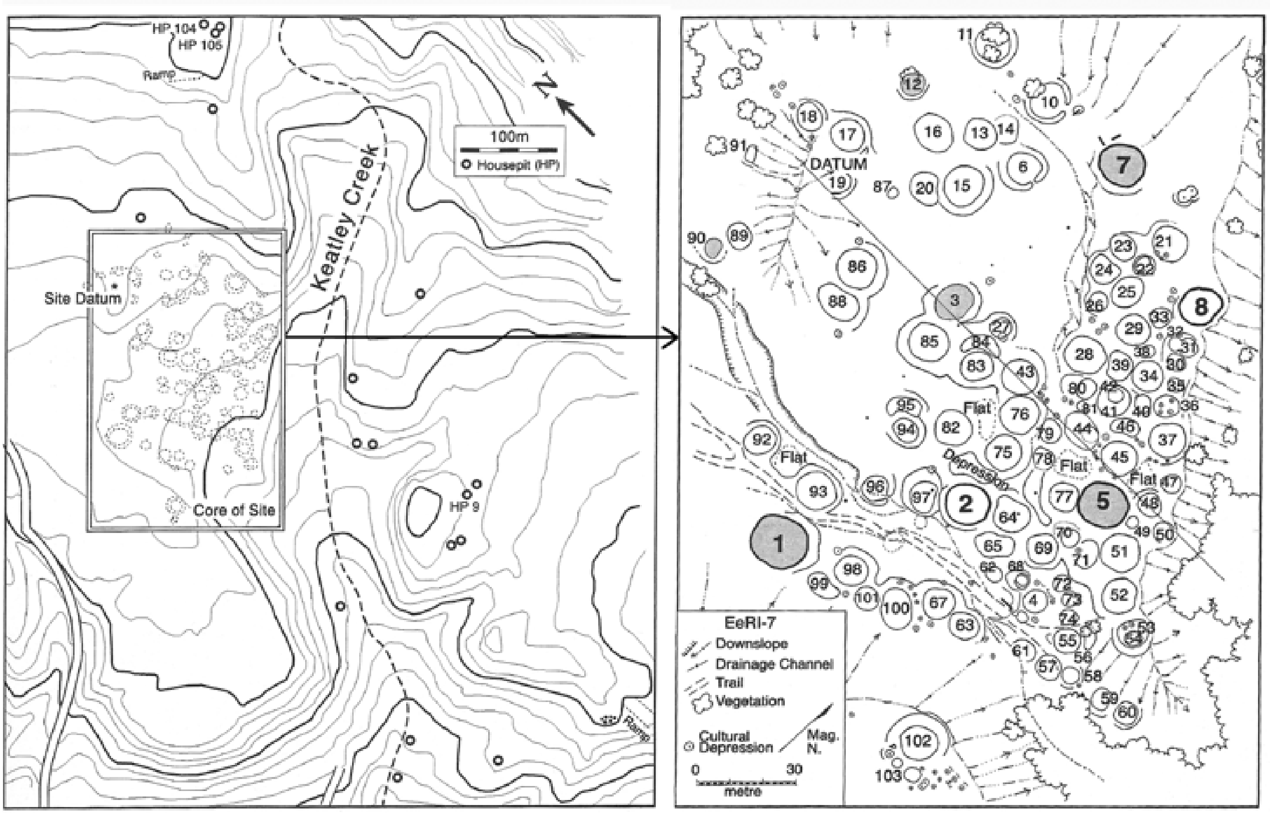


Figure 3. Map of the Keatley Creek site. Entire site area shown on the left. Site core shown on the right.

These resource conditions, together with the major travel corridors along the Seton River and Lake watershed to the coast, made this region favourable for the development of dense hunter-gatherer/fisher populations complexly organized socially, politically, economically and ritually. Unfortunately, only half a dozen of these large pithouse village sites remain relatively intact in the Mid-Fraser region due to land or industrial developments that have fully or partially destroyed some of them. The remaining pithouse village sites constitute true cultural heritage sites of great value.

Figure 4. Photograph of the Keatley Creek site.

2.2. The Keatley Creek site

The village site of Keatley Creek is the most intensively studied and important of these remaining sites. It is also one of the largest sites of complex hunter-gatherers in western Canada. Ongoing research has been conducted at the site since 1986, representing one of the longest running research programmes for any site in Canada. Over the past three decades, Keatley Creek has featured prominently in understanding the emergence and evolution of socioeconomically complex hunter-gatherer cultures in both a regional context and in more general models of the dynamics of complex hunter-gatherers in the Americas, and indeed elsewhere the world (Hayden, 1995, 2000a,b, 2001).

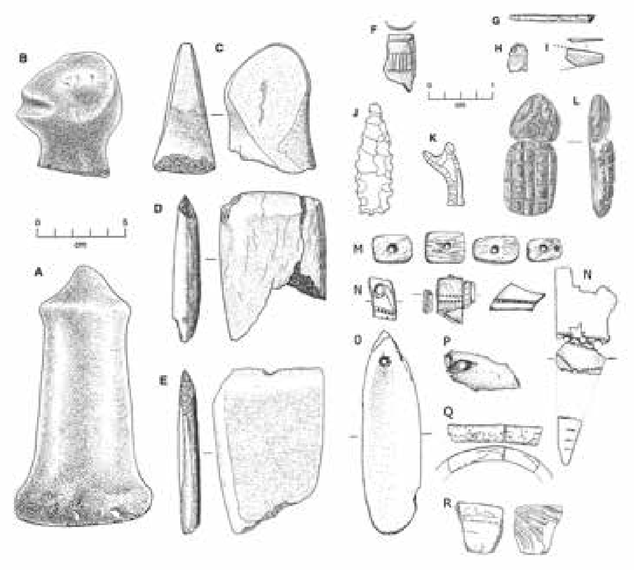


Figure 5. Items of presetige from Keatley Creek, including sculpted mauls and maul heads (A-C), nephrite adzes (D-E), a pipe fragment (F), copper tube bead and sheet (G-H), a sculpted stone reptilian pendant (L), a series of bone buttons (M), incised bone ornaments (N,P), a bone bull roarer (O), a shell bracelet fragment (Q) and a small shell adze (R). © B. Hayden. (Hayden 2005: 71-72, 99).

Keatley Creek is well positioned in regional and national archaeology to provide critical insights into early cultural developments in the Americas. Located in an impressive natural setting, Keatley Creek is an unusually large site, with the core covering over four hectares and well over 100 semi-subterranean pithouses, and peripheral structures extending over one kilometre along the back of a glacial terrace (Figure 3 and 4). It preserves some of the largest corporate group structures in the region together with early ritual structures (with specialized floor deposits) unique to the region and to Canada.

Models of population dynamics and the evolution of the village site are undergoing re-evaluation in the current research programme at Keatley Creek, however, work to date suggests that the height of population and complexity at the site occurred roughly 1,000-2,500 years ago (Hayden, 1997b, 2000a). Because of the favourable preservation conditions at this site, it is possible to track the development of the village from initial occupations of simple hunter-gatherers (foragers) during Middle Prehistoric Horizons (*c.* 4000-7000 BP) through the development of more sedentary and more complex hunter-gatherers who constructed more permanent and sometimes imposing domestic structures up to 20 meters in diameter. Some archaeologists have tried to minimise the extent of inequality and complexity represented at this and other similar sites (for instance, Prentiss et al., 2005, 2007). Yet, given the size of the community, the magnitude of the effort expended in construction, the degree of sedentism displayed, the use of prestige items (including exotic imported materials from the coast, copper and jade, Figure 5), the domestication and ritual use of dogs, and the evidence of costly feasting and rituals, it is clear that this was a community of complex hunter-gatherers replete with important socioeconomic inequalities. However, the timing and conditions surrounding these early cultural developments has become the focus of recent intensive investigations at the site (Villeneuve, 2014).

2.3. History of research at Keatley Creek

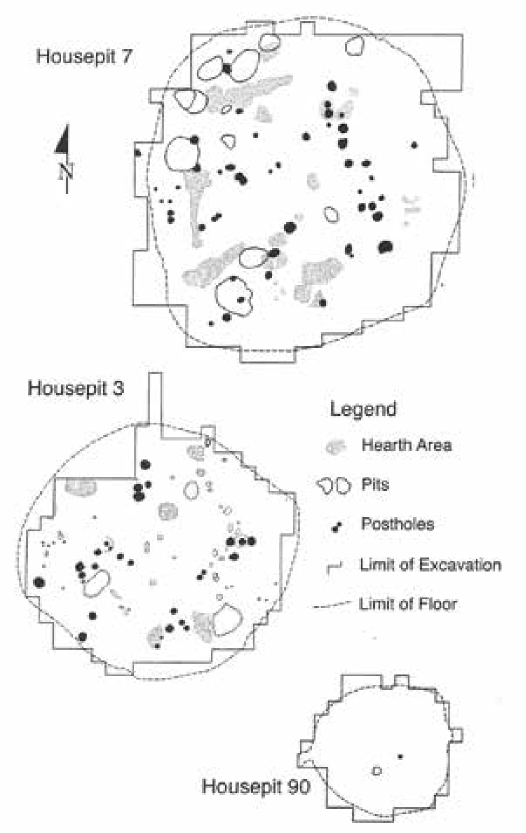


Figure 6. Living floors of small, medium, and large structures at Keatley Creek (Housepits 90, 3, and 7). © B. Hayden (Hayden 2005:50).

The majority of research at Keatley Creek has been either undertaken by Brian Hayden directly or through the assistance of his colleagues and former students in collaboration with Hayden. (I have directed excavations at the site since 2006). There have been four major research phases of research at the Keatley Creek site, with a new phase commencing in 2014. The initial phase of research initiated by Hayden between 1986 and 2000/2002 focused on socioeconomic organization (Hayden, 1997b, 2000a,b, 2004). Toward the end of this research phase ritual activity was explored (Hayden, 1998) and then further developed as part of the next phase of research at the site, which began in the early 2000s (Hayden, 2004; Hayden and Adams, 2004) and has been an ongoing focus of research (Villeneuve, 2010). A separate brief period of excavation occurred between 2000-2003 by one of Hayden's former students (Prentiss et al., 2003, 2007) who presented a revised chronology for Housepit 7 and argued for a revised site chronology and changes in resource relationships. Due to discrepancies in dating large housepits and implications for understanding the development of the site, a new research programme was launched by Hayden and me in 2010 with Social Sciences and Humanities Research Council funding to further investigate the timing and resource conditions surrounding the emergence of the village, and especially large houses.

Hayden's earlier socioeconomic research (1986-2000/2002) proved central in laying the foundation for social archaeology in the region by demonstrating how large multi-family corporate residences were organized socially, and in developing socioeconomic models for Keatley Creek as well as complex hunter-gatherers in general (Hayden, 1995, 1997a, 2000b, 2005a). Hayden identified discrete living floors for both large and small structures and mapped their features and contents (Hayden, 2000a,b, 2004 Figure 6). Through full excavation of a number of large, medium and small structures and the testing of additional structures, Hayden demonstrated that different corporate structures exploited or owned different economic resource areas. This was reflected in the different sources of lithic raw materials used by different houses (Hayden et al., 1996; Hayden, 1997a, Figure 7), and in the different ages of salmon procured by residents of larger versus smaller structures (Berry, 2000). The differential procurement of salmon implied ownership rights by large corporate groups over the most important fishing sites while continuity in the differential procurement of lithic sources implied long-term ownership of house sites extending over hundreds of years and perhaps more than a millennium (Hayden et al., 1996). These, and other indications including floor plans demonstrating muti-family organization of large houses with apparent wealth inequalities, led Hayden to propose that substantial inequalities characterized the main occupation at the Keatley Creek site and other large contemporaneous villages in the region (Hayden, 1997a, 2000b). The results from this past research were published in three edited volumes and numerous articles.

This excavation programme provided archaeologists with a much greater understanding of the economic basis and internal social structures of the large corporate groups. The project also raised a number of questions concerning the socioeconomic mechanisms by which such residential corporate groups came into existence. On the basis of ethnographic and archaeological research produced by the Keatley Creek project, Hayden concluded that large corporate groups and villages with pronounced socioeconomic inequalities developed on the British Columbia Interior Plateau under conditions of resource abundance sometime between 2,000 and 4,000 years ago (Hayden, 2000a, b).

More recently other archaeologists have argued for a much more recent development of the large villages and inequalities (for example, Prentiss et al., 2003, 2007), and that these developed under conditions of declining food resources with egalitarian social structures characterizing all but the latest occupations. However, these interpretations were based on a very limited sample from the Keatley Creek site (the northern rim area in Housepit 7) and subsequently limited samples from a nearby site (Bridge River, Prentiss et al., 2008) and limited samples in these contexts to examine resource shifts, especially in early periods of village development. Determining when large residences and indicators of socioeconomic inequality emerged in large communities such as Keatley Creek, and under what resource conditions they developed, has thus become critical to evaluating theoretical models concerning early cultural developments and adaptations of hunter-gatherers on the Canadian Plateau (Hayden, 2005b; Hayden and Mathewes, 2009). Current research at the site is testing theoretical models by examining the timing of cultural changes such as the beginning of large villages and multi-family structures, the emergence of specialized ritual structures and the occurrence of wealth-related artefacts reflecting inequality. This research is also trying to monitor subsistence changes over the occupation lifetime of structures, in relation to cultural changes, environmental shifts and technological changes. This programme focuses on the detailed excavation, recording, sampling and analysis of house rims and floors.

To accomplish these research goals, it was first and foremost critical to increase sample sizes across the site. This was greatly facilitated by using advanced methods of data collection, recording and analysis in undertaking larger scale research including the finer details needed to better assess alternative models. Excavation, recording, documentation, analysis and interpretation of complex stratigraphic sequences is now undertaken with a combination of digital, geospatial, high resolution imaging, micromorphology, palaeoethnobotanical and other analyses (Villeneuve, 2014). The following section discusses some key aspects of the updated methods as applied to specific complex and fine-grained stratigraphic contexts, and how results emerging from the integration of new approaches have implications for investigations of hunter-gatherer adaptations in the region and elsewhere in the Americas.

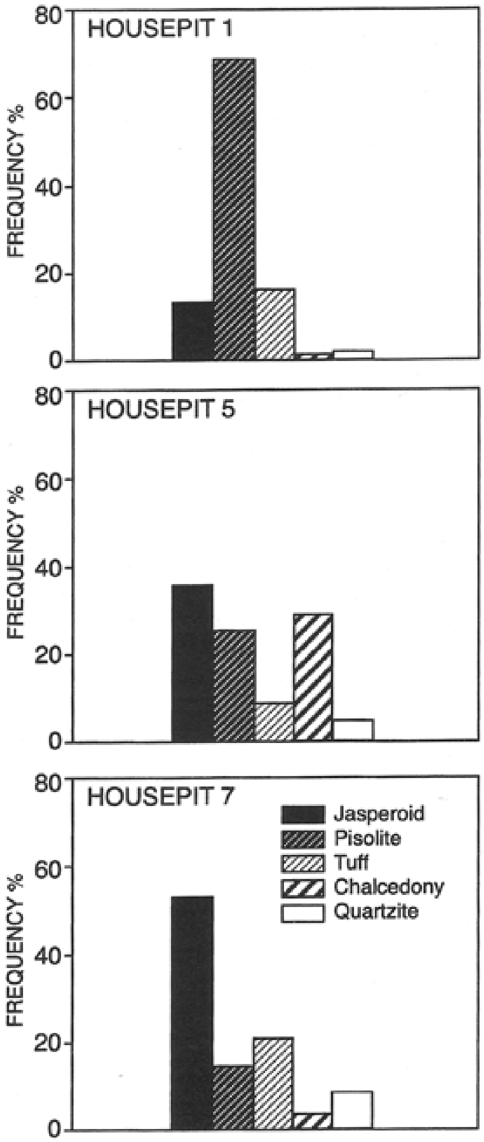


Figure 7. According to the results of past analyses, large corporate households at Keatley Creek had access to, and probably ownership over, different sources of lithic materials (Hayden et al., 1996). These histograms illustrate some of the important differences between three of the largest structures at Keatley Creek. These differences persisted in each housepit rim from the earliest to the latest occupations, spanning about 1,000 years. This indicates that the same corporate group retained ownership of both the residential structure and rights to specific resources throughout the occupation span of the structures. © B. Hayden (Hayden 2005:106).

3. Advancing methods

3.1. Contexts are key

Contexts are essential elements in evaluating theoretical models. The majority of research undertaken in the pithouse villages of the Mid-Fraser region has focused on house floor contexts. Past research into socioeconomic organization at Keatley Creek, for example, relied primarily on floors for the reconstruction of activity areas and social units or group size estimates (Hayden and Spafford, 1993; Hayden, 1997b; Hayden, 2000a, b, d, 2004). Over twenty radiocarbon dates were produced in this past research, which were used to compare contemporaneous floor assemblages (Hayden, 2000c, p. 36). To position these floor assemblages in a larger general picture of the potential development of the site, some initial radiocarbon samples from house rim midden contexts were also processed. These provided an initial idea of when certain houses (especially large houses) were built and abandoned (Hayden, 2000c, p. 37).

House floors were ideal contexts for investigating activity areas and social organization. However, floors alone are not a reliable or suitable context for addressing larger questions concerning the evolution and organization of a pithouse village site (as some archaeologists have attempted). In terms of the degree to which floor deposits were removed, covered, cleaned, maintained or prepared, there does not appear to be any general pattern to floors over time across a single pithouse village site or between sites. A housepit could be used for many hundreds of years without a major break in occupation, or it could have been used episodically and reoccupied at various times. Multiple floor deposits *might* have been left from some period of use, although floor deposits were frequently removed as part of re-roofing events, leaving only the last occupation deposits *in situ*. Thus, remnant floors (if any exist) would not provide a reliable means of reconstructing the life history of the house. There is simply too much variation in the accumulation or cleaning of floor deposits in the large pithouse village sites so far investigated, to be able to obtain a good understanding of the full potential occupation of a specific house structure, let alone to extend those results to

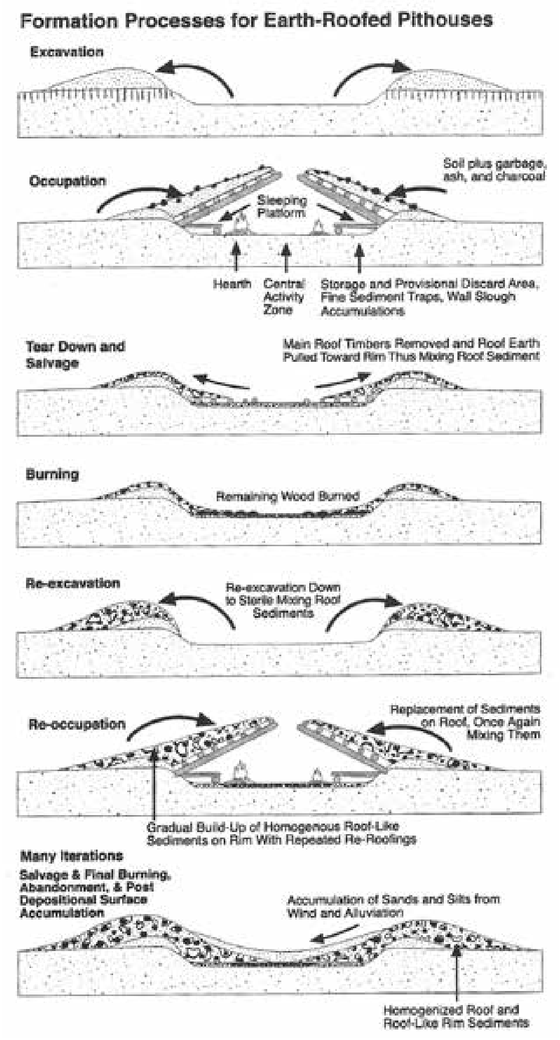


Figure 8. A schematic representation of the formation processes involved in the accumulation of rim deposits and the cleaning out of old floor deposits during the re-roofing process as represented at Keatley Creek. © B. Hayden (Hayden 2005:37)

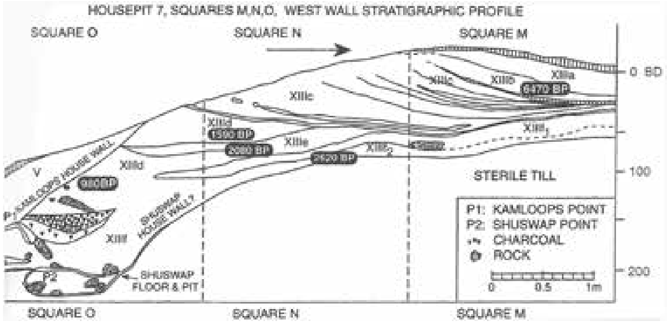


Figure 9. A cross-section profile of the northern rim of Housepit 7 as recorded in Hayden's excavations together with radiocarbon dates he obtained from these strata. © B. Hayden (Hayden 2000:37).

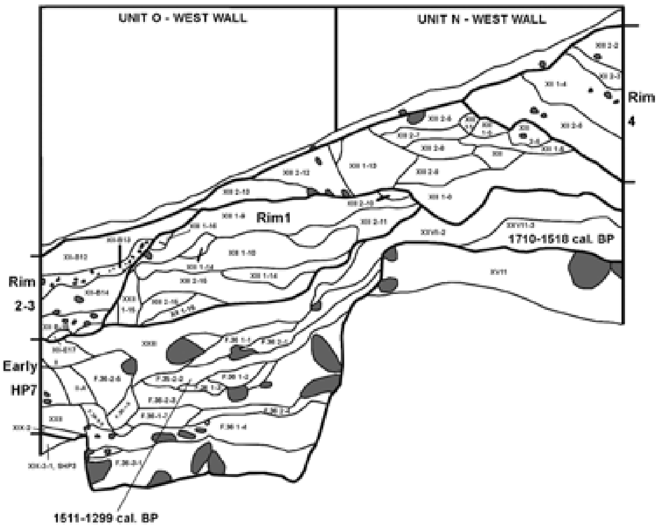


Figure 10. The cross-section profile from the same northern rim as Fig.9 of Housepit 7 as recorded in Prentiss' excavations with accompanying radiocarbon dates. Re-drawn from Prentiss et al., *2007:305.*

reconstructing the timing of early cultural developments or the evolution of a pithouse village site. To do this, it is essential to use a combination of floor and house rim midden contexts.

Rims, in particular, represent a large proportion of pithouse village architecture and activity debris (including resource remains) reflecting the history of the site (Figure 8). House rims were the primary location for the discard of household refuse. They are composed of accumulations from the initial building and occupation of a structure throughout its use life and abandonment (Hayden, 1997a). Dumping of house cleaning and construction materials (including the removal of sterile deposits from the excavation of new storage pits or the widening of a wall) can contribute to rim formation, as well as the deposition of materials from activities carried out inside houses or on the outside perimeters of houses. In addition, various natural and cultural taphonomic processes also influence the build-up, erosion or alteration of house rim middens (for example, re-roofing, fires, loessic accumulations). Due to the highly organic layers and dense lithic concentrations that often occur in large housepit rims these contexts provide an abundance of remains for analysis of resource or technological shifts throughout the use life of a house, as well as an understanding of its occupation history.

Past research has shown that rim middens can be very complex (Hayden, 2000a, 2004). Because of their complex nature, limited work was undertaken in rim deposits in the past by Hayden and his team and it was acknowledged that much more detailed methods and sampling would be required to adequately excavate and interpret rims which were then outside their research focus and funding capacities. Nevertheless, their preliminary work showed that rims are contexts that could be used for understanding the evolution of house structures (Alexander, 2004; Hutchings, 2004; Muir, 2004). These preliminary investigations suggested an early development for some large pithouse structures, but Hayden's exploratory rim investigations were not intended to be thorough or in-depth studies (Hayden, 2004; Hayden, pers. com.). Preliminary results from dating Housepit 7 rim deposits, in particular, helped provide an initial bracket for the potential time range of occupation in this structure which had implications for understanding the emergence of socioeconomic complexity at the site (Hayden, 2000c) (Figure 9, see also Figure 10 for another profile of the same wall presented by Prentiss et al. (2007), which is under further revision in the current research programme).

3.2. A new approach

To better investigate these stratigraphically complex large housepit rim contexts, and to further evaluate the timing and conditions surrounding early cultural developments at the site, it was advantageous to up-date conceptual and methodological approaches. Digital methods have ultimately led to a new research paradigm in archaeology and have transformed the way in which archaeologists can engage with archaeological contexts or materials and process or analyse information, and ultimately how archaeologists understand the past (for example, Hemsley et al., 2005; Evans and Daly, 2006; Cameron and Kenderdine, 2010; Agbe-Davis et al., 2013). Satellite imagery, for example, was not easy to obtain in the past, but now we view the world this way nearly daily through Google Maps, which has influenced our day-to-day lives as well as our research. The practical and ethical implications of operating in a digital age are perhaps not yet well understood (for example, Colley, 2012), but clearly the use of digital technologies have led to tremendous benefits in life and in the sciences, including archaeology.

This paper discusses a few highlights resulting from implementing digital oriented methods and conceptual approaches to the research at Keatley Creek. Primary focus has been on GIS related techniques as we work toward a larger integrated system for managing data (for example, Katsianis et al., 2008). A wide range of GIS applications have been used in archaeological studies for well over a decade (for example, Westcott and Brandon, 2003; Mehrer and Westcott, 2005; Chapman, 2006; Conolly and Lake, 2006; Robertson, et al., 2006). At Keatley Creek, we have only scratched the surface of the possibilities of digital applications in research, but the new developments are providing significant advantages in how we understand early cultural developments and hunter-gatherer adaptations on the Canadian Plateau.

The Keatley Creek Project has been incorporating digital methods in research since 2006 (Villeneuve, 2007, 2010, 2014) using a number of techniques that had been employed in Europe during the previous decade, and which the author became familiar with beginning in 2000 (for example, McPherron and Dibble, 2002; Sisk, 2010). With the new research programme at Keatley Creek beginning in 2010, great emphasis was placed on adopting a more scientific approach to undertaking excavations of complex stratigraphy and viewing the excavations as repeated experiments for evaluating hypotheses (Villeneuve, 2014). Methods of data collection were routinely refined as part of the experimental process. A major goal of this work was to establish a simple, practical, cost- and time-efficient, digital approach that would increase the amount of data and detail possible to record with consistency and with great accuracy. Methods included using GIS and auxiliary software, video recordings, high resolution imaging, remote sensing, and other techniques. With this new approach it is possible to view and produce or edit results (including graphics) as excavations unfold, and to complete in weeks (with greater detail, accuracy, data, and analysis capability) what used to take multiple research seasons to complete. This has made it possible to increase the number of areas sampled across the site as well as the number of samples taken within those areas, while increasing data consistency.

The original purpose or goal behind the use of advanced methods was to achieve improved resolution and understanding of complex stratigraphy especially in rim deposits. The conceptual approach behind designing and integrating new methods at Keatley Creek emerged from the application of digital techniques to the excavation and recording of complex rock shelter deposits in Europe. The complex stratigraphy of rim middens of large houses was viewed as comparable to that of rock shelters in terms of the potential range of horizontal and vertical stratigraphic variation and complexity, taphonomic processes and anthropogenic influences in mixing or recycling of deposits, and the occurrence of occupation surfaces. Thus, in implementing new methods in the excavation programme at Keatley Creek, emphasis was placed on an approach that would provide maximum interpretive potential and advance the recording and analysis of complex stratigraphy at the site.

3.3. Digital recording in excavations

In 2005-2006, when introducing digital approaches in excavations at Keatley Creek, it was necessary to take into consideration the two decades of prior excavations that were recorded using a traditional excavation system. Similar to the process other archaeological sites have gone through, digital methods are helping build an information infrastructure to be able to more successfully and efficiently conserve, access, integrate, mine and analyse data sets with the objective of advancing understanding of human cultural evolution (for example, Kintigh, 2006).

The early Keatley Creek records were archived on paper, as well as stored in Excel files for analysis, and in Photoshop or Illustrator files for simple graphics of maps and stratigraphic sections. A GIS was designed to assist with digitizing old excavation data (for example, excavation plan maps, Figure 11) and to be used in building a centralized geospatial database for the site that could also integrate analysis results and new digitally collected field data (Sisk et al., 2008). Currently, this GIS is also providing a central database for the site collections (including an inventory catalogue of all excavated materials and samples, all analysis results, photographs, paper archive images and other data). One of the primary objectives in utilizing GIS to centralize data management is to help provide more versatility with spatial and intrasite analyses in current and future research.

In 2009 and 2010, a combination of software including GIS, EDM Windows and NewPlot (McPherron and Dibble, 2002) were incorporated into excavations for digital recording, data collection, and processing using a barcode system. One of the major benefits of this system has been the ability to automatically add to (and generate) an excavation database as each item is recorded, including all of the information that was traditionally recorded on excavation cards (for artefacts, samples, and buckets), and a lot of what was traditionally recorded in field notes (such as strata changes, depths, features, burrows, and disturbances), including spatial coordinates of all items recorded (Figure 12). During excavations, this system involves a simple daily set-up requiring only a few minutes at the start of excavations and only seconds of recording as excavations are undertaken (in comparison to the amount of time that graph paper and artefact or sample card recording typically takes). This approach alone has significantly increased speed, efficiency, and organization of work flow, as well as the accuracy and amount of data retrieved in excavations. More importantly, it provides greater ability to focus on the deposits and sampling contexts, thus essentially increasing the quality of interpretations that result from the field. Because there are no artificial quadrat boundaries that constrain excavation, digital grids also facilitate excavators' abilities to follow natural stratigraphy.

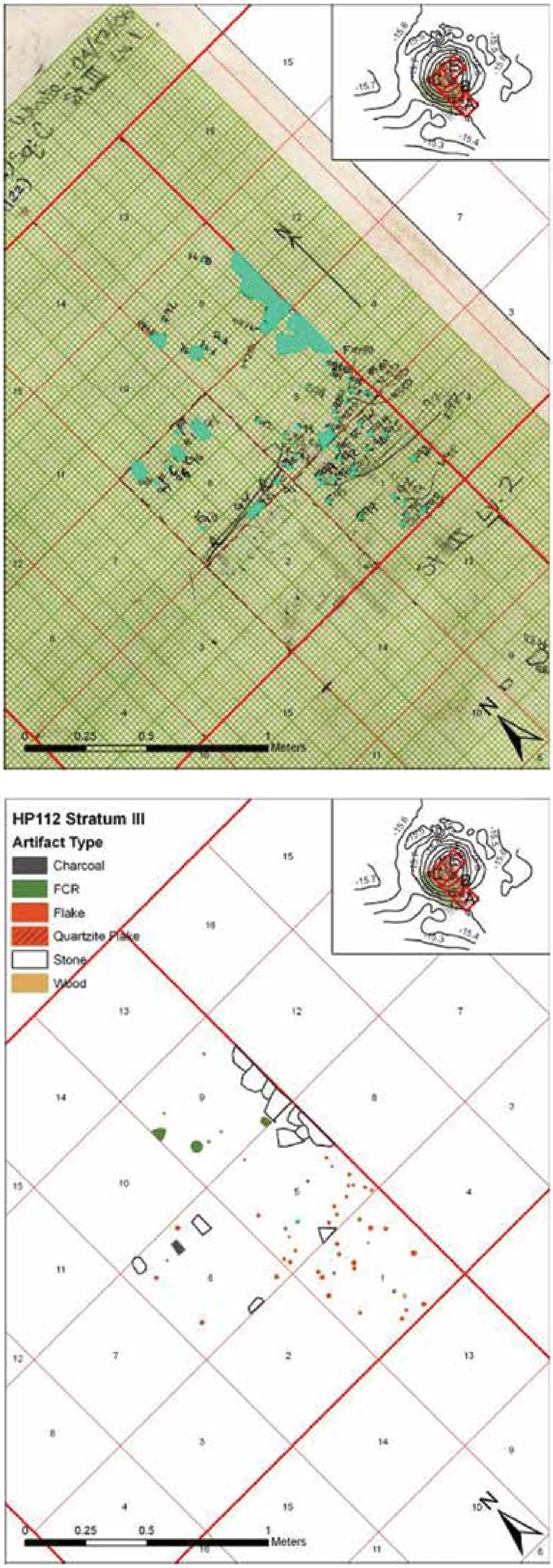
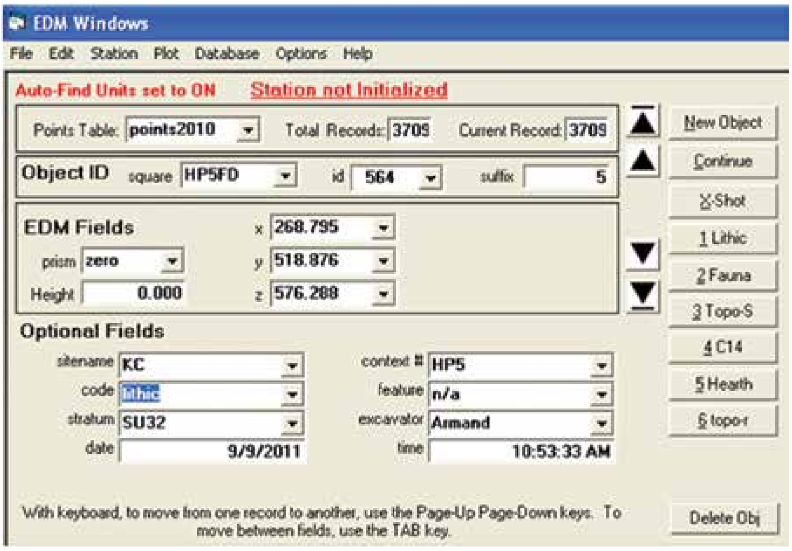


Figure 11. The process of digitising excavation plan maps using GIS. The image to the left shows a scanned excavation sheet (for Housepit 112) referenced to the digital excavation grid and digitisation of artefacts and feature data in progress. On the right are digitised artefacts coloured by type using ArcMap. This digitisation of old excavation data is contributing to a larger geospatial database for excavation data from the site that is also helping also centralise data from various analyses and collections inventories. (Figures taken from Sisk et al.*, 2008 and also reported as a chapter in Villeneuve 2010).*

This frees the excavator to focus more on following, examining, and interpreting complex stratigraphy in field excavations.

The ability to view and edit spatial data (including re-designating strata numbering or interpretations) in the field during excavations is also of great benefit to improving the quality of data that results from excavations. This includes the ability to examine artefact distributions, clustering, and orientations during excavations for stratigraphic assessments and understanding of formation processes of rim deposits. In addition, strata designations can be made more easily in all areas of excavations with a digital recording approach, providing a significant advantage over the limitations of traditional recording systems. In the past, with traditional methods, field interpretations could sometimes result in the lumping of poorly differentiated strata whereas they could later be determined to be separate deposits. The materials from these layers would thus be lumped together in one level bag (or sample bag) and could not be separated out later for analyses. On the other hand, due to the ease and speed of digital recording systems in excavations, it is possible to increase the number of distinct strata recorded (that can more easily be lumped later). Combined with the individual recording, numbering and bagging of artefacts and samples (all with point proveniences) throughout strata or features, this makes it easier to re-assign artefacts and features to new strata designations and even subdivide strata contents after field excavations and interpretations. Reducing the bulk of paper recording and processing also avoids errors that occur in recording and transferring notes or information. There are many other benefits to the digital excavation approach in excavation, including the ability to view graphics of excavations as the work is undertaken, the conservation of excavation data, and the ease of teaching or training individuals in methods.



Auto-Find Units set to ON   Station not Initialized

Points Table: points2010   Total Records: 3709   Current Record: 3709

Object ID   square HP5FD   id 564   suffix 5

EDM Fields
x 268.795
prism zero   y 518.876
Height 0.000   z 576.288

Optional Fields
sitename KC   context # HP5
code lithic   feature n/a
stratum SU32   excavator Armand
date 9/9/2011   time 10:53:33 AM

With keyboard, to move from one record to another, use the Page-Up Page-Down keys. To move between fields, use the TAB key.

Figure 12. A screen shot of the EDM Windows field recording system for Keatley Creek, as of the 2011 year (some up-dates to recording categories have been made since 2011). Field data is registered with this software that is run on a mini laptop with an XP Windows operating system, utilizing a Leica TS06 (Total Station) to record data points(also see Figure 13). EDM Windows automatically feed data into a central Access database for the entire site (that stores data from multiple excavation areas), which can then be opened and viewed using NewPlot or GIS software in the field to examine data in real time as excavations are ongoing.

Figure 13. Still of the video recording of stratigraphy descriptions in excavations, during 2011 while iPad recording was also explored for combined recording of excavation logs, photos and videos in combination with Total Station and EDM Windows recording. (Video screen shot of Russell Clark in Housepit 5 excavation trench, video recording by S. Villeneuve, video reference KCMVI0001HP52011).

3.4. Video recording of stratigraphy

Stratigraphic profiles reflect the history of a site and are essentially the story-board of excavations. Understanding the formation processes of complex rim stratigraphy, and being able to communicate that through a stratigraphic profile with results from radiocarbon dating and other analyses, is critically important to a research programme. Traditionally, profile recording has been undertaken with string, line level and measuring tapes, and recorded on graph paper under highly variable daylight conditions. In situations of highly complex strata of large housepit rims, it is seldom that archaeologists take the time to record a very detailed profile on graph paper to accurately represent all aspects of the context, nor is this feasible in most conditions. Any profile drawing on graph paper lacks the wealth of information and accuracy that digital approaches can provide.

Field notes for all stratigraphic units excavated and samples collected are now recorded using high definition video which is then transcribed for reports and high resolution imaging (Figure 13). This visual digital approach to field notes provides far more information and detail from an excavation, in comparison to what was traditionally recorded on paper for strata descriptions and measurements. Video recording tends to be quite thorough since, in our on-site interpretive recording approach, *the camera encourages the excavator to explain their reasoning or justification for strata interpretations* in greater detail than traditionally documented in writing on paper forms. Strata observations (basic colour, texture, compaction, organic content and other information) are documented with video, as well as the thought processes behind the evaluation or judgment of features, artefact patterns, disturbances, or other details that previously would have been recorded in field notes (or, that were even sometimes omitted in past field notes). Video records also provide the ability to review earlier phases of excavations during ongoing field work, and to take screen stills (images) from the video stream, to assist with strata identifications and interpretations, and the assessment of rim formation processes, as well as helping later (in the lab) in the re-examination of strata assessments when finalizing interpretations. Contexts of sampling for radiocarbon dating, for example can be re-examined with far greater information before finalizing a selection of samples for processing.

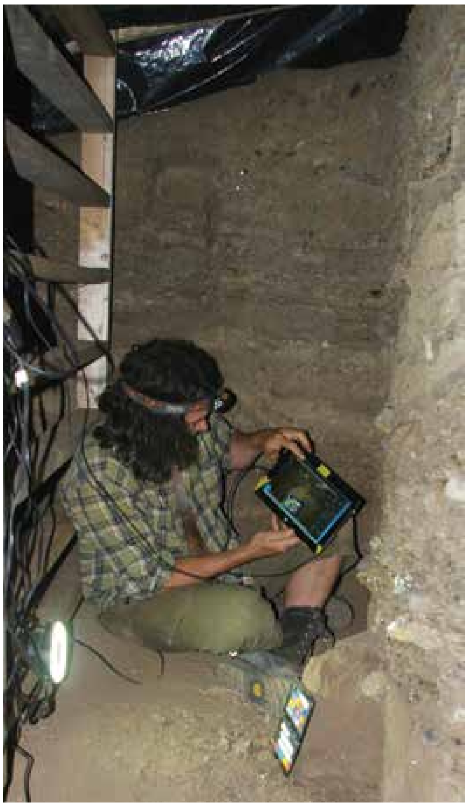


Figure 14. Photograph showing the process of collecting high resolution photographs of the excavation profile west wall in Housepit 5. A Nikon D800 camera is used with a 50mm lens and a 44LED ring light mounted on the camera lens, with a colour chart and light meter reading in LUX present. Images are captured using ControlMyNikon software and processed in Adobe Photoshop Lightroom, then stitched with PhotoScan. (Photo of Remi Farvacque in Housepit 5 excavation trench, taken by S. Villeneuve, August 2013).

Video has ultimately become one of the most powerful recording tools in the field for enhancing the process of excavating, the quality of interpretations of complex strata, and the documenting of strata descriptions. It has also advanced learning and teaching experiences which is a benefit recognized by other researchers exploring the use of video in archaeology (for example,

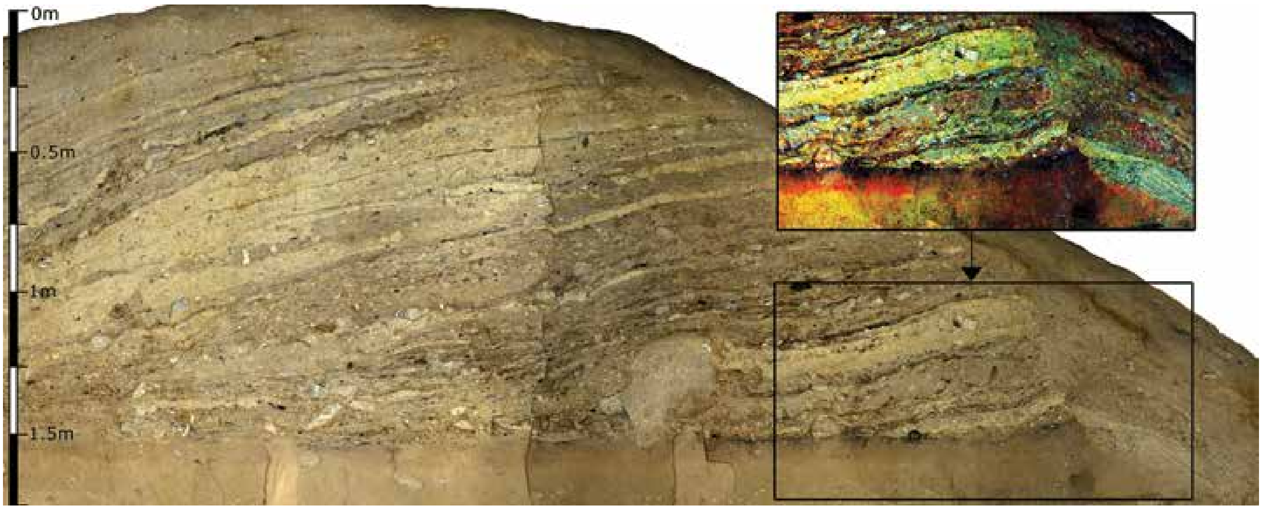


Figure 15. A compressed jpeg image of the final stitched, rectified and colour corrected high resolution photograph of Housepit 5 west wall excavation profile prepared by R. Farvacque, and further prepared by S. Villeneuve for this paper and the Keatley Creek reports (Villeneuve 2014). The box on the right shows a portion of the profile (area shown by the black box) that is enhanced using D-Stretch® software (LAB colorspace that is sensitive to artefacts caused by jpeg compression) to provide a good all-around enhancement. These imaging products are used as visual aids (as well as video records and field measurements) in the process of preparing profile line drawings, and for reference in the field when sampling (e.g. for micromorphology) and in excavation.

Colley and Gibbs, 2013). In our situation, it formerly could take years for new students to build up enough experience to critically assess, think through, evaluate, and document strata well enough to be able to deal with contexts that involve highly complex stratigraphy. Video recording, including the process of engaging students to explain observations and justify interpretations in front of a camera, and the process of transcribing video recording of stratigraphic descriptions, is helping speed up the student training and learning process so that more students can contribute to advancing research in the field. This ultimately translates to the ability to undertake more research with higher quality results.

Visualization techniques have become an important and sometimes central part of archaeological investigations (Llobera, 2010). We are finding that video recording ultimately provides (for our research) what is essentially the best form of 3-D audio and visual documentation of excavations. These documents can also be compiled into movies showing the entire excavation process for every excavation area. Other 3-D imaging techniques, such as those that utilize GIS or photogrammetry in displays of plan (top-down) views of excavations (versus profiles) (for example, Sisk, 2010) are also applied to new research at Keatley Creek for house interiors, especially for ritual contexts.

3.5. Photography and digital image processing

To further assist with stratigraphic analysis and interpretations, high resolution digital photography and photogrammetry were also incorporated into profile recording. Our starting objectives in past work (2010-2013) was simply to explore the potential of different lighting conditions and digital image resolution to help capture details of stratigraphic profiles that would aid in profile mapping of stratigraphic boundaries. Daylight conditions for example, even with shade, tend to wash out stratigraphic distinctions making certain boundaries barely noticeable. Some natural lighting can also cause shadows that reduce visibility of strata boundaries which impacts the ability to identify continuity of colours and textures within the strata. The use of LED lighting (versus standard halogen lighting) under dark conditions (at night or under dark tarps) significantly enhances strata visibility. To avoid shadows and distortion, photographs of the profile wall were taken with using direct LED lighting (5500k) ring mounted on a 50mm lens of a DSLR camera under conditions where natural light was blocked out by dark tarps. Colour charts and light meter readings (in LUX) were incorporated (Figure 14). Photographs were taken in vertical sequences across the profile wall and were cropped and stitched, then rectified using correct measurements from the profile wall with the aid of GIS. The resulting image provides far greater strata visibility than what was visible or could be recorded under normal daylight conditions (Figure 15).

Our high-resolution photographs of the stratigraphy can then be run through image enhancing software to examine stratigraphic patterns in even greater depth. At a low cost, non-specialist level, D-Stretch® was used to explore the use of such software. D-Stretch is based on remote sensing principles and was developed for, and normally applied to, rock art studies (for example, Harman, 2008; Gunn et al., 2010). However, this software can also assist with exploring digital images for enhancing strata visibility (Figure 15). Certain strata characteristics (colour, texture, organic content, sterile layers and other variations) can be made much more visible using this kind of image enhancement software, thus providing advantages to mapping strata boundaries in profile recording. Video records and GIS data are also consulted in the process of creating profile line drawing. The profile maps resulting from this approach are far more accurate, detailed and informative than profiles recorded using traditional graph paper methods under variable daylight conditions. Other data can then be incorporated into profiles drawings (utilizing GIS), including the artefact distributions and strata boundaries recorded digitally in excavations, as well as locations of various kinds of samples and the details of their results (for example, numbers, counts or percentages, and types) including radiocarbon dating, micromorphology, chemical and macro or microbotanical analyses. These digital visual aids increase abilities to examine relationships between deposits and anthropogenic contents at various scales to better assess formation processes and the significance of individual strata. These digital images alone (or enhanced with D-stretch®) can also be used during excavations to assist with following and examining strata as excavations unfold.

This approach has thus far been used strictly for visually enhancing strata boundaries and details. It is not currently used at the interpretive level since that would require much more advanced methods. However, since the basic techniques we have employed thus far have demonstrated that this approach has significant advantages over traditional profile recording, more advanced imaging is now being developed with specialists to help improve this area of research and to integrate results into analyses. Nonetheless, the results emerging from this approach demonstrate how significantly different field interpretations can be for complex stratigraphy when only traditional approaches are applied. This has important implications for understanding the formation processes of a large housepit rim and thus interpreting the evolution of the house and hence extending this to entire site or regional chronologies. Where methods can be of even greater benefit is in turning from issues of site chronology and resource conditions back to larger social questions for modelling pithouse village dynamics. A combination of detailed stratigraphic recording techniques, analysis and more comprehensive intrasite spatial

Figure 16. Artefacts recovered from ritual related contexts, including a bone button blanket (top right) and a crescent shaped biface (centre right). A rock lined hearth (bottom left) in Housepit 116 is adjacent to unique specialized floor deposits. Rock lined hearths are a feature type found only in ritual related small housepits on the southern Terrace of the site (Villeneuve, 2010). A dog burial (left) led many archaeologists to believe there was a ritual association (see chapters in Hayden 2000a, and Housepit reports in Hayden 2004). © B. Hayden.

analysis utilizing various digital methods will ultimately create a firm foundation for reformulating views about the past and processes surrounding early cultural developments involved in hunter-gatherer adaptations on the Canadian Plateau.

4. Ritual investigations

One area where the use of digital techniques can be of great benefit is in the excavation and analysis of ritual contexts. Ritual is a notoriously challenging domain of research in archaeology, in terms of the identification and interpretation of individual structures or events, and the development of ritual contexts over time. At Keatley Creek, the identification and interpretation of ritual has been a central focus of research in recent years, as well as understanding what role ritual played in early cultural developments at the site. The ritual structures identified, and that continue to undergo investigations (Villeneuve, 2008, 2010, 2012, 2014; Villeneuve and Hayden, 2008), are small and simple, but represent the first recognizable nascent development of specialized ritual structures documented archaeologically in the Northwest, and, as far as is known, in Western Canada.

Hayden first began to suspect that a number of small structures on the periphery of the site might have been ritual structures in the mid to late 1990s (Hayden, 1998). Many years of careful excavation then went into their excavation and analysis to further investigate and firmly establish that they were likely ritual structures rather than other kinds of specialized structures or residences (Hayden, 2004). Some of the more important indicators of the ritual nature were then established (Hayden and Adams, 2004). These included: their isolated location peripheral to residential areas; their distinctive types and locations of hearths (central stone ringed hearths); the unusual volumes of storage capacity; the unique assemblages of stone tools and fauna (including ethnographically documented species used in rituals such as loons); the occurrence of exotic and wealth items in usual quantities (for example, dentalium, jade, gaming bones, a unique collection of 72 bone buttons); the rarity of other artefact types; intentional destruction of structures; spatial association with large roasting pits, and; specially prepared floors (Figure16). Individually, each of these characteristics might be explicable in other terms. However, when considered together, all of these indications make a rather compelling case for an early development of this type of structure for ritual use.

In our current excavations (Villeneuve, 2014), the digital recording methods in excavations (to record stratigraphy, features, artefact distributions and sampling locations), combined with high resolution imaging of profiles and micromorphology is contributing a more refined and detailed understanding of the development of ritual activities and their change over time as well as the investments in, and construction of, ritual spaces. These methods are especially helpful where finely layered floor deposits occur. The investigation into the material remains of ritual activities is now also benefitting from the compilation of a geospatial database (the GIS digitizing of old excavation plan maps) that can be used in activity area analysis and intrasite analysis. All of these new techniques have been applied to refine criteria used to identify ritual activities and potential ritual zones, and in the analysis of the development of ritual at the site. Video recording and 3-D modelling (with photogrammetry and GIS methods) also provide new forms of documentation of these spaces. The combined visual (and audio) displays are beneficial in the analysis of changes over time in these ritual (and other) contexts. Through these new methods, our understanding of ritual behaviour at the site is being transformed and broadened. With data emerging from detailed house rim excavations combined with results emerging from ritual structures, we are starting to develop an understanding of the co-evolution of ritual and social complexity in pithouse village communities.

Why some of the first specialized types of structures in emergent complex societies should be ritual in nature rather than political, economic, or militaristic, is an intriguing question. The same pattern can be discerned in the early complex hunter-gatherer and horticultural cultures of the Near East (Hayden, 2003). In fact, there are many similarities between the Natufian culture of the Near East and the complex prehistoric cultures of the Mid Fraser River Region. As in the Near East, the first ritual structures at Keatley Creek are relatively small, and capable of accommodating only a small exclusive fraction of the community population. They appear to have been used by a very select group, perhaps linked to important economic and political roles as in the secret society organizations recorded for the Northwest area ethnographically – at least, these are the ideas and suggestions we have been evaluating and investigating at Keatley Creek and in other parts of the world.

Keatley Creek has one of the most fine-grained records in Canada for the study of such ritual structures at the transegalitarian level and we expect that results from the site will provide further important insights for understanding these issues in other parts of the world. The new directions in ritual and other research at the site should lead to revised models for pithouse village dynamics, and the evolution and organization of complex hunter-gatherers and early cultural developments on the Canadian Plateau. This research should help to make a valuable contribution to the process of identifying and interpreting ritual activities represented in the archaeological record elsewhere.

5. Conclusions

The Keatley Creek site is critical for understanding the transition from egalitarian foragers to more socially complex adaptations in early hunter-gatherer populations. The current research programme at Keatley Creek has helped to shed light on the conditions preceding and accompanying the establishment of large villages, large corporate groups, and inequalities (Villeneuve, 2014). Ritual, in particular, has been an important part of this research which has been under-theorized in studying these processes, or hardly mentioned at all in the major edited volumes on complexity (for example, Price and Feinman, 1995, 2010, although see Aldenderfer, 2010).

Together with obtaining critical new radiocarbon dates for the earliest manifestations of these traits, our recent research has also been implementing the use of state-of-the-art advanced methods to examine stratigraphic sequences and ritual structures. Digital techniques, video recording, GIS data collection and processing, micromorphology, new photographic approaches, and other features have all combined to produce a broader data set and robust new interpretations that will be used to test alternative models of these important cultural adaptations and evolutionary developments.

In summary, Keatley Creek has been an exceptional site to work at in terms of the ability to identify domestic and corporate groups (directly associated with the refuse that each produced), the preservation of deposits, and a vibrant native culture in the region directly descended from prehistoric populations. In terms of its importance, research at Keatley Creek has contributed to the development of social, economic, political, and ritual models of complex hunter-gatherers, and it continues to contribute major new insights into understanding the prehistory of the region as well as early cultural developments in general.

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4

Conclusions and the Way Forward

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The international meeting *The First Peopling of the Americas and the World Heritage Convention* was held in Puebla, Mexico, from 2 to 6 September 2013. The meeting marked an important advance of the HEADS Programme towards its mission of defining and establish a strategy of cooperation with the local government of Puebla and of establishing solid actions in order to ensure the future recognition, conservation and research of sites related to the process of human evolution, adaptation, dispersal and social development in the Americas. The Americas hold many sites that have strong links to human origins and many of these are insufficiently represented on the World Heritage List. The value of these sites is underestimated and goes unrecognized, and it is often a challenge for States Parties to conserve this heritage and manage its specific vulnerability.

The meeting was a continuation of a series of World Heritage meetings; it addressed the discussions and recommendations from the international UNESCO meeting *Human Evolution and the World Heritage Convention*, which took place on 21 to 25 March 2009 in Burgos, Spain, the *Meeting to promote African human origin sites and the World Heritage Convention*, held from 8 to 11 February 2011 in Addis Ababa, Ethiopia, *Human Origin Sites in Asia and the World Heritage Convention,* held at the Jeongok Prehistory Museum, Republic of Korea, from 24 to 28 September 2012 and, most recently, *Human Origin Sites and the World Heritage Convention* in Eurasia held at the University of Tübingen, Germany, from 25 February to 1 March 2013. Whilst the meeting in Burgos focused on sites related to Human Evolution from a global perspective and analysis, this meeting provided a regional concentration in support of the future conservation of human dispersal and adaptation sites in the Americas, as was the case following the African, Asian and Eurasian meetings. Additionally, this meeting extended beyond evaluating and defining HEADS related sites and their evolutionary features and addressed the development of the compulsory cooperation between science and conservation.

This essential collaboration was highlighted by the involvement and participation of government officials from the State Government of Puebla, SEMARNAT, CONAMP, INAH and CONABIO.

Most of the meeting's work was achieved through multilateral Working Groups, which were based on information acquired from several days of scientific sessions and site visits[1]. The scientific sessions consisted of presentations by invited experts from Mexico and representing 11 other countries, representing over 30 universities and research centres. The experts gave presentations and engaged in discussions about the arrival and dispersal of hominids to and across the Americas. The presentations approached the first peopling of the Americas from many perspectives; experts specializing in climate analysis, human palaeontology, zooarchaeology, mitochondrial DNA, property relations, neolization, the origins of agriculture and the domestication of maize and the important role of the *cenotes* submerged heritage.

The scientific sessions were enriched by site visits. The experts visited la Reserva de la Biosfera Tehuacan-Cuictlan in Tehuacán, Puebla, Mexico, which was declared a Natural Protected Area by Presidential Decree in 1998. The valley reveals important information regarding the origins of agriculture in Mesoamerica and thus regarding the peopling of the continent. It contains key information for developing an understanding of the domestication of many species of plants (maize, chilli, amaranth, avocado and pumpkin, among others). The bioreserve is also home to many endemic species, both floral and faunal. The experts also attended the Museo de la Valle de Tehuacán where the local populations of the area presented the ritual called Popoloca Ceremony.

Narratives discussed in the Working Groups include human dispersion into the continent and subsequent adaptations and social developments, such as adaptations to high altitude environments, the domestication of potatoes, maize and amaranth, the transformation of symbolic landscapes and the transformation of grassland use from megafauna to cattle ranching, time depth in living traditions and technological innovations. Other narratives discussed were human and megafaunal interactions

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[1] http://whc.unesco.org/es/eventos/1077/

and economic alternatives, plant and animal domestication and the transition from hunter-gatherers to agricultural or sedentary societies, as referenced in the last pages of the second volume of this publication.

These narratives were discussed within the contextual framework of the following criteria and concerns: current degrees of conservation, exceptional variety and chronological continuity, cultural and environmental record, and political and environmental risks necessitating international collaboration.

Among the sites discussed was Monte Verde in Chile, noted for its Outstanding Universal Value. Investigations of the site have contributed to insights into a growing body of knowledge based upon several of the aforementioned scientific narratives. The site embodies a huge temporal development, with dates as early as 14,500 years BP. The site also conveys a transcendent and significant quantity of biological, social and cultural processes related to human evolution. Technological advances are evidenced even by double-S-slip knotting. It has also been underlined the importance of the evidence of technological advances at Peru´s Huaca Prieta, that includes unifaces dated 14,400 (calibrated) BP. Unifaces from Monte Verde date to 13,500-12,800 (calibrated) BP. This correlation potentially indicates dispersion patterns.

The Working Groups focused on conservation and addressed the need for enlarging sites to include the past and current use of biodiversity in surrounding areas, and also touched upon the subject of expanding conservation procedures to include local populations in the decision-making process. The idea of expanding conservation to include mobile heritage was also discussed, and it was suggested that a Technical Group be created that would look at designing a HEADS approved protocol for designing interpretive criteria for prehistoric sites, guidelines to display collections and delve deeper into the reflection on how to use criteria viii for the benefit of HEADS sites.

Discussions also considered the Mexican Tentative List for World Heritage Sites, and in particular, the case of Tehuacan/ Tehuacan-Cuicatlan Biosphere Reserve. It was suggested that the current model for the nomination process be updated to reflect the following aspects:

Suggestions in order to begin the nomination process of this site within the collaborative nature and framework of the HEADS Thematic Programme include eliciting a meeting between mayors and state governmental entities to generate dialogue as reflected in the participation of members from the SRE, SEMARNAT, CONANP, INAH and the Governor of the State of Puebla of the Presidium of the opening ceremony of the meeting.

It is acknowledged that the HEADS Thematic Programme may provide the knowledge, international experience and resources necessary for the generation of expert technical working committees in order to advance the nomination process. This publication could be used as a tool to provide the elements for the comparative study of sites.

Results of Working Groups

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GROUP 1: The Americas (I)

The first Working Group's discussion on multidisciplinary Approaches of Colonisation and Dispersal was guided by Dr Robin Dennell. The participants who contributed to the dialogue were Dr Tom Dillehay, Dr James Chatters, Dr Dennis O´Rourke, Dr Nelson Fagundes, Dr Luis Alberto Borrero, Dr James Steele, Dr Eduardo Corona Martinez and Dr Joaquin Arroyo.

Main narratives for the Americas

i. Archaeological studies (i.e. skeletal record)
ii. Geoarchaeological processes
    a. Caves
        1. Little Fish
        2. Bute
    b. Rock shelters
        1. Pedra Fourada 2
    c. Cenotes in Yucatan
iii. Genetic-archaeological-geomorph-climatic studies (i.e. identifying landscape usage)


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- iv. Integration of genetic record of modern humans, aDNA and archaeological evidence
    - a. Modelling and reconstruction of past environments in relation to the timing of colonization, namely:
        1. Beringia
        2. Panamanian isthsmus
        3. Brazilian rainforest
- v. Isotopic analysis
- vi. Palaeoecological research
    - a. Megafaunal/ human and megafaunal interaction

Subsequent Adaptations

- i. Economic shift from sealing to whaling
    - a. Dorset to Thule (Arctic North America)
- ii. High altitude adaptation
    - a. In the archaeological sites of Peru and Bolivia
- iii. Movements across the Andes
- iv. Modifications of human biology
- v. The domestication of the potato
- vi. Transformation of grassland use by megafauna to cattle ranching as in the cases of Argentina.

Social Developments

- i. The evolutionary role of food storage
    - a. Population growth and domestication
        - i. North-west coast
- ii. Symbolic landscapes
    - a. Intercommunity development of public landscapes, geoglyphs
        - i. Pecos River area (USA)/ Coahuila, Nuevo León and Sonora in México.
- iii. Sedentism/villaje emergence, population aggregation
- iv. Evolutionary role of deferred or delayed return in economics
        - i. North-west Plateau
        - ii. Columbia/Fraser River
- v. Time depth of living traditions
        - i. Use of grasslands
        - ii. North-west coast
        - iii. Riverine environments
        - vi. Technological innovations
    - a. Clovis/Folsom
    - b. High altitude corrals (camelids)
    - c. Transition from coastal hunter-gatherers to sealing and to whaling

GROUP 2: The Americas (II)

The second Working Group's discussion guided by Dr Francois Sémah. Dr Mark Rohrig Hubbe, Dr Daniel Sandweiss, Dr Christopher Scarre, Dr Theodore Schurr, Dr Rafael Suárez Sainz, Dr Francisco Mena, Dr Augustin Holl, Dr Adriana Schmidt Dias, Dr Fernando Fernandez and Dr Guillermo de Anda Alanis participated.

Scientific Narratives related to specific sites:

- i. Human dispersion into the continent
    - a. South-east Alaska, USA
    - b. Monte Verde, Chile
    - c. Nacientes del Río Catalanes-Arapey, Uruguay
    - d. Channel Islands, California
    - e. Clovis Site, New Mexico, USA
    - f. Lagoa Santa, Brazil
    - g. Santa Elina, Brazil


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- h. Quebrada Jaguay, Peru
- ii. Human/megafauna interactions and economic alternatives
  - a. Lagoa Santa, Brazil
  - b. Monte Verde, Chile
  - c. Las Breas de San Felipe, Cuba
  - d. Head Smashed In Buffalo kill sites (1981, vi)
  - e. Quebrada Jaguay, Peru
- iii. Plant/Animal domestication/ Transition from Hunter-Gatherers to Agricultural/ Sedentary Societies
  - a. Tehuacán, Mexico
  - b. Huaca Prieta, Peru
  - c. Telarmachay, Peru
  - d. Oaxaca Valley, Mexico
- iv. Adaptation to extreme environmental conditions
  - a. Pucuncho Valley, Peru
- v. Evidence of the rise of social complexity
  - a. Brazilian shell mounds
  - b. Huaca Prieta, Peru

Criterion

- i. Exceptional Conservation
  - a. Monte Verde, Chile
  - b. Peruacu Valley, Brazil
  - c. Cenotes of Yucatan, Mexico
  - d. Lagoa Santa, Brazil
- ii. Exceptional Variety and Chronological Continuity
  - a. Huaca Prieta, Peru
  - b. South-east Alaska, USA
- iii. Cultural and Environmental Record
  - a. Pucuncho Basin, Peru
- iv. Necessity for international collaboration
- v. Environmentally and Developmentally Endangered

Some exceptional sites and regions were considered to shape some of the identified cultures:

- i. Pucuncho Basin, Peru
  1. Earliest high altitude site
  2. Significant palaeoclimatic and palaeoenvironmental records (glacial deposits, ice cores)
  3. Traditional but low density occupation (alpaca herders)—low threat
  4. Ongoing interdisciplinary research
  5. Obsidian: exploitation of key natural resources
  6. Linked to Puchuncho Basin by obsidian: Quebrada Jaguay
- ii. Lagoa Santa Region, Central Brazil
  1. Longest history of research
  2. Ongoing interdisciplinary research
  3. Early human collections
  4. Palaeontological quaternary knowledge in the Americas.
  5. Endangered by mining
  6. 1844: First suggestion of human coexistence/ interaction with megafauna
- iii. Uruguay Middle River Basin
  1. Transnational collaboration: Brazil, Uruguay, Argentina
- iv. Mexico, Oaxaca Valley
  1. Neolithic revolution
  2. Settlement type shifts
  3. Well-documented climate sequence
- v. Huaca Prieta, Peru
  1. Longest archaeological sequence

  2. Important for the history of plant domestication/ agriculture
  3. Fishing practices documented
  4. Rise of social complexity (i.e. rituals)

vi. Cave Sites (Early underwater cultural heritage), Yucatan Peninsula, Mexico
  1. Long human occupation 10/ 12 ky cal
  2. Exceptional preservation
  3. Human and palaeontological record
  4. Extreme environment
  5. Ecologically unique
  6. Potential for transcontinental collaboration
  7. Association with the contemporary Maya culture
  8. Palaeoclimatic changes
  9. International importance of reservoirs of fresh water

vii. Las Breas de San Felipe, Cuba
  1. Latest megafauna in Americas (associated with archaeological remains)
  2. Geographical dispersions linking Yucatan and Mexico
  3. Insights into palaeoclimate in the Caribbean overlap.

viii. Brazilian shell mounds (Sambaquis)
  1. Dates 8000-2000 PB (radiocarbon)
  2. Largest shell mounds on planet (over 900 recorded)
  3. The beginnings of ceramics
  4. Coastal development

ix. South-east Alaska, USA (Tlingit, Haida, Eyak)
  1. Migration knowledge
  2. Living cultures present
  3. Riverine movement, oral histories
  4. Climatic and environmental research
  5. Transcontinental contact

x. Catalanes Nacientes of Arapey Archaeological region (North Uruguay)
  1. Caves and rockshelter with early occupation (*c.* 10.000 BP)
  2. Stone structures (cairns and circules)
  3. Lithic resources – quarries and workshops of silicified sandstone, agates, opal and jasper.

GROUP 3: Conservation

The third Working Group's discussions were guided by Dr Margherita Mussi. Its expert contributors were Dr Fred Smith, Dr José Concepción Jimenez, Ms Suzanne Villeneuve, Dr Brian Matthew Kemp, Dr Jorge Ríos Allier, Dr Marcia Chame, Dr Felisa Aguilar, Dr María de la Luz Gutierrez Martinez and Dr Pilar Luna Erreguerena.
The discussions covered the following subjects:

Framing data into policies

i. Development of international interoperable database system to integrate movable and immovable heritage of the prehistoric sites.

ii. Increased biodiversity in the surrounding area
  a. Volcanic area (Tres Vírgenes Volcanic System, Baja California Sur), source of pigment/obsidian (symbolic, ritual and chronological importance), among others

iii. Methodology to articulate cultural and natural heritage management for rock art sites:
  a. Baja California Sur
  b. Sierra de San Francisco, Mexico (already inscribed on the World Heritage List; 1993, (i(iii))
  c. Sierra de Guadalupe

International reflection on the integrated preservation of bones

  a. Promote deeper reflection on the Anthropocene, as discussed by scientist and reflect on the implications for the HEADS project.
  b. Procure guidelines that are ___ for genetic analysis

Group 4: The Mexican Tentative List for World Heritage Sites: the case of Tehuacan/ Tehuacan-Cuicatlan Biosphere Reserve
The fourth group's discussions were led Dr Nuria Sanz. Participating professionals were Dr Antonio Gilman, Dr Jose Francisco Ortiz Pedraza, Dr Juan Manuel Vicent, Ms Maria Pia Gallina, Mr Fernando Reyes Dlores and Ms Cecelia Herandez.

The Recommendations formulated to begin the process were:

- i. To elicit a meeting with mayors and state governments to generate dialogue
    - a. Tehuacan, Coxcatlán, State of Puebla, State of Oaxaca
    - b. Secretary of SEMARNAT, commissioner CONANP
- ii. To carry out training of technical groups:
    - a. biological
    - b. cultural
- iii. To develop a detailed cultural and natural cartography of the site
- iv. Research should be focused on the archaeology of landscape and cultural occupation in the different stages of the establishment of cultures found in the Valley over 10,000 years
- v. To generate a detailed map using GIS technology including land use, erosion, the distribution of plant species in the soil, groundwater, land, etc.
- vi. To update the MacNeish studies with the implementation of new technologies.
- vii. The first site of the domestication of maize is known; but it is necessary to raise awareness of the importance of the genetic heritage of maize and its related cultural preservation.
- viii. A social development plan is necessary, including the implementation of standards of living according to the combines efforts of the local people to the traditional use of biodiversity.
- ix. To assist the relevant government bodies responsible for agrodiversity in the country, such as CONABIO and SAGARPA.

While this publication is going to press, the candidature of the site has been submitted to the World Heritage Centre for evaluation. We thank the Federal, State and Local Authorities for their commitment and engagement as proof of the outstanding value of this HEADS meeting on the Americas. No better conclusion could be achieved.

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