It's Getting Better All the Time: Comparative Perspectives from Oceania and West Africa on Genetic Analysis and Archaeology

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Abstract Technological advances are making genetic data collection and analysis feasible on a scale unimaginable only a few years ago. Early genetic research using mitochondrial DNA and the Y chromosome provided important insights for macroscale modeling of regional and continent-wide population movements, but the capacity to study the entire genome now opens an era of finer-grained, mesoscale studies of regional and local population histories that are more compatible with the scale of archaeological analysis. The utility of integrating both types of data is illustrated by a case study from Oceania, where genetic studies were used to evaluate two models for the geographic origins of the populations that colonized Polynesia beginning ca. 3000 BP, bringing with them the distinctive Lapita cultural assemblage. A second case study considers the application of genetic studies to an understanding of Fulbe history, especially that of the pastoral Fulbe. Both archaeological and genetic data are underdeveloped for the key Fulbe homeland regions of Mauritania and Senegal, but recent research in the Middle Senegal Valley permits some conjectures on the history of Fulbe nomadic pastoralism. The article concludes with suggestions for a multidisciplinary research agenda to expand and upgrade the quality of relevant archaeological data, incorporate biodistance studies of human skeletal material, and improve and expand genetic sampling using more historically sensitive collection protocols.

Résumé Les avancées technologiques permettent la collecte et l'analyse de données génétiques à une échelle inimaginable ne serait-ce qu'il y a quelques années. Les premières recherches génétiques utilisant l'ADN mitochondrial et le chromosome Y ont

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fourni des renseignements importants pour la modélisation à la macro-échelle des mouvements de population régionaux et continentaux. Mais la capacité d'étudier l'ensemble du génome ouvre maintenant une ère d'études plus précises à la méso-échelle —études de l'histoire des populations locales et régionales plus adaptées à l'échelle de l'analyse archéologique. L'utilité de l'intégration des deux types de données est illustrée par une étude de cas située en Océanie, où les études génétiques ont été utilisées pour évaluer les deux modèles sur l'origine des populations qui ont colonisé la Polynésie, dès 3000 ans BP et apporté avec eux l'ensemble culturel distinctif appelé Lapita. Une deuxième analyse examine l'application des études génétiques à une meilleure compréhension de l'histoire des Peuls (Fulbé), en particulier celle des Fulbé pastoralistes. Les données archéologiques et génétiques sont sous-développées pour les foyers de population Fulbe en Mauritanie et au Sénégal, mais des recherches récentes dans la vallée du Moyen-Sénégal permettent quelques hypothèses sur l'histoire du pastoralisme nomade Fulbe. L'article conclut avec des suggestions pour un programme de recherches multidisciplinaires destiné à élargir et améliorer la qualité des données archéologiques pertinentes, d'intégrer des études d'affinité biologique de matériel squelettique humain, et d'améliorer et d'élargir l'échantillonnage génétique en utilisant des protocoles de collection plus sensibles à la dimension historique.

Keywords Fulbe history · Genetic · Migration · Pastoralists

Introduction

Over the past two decades, genetic analysis has become an important tool for exploring past population movements. Mitochondrial DNA (mtDNA) and the non-recombinant portion of the Y chromosome (NRY) have been used to infer the origin and directional spread of genetic variants present in modern DNA, permitting the modeling of, for example, the movement of modern humans out of Africa, the peopling of the Americas, the spread of early farmers in Europe, and the Bantu expansion (Scheinfeldt *et al.* 2010; Soares *et al.* 2010; Tishkoff *et al.* 2009; Underhill & Kivisild 2007). Where archaeology has documented the spread of technologies (*e.g.*, food production) and/or cultural traits, genetic studies can, in some cases, help differentiate between past migration of peoples (demic diffusion) and movement of artifact technologies and languages without genes (cultural diffusion). Recently, new technologies have made it possible to go beyond mtDNA and NRY studies and analyze hundreds of thousands of genetic variants from across the entire genome to explore these questions. Combined with the increased geographical and temporal resolution made possible by rapid, automatic sequencing of the mtDNA and NRY genomes, this heralds a new phase in analysis that may result in a greater alignment in scale of genetic and archaeological data. In particular, more precise dating of the appearance and spread of genetic variants will encourage more detailed arguments linking genetic patterns with well-dated archaeological phenomena. Genetic analysis may transcend its current emphasis on macroscale processes at a continental or even global level and target mesoscale processes of regional and local differentiation that are more compatible with the scale of archaeological analysis. In this article, we explore how archaeological, genetic, and, to a lesser extent, linguistic evidence can be

deployed in an integrated research program to address specific historical questions regarding population movements and interactions involving gene flow.

We present two illustrative case studies. The first is from Oceania, where an expansive migration of Austronesian language speakers in the late fourth millennium BP pushed into previously uninhabited islands in Polynesia, accompanied by the distinctive Lapita cultural assemblage, which also appears in Melanesia. Genetic analysis attempts to identify the source area(s) of this population expansion. Did newcomers from the Austronesian language source area in Southeast Asia expand into Melanesia and Polynesia beginning 3,300 years ago, introducing the Lapita assemblage along the path of their migration, or was it a more complex process involving local development of Lapita by Melanesians who then carried it to Polynesia? This case study utilizes fairly extensive genetic sampling of diversity in New Guinea and the Bismarck Archipelago, the region in Melanesia with the earliest Lapita sites. As we shall see, even when relevant archaeological and genetic data are relatively abundant, interpretation is difficult, but in this case, it was possible to refute two of the proposed migration models.

The second case study considers whether genetic analysis can shed light on particularities of the history of the Fulbe (Fulani, Fellata, Peul), a pastoral group that is widely distributed across the Sudanic region of Africa. Linguistically, they belong to the family of Atlantic languages, yet arguments have been advanced (supported by the Fulbe's own oral histories) for origins in the Near East, Egypt, or elsewhere in northeast Africa. As we know them ethnohistorically, the pastoral Fulbe have a number of distinctive characteristics: a high frequency of physical traits suggestive of Mediterranean (North African, Near Eastern) and sub-Saharan admixture (Hiernaux 1975); Fulfulde language, a distinctive, cattle-based pastoral system and ideology, high levels of mobility, and low levels of archaeological visibility. When and where did the component elements of this Fulbe package of traits emerge? Can a genetic signature of an early demic expansion from the northeast be detected? Or would any such signature be overwritten by the complexities of the Fulbe's recent historical diaspora from west to east? Can genetic analysis reveal anything about the relative antiquity of the introduction of DNA from northern populations (Europe, North Africa, and the Near East) into populations ancestral to the Fulbe? We review the genetic studies conducted to date and discuss their limitations. Archaeological data are essential to the investigation of past pastoral systems and cultural patterns with possible links to Fulbe prehistory. However, the current state of archaeology in much of the relevant area of Africa provides very limited information for our inquiries, with the exception of the Middle Senegal Valley homeland of the historic Fulbe. Additional sources of evidence will be needed to tease apart the tangled deep-time history of the Fulbe. Based on current evidence, we propose that certain cultural aspects of the ethnohistoric Fulbe package, namely, specialized, semi-nomadic pastoralism, developed only in the last millennium out of more generalized agropastoral precursors. Evaluating this proposal and the other Fulbe components will require high quality, multidisciplinary data. We conclude with suggestions for a research agenda designed to upgrade the quality of relevant archaeological data, incorporate bio-distance studies of human skeletal material, and expand and improve genetic sampling using more sophisticated collection protocols, additional population samples, and additional genetic loci for analysis.

The Analysis of Genetic Variation

Uniparentally Inherited Genetic Variation—mtDNA and NRY

MtDNA and NRY have two characteristics that make them very useful for investigations of human demographic history: like all chromosomes, they have noncoding regions (*i.e.*, regions of DNA that do not code for genes) that can accumulate mutations much faster than coding sectors where mutations may affect function, and they are inherited uniparentally without recombination (the shuffling of chromosomes that occurs between the 22 paternal and maternal autosomal chromosomes each generation). Thus, the pattern of accumulated mutations is passed down intact, exclusively from mother to child in the case of mtDNA and from father to son for NRY, allowing the reconstruction of maternal and paternal population histories. Through time, new variants continue to arise through mutation, with two types of variant particularly relevant for studies of past population movements:

1. Biallelic variants, including single nucleotide polymorphisms (SNPs), which result from a mutation in a nucleotide base (abbreviated as A, C, G, and T) producing a second form, or allele, at a particular position on the chromosome; and in/dels, involving the insertion or deletion of one or more bases at a particular position (Fig. 1).
2. Multiallelic variants, particularly single tandem repeats (STRs, or microsatellites) which are mutations involving repetition of a short sequence of two to six bases at a particular position (Fig. 1); the number of repeats defines each allele.

By studying the patterning of biallelic variants in primarily the noncoding, hyper-variable segments (HVS) of the mtDNA, it has been possible to identify almost 7,000 sequence variants, which define particular lineages called haplotypes. These have been partitioned into approximately 90 mtDNA haplogroups, each one defined by a small set of shared biallelic SNP or in/del polymorphisms (Brown & Brown 2011, p. 177). The haplogroup mutations arose in a cumulative fashion over time, so that a haplogroup sublineage contains all the mutations of its parental lineage. The same principle underlies the recognition of NRY haplogroups. Figures 2 and 3 show genealogies of mtDNA and NRY haplogroups respectively. MtDNA haplogroup B, for example (Ruiz-Pesini *et al.* 2007; van Oven & Kayser 2009), contains its own defining mutations (including a 9-bp deletion) as well as the mutations that define haplogroups R, N, and L3. Similarly, NRY haplogroup O contains its own defining mutations (including M175) as well as the mutations that define haplogroups K and F (Karafet *et al.* 2008). These haplogroup variants are assumed to have arisen only once in modern human history [although this is not always the case (*e.g.*, Redd *et al.* 1995)]; therefore, individuals that share the same haplogroup variants are assumed to share ancestry with the last common ancestral population containing that haplogroup.

reference strand of DNA:	AATGCAACCGTGAAGGTCTACCGTTATATGAGTGCA
SNP:	AATCAACCGTGAAGGTCTACCGTTATATGAGTGCA
insertion:	AATGAGGCCAACCGTGAAGGTCTACCGTTATATGAGTGCA
6 bp deletion:	AATG-----TGAAGGTCTACCGTTATATGAGTGCA
STR:	AATGTTTATTATTATTATTATTATTATCAACCGTGAAGGTCTC

Fig. 1 Illustrative examples of SNP, in/del, and STR variants

mtDNA Haplogroup Tree

Fig. 2 An mtDNA haplogroup tree. Each branch represents a haplogroup lineage within haplogroup L3

The geographic distribution of the various haplogroups suggests a process of migration from Africa, gradually spreading across the world (Cann *et al.* 1987; Garrigan *et al.* 2007; Underhill *et al.* 2001).

Because uniparentally inherited mtDNA and NRY are not subject to the unpredictable shuffling that occurs during recombination, they can be used to reconstruct

NRY Haplogroup Tree

Fig. 3 A Y chromosome haplogroup tree. Each branch represents a haplogroup lineage within haplogroups C:T

several demographic parameters, including the time to the most recent common ancestral population, effective population size (the number of breeding individuals in the ancestral population), past gene flow, and past migration events. Estimating the time that has elapsed since a haplogroup came into existence (the coalescence time) considers the amount of diversity present within each haplogroup. Since greater diversity is the result of a larger number of mutations, which accumulate as a function of time since the emergence of the founding mutation(s) of the haplogroup, it is possible to assign an approximate date to that event if the mutation rate (generally assumed to be constant) can be estimated. This type of molecular dating requires some important caveats: when hyper-variable variants (from mtDNA or NRY) are used to estimate the absolute age of a haplogroup lineage, any variant within the lineage that has arisen more than once will bias the estimated age, and the absolute ages are dependent on an accurate mutation rate. Many studies include extremely large confidence intervals to compensate for these uncertainties.

When these analyses are used to infer migration patterns, it is generally assumed that the contemporary population with the highest levels of within-haplogroup diversity descends directly from the population in which the haplogroup arose. This assumption is based on two properties of population genetic modeling: The longer a haplogroup lineage has been in existence, the more mutations accumulate within it; and populations that migrate away from the source population generally carry only a subset of the variation present in the source population (sometimes referred to as a bottleneck or founder effect). Thus, analyses of haplogroup diversity in the source and migrant populations can be used to estimate the time that the two populations separated from each other (*e.g.*, Brown & Brown 2011, p. 225). However, diversity can be affected at any point by the random effects of genetic drift (random fluctuations of allele frequencies in a population each generation), especially in small populations, and this may obscure demographic inference.

For all its advantages, there are limitations to the analysis of mtDNA and NRY. To begin with, they represent a very small proportion of the overall genomic variation (~1.8 %) of an individual or population. MtDNA or NRY provide information on only one of the 256 lineal ancestors that contributed to the genetic makeup of an individual over a seven generation span. It therefore tells a very partial historical tale. In addition, both loci have a small (0.5) effective population size (one copy of the mtDNA and NRY is present in each individual) relative to the rest of the autosomal chromosomes (two copies are present in each individual) and are therefore more susceptible to the effects of genetic drift. In addition, there is evidence, though somewhat contentious, that these loci have been affected by natural selection (Kivisild *et al.* 2006), and if/when this is the case, variation at the entire locus will be affected (and often reduced) also obscuring demographic inference, because both the mtDNA and NRY are inherited as single units. Therefore, caution must be used in the interpretation of mtDNA and NRY data.

Anthropological geneticists have often used mtDNA and NRY to study human migration patterns (*e.g.*, Belezal *et al.* 2005; Karafet *et al.* 2002; Malhi *et al.* 2004; Manni *et al.* 2002). Many studies have characterized the distribution of mtDNA and NRY haplogroups worldwide. For example, mtDNA haplogroup B is common in populations residing in Asia, the Americas, and the Pacific (Friedlaender *et al.* 2005;

Merriwether *et al.* 1999; Ruiz-Pesini *et al.* 2007), and the NRY haplogroup O is common in populations residing in Asia and the Pacific (Kayser *et al.* 2003; Scheinfeldt *et al.* 2006; Underhill *et al.* 2000). When the same haplogroup occurs in two different areas, migration is assumed to have occurred. In particular, the geographic region (the region in which the sampled populations reside) where the haplogroup is most frequent and most diverse is often assumed to be the geographic location in which the haplogroup emerged.

These methods have inherent difficulties, however. Inferring the geographic location of past genetic events, such as the emergence and spread of a haplogroup based on present day haplogroup frequencies and distributions, assumes geographic continuity of past and present populations. This is particularly problematic in areas where climate change has resulted in major population shifts, *e.g.*, the successive episodes of repopulation and depopulation in the Sahara since the last glacial maximum. In addition, characterization of haplogroup distribution and genetic diversity depends on adequate population sampling, as small sample sizes are unlikely to provide an accurate representation of haplogroup and haplotype frequencies, and sampling protocols must take care to avoid consanguineal kin, as an obvious example. Especially in the case of older samples included in haplogroup databases, sampling protocols are not always described. Where the population sample is inadequate and/or the assumption of geographic continuity of past and present populations is invalid, mtDNA and NRY haplogroup analyses can lead to erroneous conclusions regarding past migrations and gene flow.

Autosomal Genetic Variation

Over the past 10 years, it has become easier and cheaper to collect genome-wide autosomal data. The advantage of genome-wide data is that they provide a more comprehensive picture of genetic variation (because they represent a much larger proportion of overall genetic variation than the mtDNA and NRY), but one of the challenges in using genome-wide data is that recombination severely complicates the reconstruction of genealogies for a given gene or region (patterns of recombination can actually be used in demographic modeling, and we provide an example further on using lactase persistence). Therefore, it is more difficult to infer the direction and timing of past migrations and gene flow. Additionally, many of the available sets of genome-wide autosomal variants (especially SNPs) are limited by the ascertainment scheme used (the way in which the variants were identified as significant and chosen for study). For example, many of the available genome-wide SNP arrays include variants that were identified in non-African populations, and it is unclear to what extent this ascertainment introduces a bias into the data and thus a bias into the application of these data to demographic inferences for African populations.

In the next section, we outline an example from Oceania illustrating how linguistic patterns and archaeological data have framed specific questions for genetic analysis about the source and path of population histories and migrations in Melanesia and Polynesia. This body of work illustrates contributions of genetic data to the study of population histories as well as limitations inherent to the use of genetic data.

Pacific Case Study: The Austronesian Expansion

Sahul, the joined landmass of Australia and New Guinea during the low sea levels of the Pleistocene, was colonized by some of the earliest anatomically modern humans to leave Africa (Fig. 4). Migrants arrived in Papua New Guinea by 40–60 kya (dated with thermoluminescent and radiocarbon dating; Chappell *et al.* 1994; Groube *et al.* 1986; Roberts *et al.* 1995) and sailed (over the horizon) to the Bismarck Archipelago as early as 40 kya (dated with radiocarbon dating; Leavesley *et al.* 2002). These early inhabitants likely had sophisticated boating skills, practiced a coastal/marine lifestyle, and were able to utilize both terrestrial and marine resources using a relatively simple toolkit comprised of stone flakes, core tools and axes (*e.g.*, Kirch 1997; Spriggs 1997; Summerhayes 2007).

Archaeological evidence demonstrates significant population movements subsequent to initial settlement within the region (*e.g.*, Spriggs 1997). During the late Pleistocene (18–20 kya), non-native faunal remains appear at sites in the Bismarcks, and obsidian appears at distances as far as 350 km from its source (*e.g.*, Kirch 1991; Summerhayes 2007), indicating regional trade and technological diversification. Additional technological innovations that emerged in the Holocene (4–10 kya) include tree cultivation and shell technologies (*e.g.*, Spriggs 1997).

Not until roughly 3.1 kya is there evidence that people migrated into Remote Oceania (the region east of the Solomon Islands including the Reef Islands, Tikopia, Vanuatu, New Caledonia, Fiji, Samoa, and Tonga as well as other regions of eastern Polynesia and Micronesia) (Summerhayes 2007). The pottery found at these sites shares a distinctive dentate stamped style termed Lapita (*e.g.*, Kirch 1997; Spriggs 1997). These sites also include faunal remains from non-native pigs, fish hooks, trolling lures, stone adzes, shell scrapers, peeling knives, anvil stones, shell rings,

Fig. 4 Pacific map of areas mentioned in the text

polishers, sling stones, discs, needles, tattooing chisels, and net sinkers (Kirch 1997; Spriggs 1997; Summerhayes 2007); however, some of these (*e.g.*, pig remains) were found at earlier sites in the region (>6 kya, reviewed in Summerhayes 2007). The Bismarck Archipelago is thought to be the location from which the expansion into Remote Oceania emerged because it contains the earliest Lapita sites (~3.3 kya), which are at least 200 years older than Lapita sites in Vanuatu, New Caledonia, Fiji, and Polynesia (*e.g.*, Kirch 2002; Summerhayes 2007). Some archaeologists interpret the pattern and distribution of Lapita pottery and the artifacts found at Lapita sites to support a long-range “out of Asia” model in which Neolithic Southeast Asian migrants arrived in Melanesia and rapidly spread into Remote Oceania (*e.g.*, Diamond 1988; Kirch 1997). Others argue that most artifact technologies found at Lapita sites emerged in Melanesia, and the first migrants into Polynesia were primarily Melanesians (*e.g.*, Terrell 1988; White *et al.* 1988). This scenario is one that can be tested with genetic data because the question to be addressed is relatively simple: What is the extent to which people moved from Southeast Asia into Melanesia and from either Southeast Asia and/or Melanesia into Polynesia. To evaluate this question, frequencies and distributions of haplogroups in samples from numerous populations in Southeast Asia, Melanesia, and Polynesia have been mapped. The clinal distribution of particular haplogroups may be a signature of past migration, and genetic diversity within haplogroups can be used to estimate the direction of past migrations as well as the time that has elapsed since these lineages were carried along with the migrating peoples.

The populations sampled speak either Austronesian or non-Austronesian languages. The Austronesian language family is estimated to have originated 5–6 kya in Southeast Asia (Pawley and Ross 1993). The contemporary residents of the Polynesian islands speak languages that belong to the Oceanic branch (containing 460 languages including all of the Austronesian languages spoken in Melanesia, Micronesia, and Polynesia). The linguistic data from the region have been interpreted to support the long-range “out of Asia” model of Austronesian expansion in which Neolithic Southeast Asian migrants speaking proto-Austronesian languages traveled rapidly through Melanesia and into Polynesia (Pawley and Ross 1993; Wurm 1967) with very little interaction with Melanesian inhabitants. Furthermore, linguistic evidence suggests that the proto-Oceanic branch of the Austronesian language family emerged in the Bismarck Archipelago prior to the colonization of Polynesia (Pawley and Ross 1993), which is consistent with the initial emergence of Lapita pottery in the Bismarcks. Non-Austronesian (or Papuan) languages are found primarily in Melanesia, with the largest concentration (some 800 languages) in highland New Guinea. The relationships among these languages are ancient (>20 kya) and thereby difficult to reconstruct (Dunn *et al.* 2005; Foley 1986; Pawley 2000; Ross 2005).

The earliest genetic studies focused on the distribution of mtDNA variation, and in particular the distribution of a 9-bp deletion (which defines Haplogroup B), that was interpreted to be a genetic marker of the “Austronesian expansion” since it is common in Southeast Asia but absent from highland New Guinea population samples (Hertzberg *et al.* 1989; Stoneking *et al.* 1990). More recently, mtDNA work (Melton *et al.* 1995; Redd & Stoneking 1999) revealed the presence of an additional set of variants within haplogroup B that define a sublineage, termed the “Polynesian motif” due to the geographically restricted distribution of this lineage (it has not been

found anywhere west of Indonesia, except in Madagascar, Fig. 5). Not only is the “Polynesian motif” a sublineage of haplogroup B and therefore a descendant of Haplogroup B, but an intermediate/precursor mtDNA lineage to the “Polynesian motif” (the “Polynesian motif” minus one mutation at position 14022) has been found in Southeast Asia [the populations with the highest mtDNA diversity within this intermediate lineage live in Taiwan (Merriwether *et al.* 1999)]. This geographic distribution of the precursor “Polynesian motif” and “Polynesian motif” variants is consistent with a west-to-east migration of Polynesian ancestors from Southeast Asia. The “Polynesian motif” is common throughout sampled Melanesia populations (although less so in some of the non-Austronesian speaking populations including the Ata, Baining, and Sulka (Friedlaender *et al.* 2007)) and is almost fixed (reaching 100 %) in sampled Polynesia populations. This distribution (west-to-east increase in the frequency of the “Polynesian motif”) has been used to support the “out of Asia” model in which Southeast Asian Neolithic migrants rapidly spread through Melanesia and into Polynesia with very little gene flow.

However, more recent mtDNA studies (Pierson *et al.* 2006; Soares *et al.* 2011) based on whole mtDNA sequencing and analysis of the variation within the “Polynesian motif” lineage have resulted in a revised age estimate of the emergence of this lineage in the Bismarcks (6,650, 95 % CI, 4,500–8850; and 6,950, 95 % CI, 3,600–10,400, for maximum likelihood and complete genome clock molecular dating methods, respectively). Despite the wide confidence intervals, the combined results

Fig. 5 mtDNA haplogroup B4a allele frequencies in the Pacific (data from Friedlaender *et al.* 2007)

include evidence that it was present in Melanesia long before the emergence of Lapita pottery and Oceanic–Austronesian languages. The haplogroup may thus represent indigenous Melanesian and not recent Southeast Asian ancestry

These findings would bring the mtDNA data in line with Pacific NRY data, which is more consistent with archaeological interpretations of a primarily Melanesian origin of the migration into Polynesia with only occasional contributions from Southeast Asian migrants (Kayser *et al.* 2003). Specifically, haplogroup O, which is most common in SE Asia (ranges between 64 and 100 %; Fig. 6), is not especially common among either non-Austronesian- (1.7 %) or Austronesian- (11.1 %) speaking populations in Melanesia (Scheinfeldt *et al.* 2006). In addition, estimates of variation within the haplogroup O lineage are higher in Southeast Asia than either Melanesia or Polynesia (Capelli *et al.* 2001). The low frequencies of NRY haplogroup O in Melanesia and Polynesia are consistent with the high frequency of mtDNA haplogroup B in Melanesia and Polynesia, only if we accept that the “Polynesian motif” emerged in Melanesia long before the Lapita cultural complex. If recent Southeast Asian migrants were responsible for introducing the Lapita complex into Melanesia, the expectation is that the most common Southeast Asian mtDNA and NRY haplogroups would be well-represented in Melanesia, yet only the “Polynesian motif” is (Friedlaender *et al.* 2007). With the revised age estimate for the “Polynesian motif” in Melanesia predating the Lapita complex, the case for recent Southeast Asian origins for Lapita has been weakened.

Fig. 6 NRY haplogroup O allele frequencies in the Pacific (data from Cox and Lahn 2006; Scheinfeldt *et al.* 2006)

Since 2008, four genome-wide autosomal studies in the Pacific were reported. Kayser *et al.* (2008) focused on individuals from Polynesia and compared them with a Han Chinese population sample from Beijing and a population sample from Papua New Guinea. Kimura *et al.* (2008) analyzed genome-wide SNP data from a Papua New Guinea Gidra (Papuan) population sample and from a Polynesian population sample living in Tonga. Friedlaender *et al.* (2008) analyzed a genome-wide set of autosomal markers in a larger Pacific sample including a larger regional sample from Melanesia to better understand the patterns of genetic variation within Melanesia. Finally, Wollstein *et al.* (2010) performed a genome-wide analysis of population samples from Papua New Guinea, Fiji, and Polynesia. If we combine the results from all four reports, we find low but detectable levels of past gene flow between Melanesians and Southeast Asians. These results are consistent with the mtDNA and NRY data from Melanesia and with the interpretation that the “Polynesian motif” was present in Melanesia prior to the emergence of the Oceanic branch of the Austronesian language family and Lapita pottery and therefore is not a marker of long-range, agricultural, Southeast Asian migrants.

With regard to the origins of the Polynesian expansion, however, the autosomal data do not agree with the combined mtDNA and NRY data that support a primarily Melanesian origin of the Polynesian expansion. While Kimura *et al.* (2008) inferred relatively large amounts (>50 %) of Melanesian ancestry in their Fiji population sample, Wollstein *et al.* (2010) and Kimura *et al.* (2008) both estimate roughly 30 % Melanesian ancestry in their Polynesian population samples, Kayser *et al.* (2008) estimate that, on average, contemporary Polynesians share roughly 20 % Melanesian recent ancestry, and Friedlaender *et al.* detected even less recent Melanesian ancestry (and this only from Oceanic-speaking Melanesians living in New Ireland). This discrepancy may be due to the fact that all of the autosomal studies included modest Polynesian population samples. Another possibility is that the past gene flow that is being detected with the autosomal data among Southeast Asians, Melanesians, and Polynesians occurred farther back in the past (well before 3 kya), consistent with a model proposed by Oppenheimer and Richards (2001).

Thus, the addition of more recent, higher resolution genetic analyses in the Pacific has contributed to a better understanding of population histories within Melanesia, where the population samples are relatively dense, including a better understanding of the degree to which Southeast Asian and Melanesian populations interacted with each other over the past few thousand years. However, recent genetic work has also resulted in additional questions regarding past migrations in Polynesia, where the population samples remain modest. Within Melanesia, we find relatively low amounts of shared recent ancestry with Southeast Asians, even in populations that speak Austronesian languages (*e.g.*, Scheinfeldt *et al.* 2006), indicating a poor correlation between genetic and linguistic variation in Melanesia. With regard to the interpretation of the Lapita cultural complex in Melanesia, no simple model of innovation within Melanesia or intrusion from Southeast Asia can account for the pattern of genetic variation in the region. Rather, the genetic data are more consistent with models such as the “Triple I” model proposed by Green (1991) that includes innovation, intrusion, and integration to explain the emergence of the Lapita cultural complex in Melanesia.

The study of Polynesian population histories is limited by the poor sampling included in the genetic studies, so it is more difficult to have confidence in any specific model of past migration; however, both the strict “out of Asia” model of migration (also known as the “express train” model, which allows for very little Melanesian involvement) and the strict indigenous Melanesian (which allows for very little southeast Asian involvement) can be rejected with the available genetic data (e.g., Kayser *et al.* 2008).

The Fulbe case study from West Africa that follows also revolves around questions of migration and population interaction (gene flow) that may be illuminated by a combination of archaeological, linguistic, and genetic analyses. However, the state of such studies is far more nascent in West Africa, where we will see that archaeology is plagued by poor documentation and vast gaps in even basic culture history, genetic studies are hampered by inadequate sampling, and linguistic approaches to the past of the relevant Atlantic language groups are completely undeveloped. In addition to outlining the current state of knowledge, we also present proposals for future interdisciplinary research.

The Fulbe

The Fulbe ethnolinguistic group, comprising >10 million people who speak Fulfulde languages, have traditionally had pastoral or agropastoral subsistence systems based on cattle and a distinct element of mobility, ranging from fully pastoral, to transhumance by youths who travel seasonally with cattle while older males farm, to seasonal movement by mixed farmers after the harvest (Abu-Manga 1999: 54). They have been historically documented for the past seven centuries, associated with continuous waves of migration by lineages that trace their origins back to the Middle Senegal Valley (Futa Tooro) (Fig. 7). From Futa Tooro, the Fulbe migrated to the Macina region of the Middle Niger and the Futa Jallon of Guinea by the fourteenth century. This movement may have been prompted by the southward push in the western Sahara of the Sanhaja/Azenagh Berbers seeking to avoid the Arab tribes (Ma'quil, Banu Hassan) that were consolidating gains in the thirteenth and fourteenth centuries (Norris 1986).

Fig. 7 Distribution of Fulbe populations: vertical lines show known precolonial distributions; horizontal lines show distribution in the nineteenth century (after Boutrais 1994, pp. 138–139)

It is at this time that the Fulbe first appear in a European document: The 1339 map by Majorcan mapmaker Angelino Dulcert includes “Felle” (Fula) and “Tochoror” (Tukolor or Takrur), located to the southwest of Ganuya (ancient Ghana) (Roncière 1925, pp. 56, 114). The Tukolor historically are Fulfulde-speaking settled agriculturalists living in the Middle Senegal Valley (MSV) floodplain. It is not known how far back their Fulfulde linguistic identity extends, as the ethnic name references the early MSV polity of Takrur, of unknown linguistic affiliation, and several different ethnic groups claim historical presence in the MSV, including Serer and Soninke. The great eastward migration of Fulbe from the Macina began in the fifteenth century according to the Kano Chronicle, reaching Katsina and Kano by the 1460s and then Borno and Adamawa. By the seventeenth century, the Fulbe had penetrated to southern Darfur, via Baguirmi and Wadai (Braukamper 1993). In the seventeenth and eighteenth centuries, Islamized Fulbe traveled as itinerant scholars and marabouts; the eighteenth and nineteenth centuries saw expansionist jihadist movements led by Fulbe theocrats such as Seku Amadu, Usman dan Fodio, and Ahmadu Bello. Segments of Fulbe society became settled, while others retained the pastoral life of the *Fulbe ladde* (bush or nomadic Fulbe), of which the Wodaabe of Niger are the iconic example (Dupire 1962; Blench 1999). The nomadic Fulbe continued to spread by “migratory drift” (Stenning 1959), entering new areas to the south opened up by deforestation in the twentieth century as they sought to avoid colonial taxation. Some Fulfulde speakers moved back to the Futa Tooro from Macina under French rule.

The question of Fulbe origins has been the focus of considerable historical interest and speculation. European colonizers were impressed by the success of Fulfulde speakers in the eighteenth to nineteenth centuries in creating states and spreading Islam across a vast swath of the Sahel and savanna (Robinson 1975). In an era of racially framed historical scenarios, the distinctive physical appearance of the Fulbe prompted theories of distant origins; source areas in India, Malaysia, and Syria, as well as Ethiopia, the Nile Valley, and Libya have at various times been proposed (Brasseur and Brasseur 1981; Tauxier 1937), with claims of Hamitic affiliation prominently featured. Greenberg's (1949, 1963) definitive classification of Fulfulde as a West Atlantic language contravened such conjectures, and Murdock (1959) followed him in emphasizing the local emergence of the Fulbe in the vicinity of the Senegal Valley. Tauxier is still occasionally cited as the authority for Fulbe origins in the northeast (e.g., Cerny *et al.* 2006). Another source with a long shelf life is Dieterlen and Ba's (1966) intricate interpretation of certain scenes in the Tassili rock art as depictions of Fulbe rituals and ceremonies. The notion of a discernible Fulbe identity extending back millennia to the Central Saharan pastoralists had a number of adherents at one point (Simoons 1971, p. 435, note 18). Today, there is greater skepticism over the earlier interpretations of the rock art (Smith 2005, 136–137).

The Egyptian origin of the Fulbe was a central element in Cheick Anta Diop's influential work, *The Cultural Unity of Black Africa* (1959) as well as that of his main follower today at the University of Ch.A. Diop, A.M. Lam (*De l'Origine Egyptienne des Peuls* 2003). The Fulbe continue to hold a prominent place in discussions of the African past, reflecting in some cases their continuing ideological significance and the persistence of essentializing racial discourse. Online fora provide examples of the intense reactions that can be provoked by suggestions of non-African genetic ancestry in Fulbe populations.

In the following section, we will review the evidence for Fulbe genetic history. One problem common to many of these studies is the reliance on the ethnic classification “Fulbe” as an analytic category for studies of local populations spread over a vast area. While a strong, common cultural identity and ideology characterizes all pastoral Fulbe groups, and a common language is spoken by a far wider diversity of Fulbe, their genetic history is strongly influenced by local patterns of intermarriage and shifting identity choices. We will outline some of the historical patterns after summarizing the genetic data, which support a fairly deep West African ancestry for Fulbe with scant evidence for an Egyptian or northeast African component. Both the mtDNA and NRY of sampled Fulbe populations have a low frequency of Eurasian lineages. In Fulbe populations from Mali, Cameroon, and Sudan, relatively high frequencies of the -13910^*T allele associated with lactase persistence in Europeans provide additional evidence for gene flow from the Mediterranean basin, North Africa, or the Near East. Additional genetic analysis may help identify the route of introduction and chronology of this admixture. We then review the archaeological evidence relevant to Fulbe history, as we currently understand it. The state of currently available genetic and archaeological evidence is inadequate, but this can be remedied by rigorous interdisciplinary research with contributions from archaeology, bioarchaeology, genetics, and linguistics. We agree with Wylie (2002) that the most robust results are generated when different disciplinary investigations are structured to contribute diverse evidential elements that independently illuminate the research question at hand.

Genetic Analysis

As discussed earlier, genetic analysis is used to infer past population movements and biological affinities from spatial distributions of allele and shared haplotype frequencies, focusing on comparative genetic diversity and similarity or difference among tested populations. The earliest genetic analyses on Fulbe populations were done using classic protein polymorphisms—that is to say, the functional products of genes, such as Rh factors, and gamma-immunoglobins (Gm). Based on the Rh variant frequencies, Fulbe from Senegal were most similar to Afroasiatic speakers (*e.g.*, Galla, Rendille, Amhara) in Ethiopia, but clustered with West African groups when Gm variant frequencies were plotted (Excoffier *et al.* 1987; Blanc *et al.* 1990). In addition, Cavalli-Sforza *et al.* (1994, pp. 181–182) studied classic protein polymorphisms and showed that Serer, Wolof, and Fulbe in Senegal form a discrete genetic cluster. However, since these factors are subject to natural selection, similarity in frequencies may reflect similar selection pressures rather than close genealogical relationship.

MtDNA and NRY Studies

Only in the last few years has the technology for rapid and cost-effective DNA sequencing become available, permitting relatively high resolution studies using many genetic markers (*e.g.*, Cerezo *et al.* 2011; Barbieri *et al.* 2012). Much of the earlier literature on mtDNA and NRY analysis in Africa is of lower resolution, with

only broad patterns of genetic variation revealed. Although the sampling of West African populations in general and the Fulbe in particular is problematic—characterized by small samples and undocumented collection protocols as well as serious gaps in geographic and population coverage—nevertheless, certain patterns are of interest.

MtDNA studies demonstrate the similarity of Fulbe populations in Guinea Bissau and Senegal to their neighboring northern Atlantic speakers—Wolof and Serer (Rosa and Brehm 2011). Furthermore, Fulbe mtDNA haplogroup frequencies are markedly similar in all sampled Fulbe groups from the Atlantic coast to the Chad Basin. The dominance of West African mtDNA lineages L1b/b1, L2c, and L3b/d affirms that maternal inheritance in the Fulbe is decidedly West African (Cerezo *et al.* 2011; Cerny *et al.* 2006, 2011; Gonzalez *et al.* 2006; Rosa *et al.* 2004—it should be noted that these haplogroups have time depths of between 120,000 and 60,000 ya [Underhill and Kivisild 2007] and may have expanded from LGM refuge areas into the Sahara during the early Holocene wet period). Variable but low frequencies of North African haplogroup U6, thought to be related to a southward expansion of the Berbers, occur particularly in the western Fulbe samples and also at higher frequencies among their northern neighbors, the Maure (Gonzalez *et al.* 2006; Rosa *et al.* 2004). These may indicate a north–south route for gene flow along the northwestern margin of Africa. In addition, Eurasian haplogroups (e.g. U5, J1b, and V) that have spread to North Africa are variably present in low frequencies in most sampled Fulbe groups (Cerny *et al.* 2006; Rosa *et al.* 2004).

Early mtDNA studies sampled settled Fulbe (Rosa *et al.* 2004; Scozzari *et al.* 1988; Watson 1996, 1997), who tend to resemble neighboring settled populations. Cerny *et al.* (2006, 2011) demonstrated that, by contrast, the mtDNA and NRY of nomadic Fulbe sampled in several countries from Mali to Chad differs from that of neighboring farming populations, as well as previously sampled populations of settled Fulbe, Wolof, and Serer. Unfortunately, nomadic Fulbe from Senegal have never been sampled adequately, so we do not know the extent to which the migrants resemble that putative source population. With the exception of the Songhai and Fulbe in Mali, farmer and pastoralist groups shared very few haplotypes, demonstrating a lack of gene flow between these two groups (Cerny *et al.* 2011). Gene flow among pastoral Fulbe, despite the distances involved, appears to be extensive.

Y chromosome studies have benefited from recent advances in mutation detection technology and phylogeographic methodology, permitting dramatic increases in both haplogroup recognition (from 153 in 2002, to 311 in 2008; Karafet *et al.* 2008), and genealogical resolution as additional markers within haplogroups have been identified. One result has been the renaming of certain NRY lineages as the sequence of genetic differentiation has become clearer. This means that earlier and more recent studies may use different names for the same lineages. For the purposes of this discussion, we reference haplogroups with the nomenclature provided in Karafet *et al.* (2008), and we use the lineage/sublineage alphanumeric label followed by the defining basal SNP mutation for clarity. Unfortunately, most of the West African studies predate these advances in lineage and sublineage definition, so the degree of resolution is very low and often inconsistent across studies. It is possible to say only that West African Fulbe are characterized, along with almost all sub-Saharan West African populations, by a very high relative frequency of haplogroup E1b1 (PN2) and several of its sublineages (Fig. 8)—

Fig. 8 Fulbe NRY haplogroup tree. Four population sample haplogroup frequencies are displayed: Guinea-Bissau (Rosa *et al.* 2007), Burkina-Faso (Cruciani *et al.* 2002), Cameroon (Cruciani *et al.* 2002), and Sudan (Hassan *et al.* 2008). SNP lineages that were not tested in a particular study are labeled NT

80–90 % in Fulbe samples from Senegal (Semino *et al.* 2002 pooled with other Senegal populations), Burkina Faso (Cruciani *et al.* 2002), and Guinea Bissau (settled Fulbe—Rosa *et al.* 2007). In addition, Cerny *et al.* (2011) report that most of the STR haplotype clusters identified in samples from pastoral Fulbe from Mali, Burkina Faso, Niger and Chad are referable to two sublineages of E1b1 (PN2) defined by the M2 (common in West and Central Africa) and M35 (more common in northern and eastern Africa) SNPs.

The only other haplogroups reported in West African Fulbe samples are E1a, E2, A, and R1, all at frequencies of ≤ 10 % (Cruciani *et al.* 2002; Rosa *et al.* 2007). The last haplogroup, R1, is common in Europe and is particularly geographically structured across sampled Fulbe (Cruciani *et al.* 2010): 1 % in West African Fulbe, 11 % in Fulbe from Cameroon, and 54 % in Fulbe sampled in Sudan (Hassan *et al.* 2008). A sublineage of R1, R1b1a (V-88), is thought to have entered north Africa 5–11 kya, where it is still present in low frequencies, but has reached notably high frequencies in the central and eastern Sudan, and appreciable frequencies in a Fulbe population sample from Niger (14 %) as well as in northern Berbers and Arabs (3–27 %; Cruciani *et al.* 2010). Figure 8 summarizes the main differences among the Y-chromosome haplogroups of western, central (Cameroonian), and eastern Fulbe populations. These are considerable, and they shed light on some aspects of the recent population history of the Fulbe. We will return to this after considering the autosomal data.

Genome-Wide Autosomal Studies

In a landmark study, Tishkoff *et al.* (2009) studied over 1,300 microsatellite (STR), indels, and SNPs from across the autosomal genome for 113 African population

samples. The authors used the software package STRUCTURE to estimate the relative proportions of genetic ancestry for each individual without any *a priori* information related to geography or ethno-linguistic identity. STRUCTURE is a Bayesian method that divides each individual into one or more genetic groupings called ancestral allele clusters (AACs). Each vertical bar in the STRUCTURE graphic represents a single individual, and heterogeneous ancestry is indicated by different-colored AACs. The West African samples from the savanna and forest generally are the least heterogeneous, with primarily AACs shared with other speakers of languages belonging to the Niger–Congo/Kordofanian language family (Fig. 9, shown in orange). In Cameroon, AACs shared with Chadic and Central Sudanic speaking populations (maroon) are significant. In addition to moderate levels of shared AACs with other Niger–Kordofanian speakers, the Fulbe from Nigeria and Cameroon have a striking incidence of a distinctive AAC (fuschia) that is shared in moderate to low levels with the Mozabite sample from northern Algeria and the Mandinka sample from Senegal. The Adamawa Fulbe, who have settled and become farmers, show considerable mixing with neighboring populations, such as Hausa and Baggara (Shuwa) Arabs. The Mbororo pastoral Fulbe, however, show far less admixture, consistent with the observations of Cerny *et al.* (2006, 2011). European/Middle Eastern AACs (blue) are found in low frequencies in most West African populations, including the Fulbe, but are of course more numerous in the Baggara Arab population.

More recently, ADMIXTURE analysis (a clustering program similar to STRUCTURE) by Henn *et al.* (2012) suggests an absence of northeast African ancestry among the Fulbe (pastoral Wodaabe from Nigeria were sampled), and confirms a mixed sub-Saharan and northwest African (possibly Berber) ancestry, possibly of some antiquity (Fig. 10).

From the genetic data available in these studies, several aspects of Fulbe population history can be highlighted. First, most of the Fulbe sampled across West Africa

Fig. 9 STRUCTURE plot of ancestral allele clusters (AAC) for sampled populations in North Africa and West Africa. Each vertical bar represents an individual (from Tishkoff *et al.* 2009, Fig. 4, reproduced with permission of the AAAS). This figure appears in color in the online version of this article

Fig. 10 ADMIXTURE plot of population structure of North African and neighboring populations (taken from Henn *et al.* 2012, Fig. 1). This figure appears in color in the online version of this article

are drawn from a West African mtDNA gene pool. The incidence of European or North African mtDNA lineages is quite low. Fulbe Y chromosome diversity is geographically structured, however. Western Fulbe generally resemble other West African populations, while Central and Eastern Fulbe groups testify to gene flow due, at least in part, to the recruitment of males from Central and Eastern Sudanic neighboring populations, a pattern that is particularly striking in the NRY sample from Fulbe in Sudan (comparable mtDNA data are not available for the eastern Fulbe). Given the recent arrival (<400 years) of the Fulbe in the central and eastern Sudan, this pattern is likely to be of recent date. With evidence in hand for local and regional differences in gene flow among settled vs. pastoral Fulbe, and western vs. eastern Fulbe populations, the temptation to extrapolate results from one or two sampled populations to all Fulbe (*e.g.*, Hassan *et al.* 2008; Tishkoff *et al.* 2009, supporting material, p. 16) should be resisted. Fulbe genetic history is marked in certain areas by significant population mixing, intermarriage, and shifts in ethnic identity in recent centuries, as we outline in the next section. This has implications for the kind of population sampling that needs to be done if we are to achieve the finer resolution that will take us from macro- to meso-scale inference and better alignment with archaeological data and priorities.

Discussion

To conclude the review of available genetic studies on the Fulbe, we would emphasize the importance of incorporating into research design and genetic sampling protocols the evidence of recent population history and marriage practices. Some genetics researchers have been aware that language boundaries are permeable and even strict endogamy rules get broken (*e.g.*, Blanc *et al.* 1990; Coia *et al.* 2009; Spedini *et al.* 1999), while others have seemed oblivious to the importance of understanding the history and culture of their linguistically categorized objects of study. Genetic analysis has demonstrated that endogamy is more strictly observed by pastoral than by settled Fulbe (Cerny *et al.* 2006, 2011). Along the Senegal Valley, pastoral Fulbe women are reportedly never given in marriage to non-pastoralists (Kyburz 1994:54). Once Fulbe become sedentary, however, gene flow with neighboring settled populations increases (Dupire 1994).

In the context of the nineteenth-century Fulbe theocratic states established across the Sahel, political power in some cases resulted in “Fulbeization” of local populations, including former slaves who adopted the Fulfulde language and, to varying degrees, Fulbe identity (Schultz 1984; Keita *et al.* 2010). This has

also operated in the reverse sense—Fulbe have been assimilated by Hausa in parts of northern Nigeria (see Blench 1990 for details on the local complexities of Fulbe identity and language in Nigeria). Further east, Fulbe frequently intermarry with Baggara Arabs, who abandoned camel-rearing and adopted the mixed cattle-herding/millet cultivation economy of the Fulbe, while maintaining their Arabic language (Abu-Manga 1999, p. 53; Braukamper 1993). This intermarriage is reflected in the STRUCTURE autosomal data analysis (Fig. 9). This raises the important question of gene flow among different pastoral groups. The Fulbe have historically lived in proximity to other pastoralists: Berbers and Maures in the western Sudan, Tuareg in the west-central Sudan, Koyam and Shuwa in Borno, Teda in Chad, Baggara Arabs in the central eastern and eastern Sudan. Particularly in times of epizootics (such as the great rinderpest and bovine pneumonia epizootics in the nineteenth century) and drought, when herd losses are catastrophic, intermarriage and assimilation with other pastoral groups may provide a way to maintain a pastoral way of life and, in the case of other cattle herding groups, to rebuild herds through bridewealth payments in livestock. These examples are fully consistent with our understanding of ethno-linguistic identity as fluid and situational (Barth 1969) and contradict any reified notion of “the Fulbe” as an analytic category for which genetic observations on one population can be applied more broadly to the entire group. For this reason, anthropologists have repeatedly cautioned against treating gene history as ethno-linguistic history (Brown and Pluciennik 2001; Keita *et al.* 2010; MacEachern 2000).

The guiding notion of genetic studies of population history is that gene/allele distributions are “structures” that reveal aspects of history. However, the interpretation of historical process from genetic patterns depends on the models used, as seen in the Pacific case study previously discussed. These in turn depend significantly on “one’s understanding of the biology of the traits, social processes and histories of the region” (Keita 2005, p. 139). Genetic sampling, in addition to targeting underrepresented groups and geographical areas, should pay much more attention to the collection of historical data along with their blood or saliva samples, including recent family histories and migration routes and intermarriage patterns (Keita *et al.* 2010). As the resolution of phylogeographic analysis becomes increasingly refined with regard to both timescale and distribution of novel genetic variants, meaningful interpretation will require concomitantly fine-grained local and regional historical data and population data sets adapted to the geographic and historical scale of the events under investigation (Coia *et al.* 2009). For archaeologists, the difficulty with phylogeographic approaches is that distributions of modern genetic diversity across geographic space are palimpsests of many layers of gene flow and drift resulting from a variety of cultural and historical processes—and it is precisely these processes, which need to be teased out at a fairly high degree of temporal resolution, that are of primary interest (Brown & Pluciennik 2001; MacEachern 2000). The genetic data that have been available until recently for interpreting Fulbe population history are very blunt tools for the kind of analysis needed. As more intensive sampling protocols reveal regional population structure, and more informative genetic markers are identified; however, the resolution of genetic studies will continue to increase, generating more detailed insights using mtDNA, NRY, and genome-wide autosomal data.

Archaeology and Fulbe History

Clear and unambiguous evidence for the Fulbe extends no further back than the historical documentation in the fourteenth century. Archaeological identification of the pastoral Fulbe is difficult due to their very low archaeological visibility (MacDonald 1999) (Fig. 11). Their material culture is notably ephemeral in the Sahel, with a predominance of organics such as animal skin, grasses, and calabash (Smith 2005). Based on ethnohistoric observations, we might conclude that the Fulbe would be primarily visible archaeologically as palimpsests of dung deposits from livestock pens, and ash and debris from fires for cooking and keeping insects at bay. With such limited evidence for material culture, and absent a unique Fulbe pottery industry (pastoral Fulbe purchase any pottery they may use from settled populations, *e.g.*, Gueye 1998, p. 116), it is not an easy proposition to use the direct historical method to trace the Fulbe backwards in time from the present. The only ethnoarchaeological study conducted on Fulbe occupation sites focused on settled groups in Cameroon (David 1971) and included a caveat that the observations could not be extrapolated to mobile Fulbe groups.

What we do not know is how far back in time the historic Fulbe pattern of high mobility and low archaeological visibility extends. It is possible that their specialized pastoralism, which depends crucially on the exchange of dairy products for grain and other subsistence and craft items, is a fairly recent phenomenon. Most theories of the origins of this type of symbiotic pastoralism involving herders and farmers who form a single economic unit see it as a later development out of mixed farming, enabled by the development of markets, complex social organization, and interregional contacts (Anfinset 2010, Ch. 5; Sadr 1991, pp. 5–11).

Based on the recently established archaeological sequence covering the period 2500–1000 BP in the Futa Tooro traditional homeland of the Fulbe, we propose that the ethnohistoric Fulbe pastoral system first developed out of an earlier agropastoral economy in the late first/early second millennium CE, when reliable agricultural surpluses first became available in the Middle Senegal Valley and there was a rapid

Fig. 11 Recently abandoned Fulbe pastoral camp near Djenné, Inland Niger Delta, Mali. The scale marker is 20 cm long, and it is placed in the interior area of what was a straw hut. Other than burnt areas where cooking fires were lit, there is little durable material evidence of the site's occupants

development of markets and political complexity. Focusing on the archaeology of northern Senegal/southern Mauritania provides our best opportunity to study the context and trajectory of the historical emergence of the Fulbe, we suggest, in view of Futa Tooro's key role in Fulbe history, genetic evidence for West African ancestry, and the classification of Fulfulde as a North Atlantic language closely related to Serer and Wolof. We provide an overview of available evidence for settlement and economy in the Middle Senegal Valley beginning with its initial occupation by agropastoralists ca. 2500 BP at a time of increasing aridity (Fig. 12) (McIntosh *et al.* 2012).

Agropastoralists from the north colonized the levees of the central MSV at this time. They occupied the site of Walalde from 2500 BP (800–400 cal BC) to 2200 BP (400–200 cal BC), creating a 5-ha mound with deposits up to 4.5 m deep. It represents fairly intensive occupation by people who consumed (and presumably herded) primarily cattle and some small livestock, occasionally hunted wild antelope and fished on a very limited basis (Deme 2003; Deme & McIntosh 2006). Domesticated millet (*Pennisetum glaucum*) dominated the macrobotanical remains (Murray & Deme *in press*). Dozens of small, terracotta horned figurines were found, many in apparent association with burials; these are interpreted as schematic representations of short-horned cattle (Fig. 13), signaling the kind of symbolic investment in cattle that we associate with pastoral societies such as the Fulbe. A small number of struck lithics in the earliest deposits, accompanied by iron tools, suggests that technology at the site was in transition from stone to iron. Abundant iron production debris (tuyeres, slag) was recovered from the upper deposits (400–200 cal BCE).

The precursors of and regional context for Walalde are poorly known. Agropastoralists with a millet and livestock-based economy inhabited sites on the *dhar* and *baten* (plateau and lake) landscape around Tichitt and Walata/Nema for over a thousand years until increasing aridity resulted in abandonment of the stone-built settlements on the *dhar* ca. 1000 BCE. Little is firmly established regarding the development of these societies or their subsistence economies during this period.

Fig. 12 Map of sites and regions mentioned in the text

Fig. 13 Horned terracottas from Walalde. The human head is also of great interest (from Deme & McIntosh 2006, p. 334)

Munson's (1971) pioneering efforts to develop a ceramic sequence based on excavated and ^{14}C -dated assemblages were not pursued and refined by subsequent researchers, with the exception of recent research around Dhar Nema (MacDonald *et al.* 2009). Most of the published information seems to be based on deflated surface collections and ^{14}C dates of uncertain association (Amblard-Pison 2006). However, one pattern of interest for our purposes can be highlighted from Munson's work. Between 2800 and 2100 BP, there was a major shift in the pottery assemblage. The earlier "classic" Tichitt assemblage dominated by simple round bottomed bowls was largely replaced by everted rim jars (Munson 1971; MacDonald *et al.* 2009). New decorative motifs appear that link the first millennium BCE Tichitt assemblages with the earliest agropastoral assemblage at Walalde, as well as with pastoral assemblages around Bouhdida on the Atlantic coast (Deme and McIntosh 2006; Vernet 2001). These distinctive motifs include long, or "running" comb [long, straight lines of crisp impressions that suggest a tool at least 5 cm long—perhaps a twine wrapped knife such as the *furgu* used today by the Tukolor (Gueye 1998)], zoned comb impression (zones delineated by incision and filled with straight or rocker-comb), guilloche cordons, and "lozenge" motifs consisting of an incised oval with incised or impressed fill) (Munson 1971; Amblard Pison 2006: pp. 184, 198, 205, 207; Vernet 1993) (Fig. 14).

Fig. 14 Shared, distinctive ceramic decorative styles and motifs from Walalde, the Nouakchott area (Imbich Est) and the Lake Rkiz area: “running comb” from Walalde (1a,b) and Lake Rkiz (1c); guilloche from Walalde (2a,b) and Imbich Est (2c,d); outpressed nubbins from Walalde (3a,b) and Imbich Est (3c); partial lozenge motif (Walalde 3d) (photos of sherds from Mauritania courtesy of R. Vernet)

The Bouhdida surface assemblage from Imbich Est has been described in some detail (Vernet 1993, 2001), permitting identification of its affinities with Walalde pottery. Dated ca. 2600–2200 BP, these sites were apparently occupied by cattle herders who also fished and used both stone and copper tools (Vernet 1993). The source for the abundant copper assemblage was Akjoujt, located <100 km away. Akjoujt copper was also documented at Walalde, where copper earrings had the arsenic-rich compositional signature of that copper source (Deme & McIntosh 2006). Based on the distribution of surface copper artifacts recovered in Mauritania, Deme & McIntosh (2006) suggest that copper moved with and among pastoralists who pastured herds seasonally in the interdunal depressions of southwest Mauritania; close affinities between Walalde and the Lake Rkiz area have also been noted (Deme & McIntosh 2006). Contact—likely indirect—between Bouhdida and Walalde and North Africa is indicated by copper earrings at both sites in a Punic style known from jewelry in Moroccan graves of the eighth to sixth centuries BC (cp. Deme & McIntosh 2006, p. 335; Jodin 1966, p. 71; Ponsich 1967, pp. 34, 91, 196; Vernet 1993, p. 347).

Increased interaction with the north may have involved gene flow. Munson and others suggest that the appearance of two-wheeled chariots and horses on the rock engravings in Mauritania probably signals the arrival of Berber language speakers at about this time. While we have no information on the physical anthropology of the makers of Bouhdida and Tichitt pottery in the mid-first millennium BCE, analysis of the one intact Walalde cranium indicates a definitively sub-Saharan morphology (Ribot 2011).

The arrival of agropastoralists in the MSV ca. 2500 BP correlates broadly with a decline in the number of archaeological sites in southern Mauritania (Bathily *et al.* 1998) and a period of fluctuating climate trending towards greater aridity. Walalde is the only MSV site currently documented from the first millennium BCE. A multi-season project of intensive survey and excavation at 11 sites in the same sector as Walalde has provided initial insights into the continuation and development of agropastoral societies during the first millennium CE (McIntosh *et al.* 2012). The focus of the project was a 460-km² area centered on the village of Cubalel in an interior floodplain known as the Ile à Morphil, within the broad area historically attributed to the early polity of Takrur. Within this study region, sites were distributed primarily on the 9–10-m-high levees that generally remain above the annual floodwaters. Sites can be categorized as mounds (0.5–5 m of accumulation) and flat surface scatters. Mounds occur only on the levees, and generally range in size from 1/2 to 4 ha. Only a handful of sites exceeded that, reaching 12 ha exceptionally. Excavations at both mounds and flat scatters revealed subsurface deposits from a series of occupation and abandonment episodes.

The mounds were built up of domestic debris associated with wattle and daub houses, and hundreds of burnt features, including hearths, ashpits, and burnt wall material. The frequent burning anchored and helped to consolidate the otherwise easily eroded sandy loam deposits. The mound with the most extensive accumulation—C3—provided a sequence that covered most of the first millennium CE, and the changes in material culture documented there were confirmed at the other Cubalel mound sites also occupied during the first millennium. All in all, 36 radiocarbon dates anchor the sequence at eight sites. The pottery assemblage changes rather rapidly through time, making it an excellent chronological tool.

The overall pattern of the archaeological evidence in the Cubalel region throughout the first millennium CE is consistent with semisedentary agropastoralists living for extended episodes on the high levees. Repeated construction and decay or burning of wattle and daub structures resulted in rapid mound accumulation, despite episodes of mound abandonment. The relation of flat sites to mounds needs a great deal more investigation, as surface collection and excavation focused almost exclusively on the latter. Test excavation at one of the flat sites revealed deposits extending down 0.85 m with numerous ash-pits and hearth-like burned features, dating to 600–800 CE. The pottery was no different in appearance or quantity from that found in contemporaneous mound site deposits.

Subsistence at all sites appears to be generalized, with primarily domestic animals and cereals, but significant hunting, fishing, and gathering of wild plants. Dog bones are frequently charred, suggesting consumption. The emphasis in the faunal assemblage shifts from cattle at Walalde in the first millennium BC to sheep and goat at Cubalel sites in the first millennium CE. The reasons for the shift may have to do with altered consumption practices and/or changed climate circumstances—but it is noteworthy that the dominance of ovicaprids continues despite the return of wetter conditions later in the first millennium CE. The cattle at all sites are in the middle size range recognized by MacDonald and MacDonald (2000, p. 131), comparable in size to modern Ndama breeds, although one very small specimen (West African dwarf shorthorn size category) was recorded from Walalde (C. Cain, in Deme 2003).

Flotation was systematically undertaken in every level and pit feature. Pearl millet is present at all sites as the primary domesticated cereal crop, accompanied by very low but consistent levels of fonio. Sorghum, cultivated in the clay basins of the floodplain as a flood recession crop historically in the MSV, is notably and surprisingly absent in all sites and levels prior to the end of the first millennium. It would appear that the floodplain basins were largely used for pastureland during this period. This finding has significant implications for agricultural productivity and the possibility of grain surpluses, which historically have come from the double cropping of millet and sorghum that is uniquely possible in the floodplain. Grain surpluses, in turn, are a crucial factor in specialized pastoral systems that are based on the exchange of milk products for grains and craft items.

Site size remained very small and site density low in the study region for the first seven centuries of the first millennium CE, suggesting that subsistence productivity was low. The near-exclusive reliance on millet would have involved a significant segment of the population in cultivation on the levees during the summer rainy season. At this same time, another segment (young men?) would have moved the livestock both to seek higher quality forage and to keep the cattle away from the fields. This type of system produces labor bottlenecks (for weeding and harvesting millet) that limit subsistence productivity (Swift 1979). A notable increase in site density and site size in the late first/early second millennium likely reflects the resolution of these labor constraints through increased specialization, which became absolutely essential when *décrué* cultivation of sorghum began. Full-time farmers in the floodplain could retain their traditional agropastoral identity by outsourcing herd transhumance to specialized pastoralists, as do the Tukulor. More options for longer seasonal transhumance may have become available with the emergence of political structures capable of assuring safe passage for herds. In this way, both the pastoral and agricultural sectors of the MSV economy could expand. The use of slaves (*jeyabbe*) in the agricultural sector was important for surplus production historically (Robinson 1971, p. 26), but we do not know how far back in time this goes.

This hypothetical outline posits that food-producing economies in northern Senegal shifted over the past 3,000 years from more generalized agropastoral subsistence economies that incorporated wild components where opportunities existed, to more specialized economies, including that of the pastoral Fulbe, in the past millennium. Alternatively, broad spectrum consumption patterns may reflect the operation of local subsistence exchange systems linking specialist herders with fishers, cultivators, or hunter/collector specialists (McIntosh 1993). Given the diverse dimensions of local subsistence systems, either is a possibility. Determining which model is a better fit for the development of subsistence systems in our focus area will require high-resolution, problem-oriented archaeological research that is grounded in more extensive excavation and survey within regionally focused projects. Special attention must be paid to the identification of specialized, highly mobile pastoralists archaeologically. Both Cribb (1991) and Sadr (1991) have developed strategies for this, utilizing intensive regional surveys to locate the various interacting mobile and sedentary components in the archaeological landscape, and carefully considering artifact densities and depth of deposits. An excellent starting point would be a systematic examination of the flat, more ephemeral surface sites in the MSV, and an extension of the area investigated to the area south of the floodplain, where

pastoral transhumance routes were located historically. Recovery of larger faunal samples through more extensive excavation should provide data on cattle diversity (assessed by the size categories present—MacDonald & MacDonald 2000) and herd structure (differential off-take patterns) at different sites.

Thus far, we have focused on the historical development of the distinctive, traditional Fulbe pastoral system within the geographical area of the northern Atlantic languages. However, another part of our inquiry concerns the distinctive genetic profile of the Fulbe. Therefore, the final section of this paper will consider ways to investigate the context and chronology of these elements, namely, the distinctive AAC clusters noted by Tishkoff *et al.* (2009; documented primarily for sampled Fulbe populations further to the east), the European lactase persistence allele and haplotype, and the low frequencies of mtDNA and NRY lineages of North African, Mediterranean, or Near Eastern origin. Lactase persistence is particularly interesting.

African pastoralist populations appear to have a variety of alleles that allow them to continue producing into adulthood the intestinal enzyme lactase that is responsible for the digestion of the milk sugar, lactose (Ingram *et al.* 2007; Tishkoff *et al.* 2007). For most of the world's population, lactase production declines after weaning, and they cannot digest milk without experiencing some degree of intestinal distress, unless the milk sugar has been broken down by bacteria through culturing or fermentation prior to consumption (Ingram *et al.* 2009). The lactase persistence trait makes the drinking of raw milk possible, and this is thought to have conferred a definite selective advantage for African pastoralists in hot, arid conditions where food and clean, uncontaminated water or other fluids are scarce (Ingram *et al.* 2009:588). Four SNPs located approximately 14,000 bases upstream of the lactase gene have been demonstrated to significantly affect the regulation of lactase production, suggesting a causative role in the mechanism of lactase persistence (Tishkoff *et al.* 2007). Two of these appear to have originated in East Africa, one in the Arabian peninsula where it is associated with camel pastoralism and the drinking of camel milk, and one in Europe (Enattah *et al.* 2008; Tishkoff *et al.* 2007; Fig. 15). The 13910*T allele is found at very high frequencies in Europe in a genomic region of reduced diversity and extended linkage disequilibrium (regions where recombination has not yet shuffled the area of DNA surrounding the allele), which suggests relatively recent, strong positive selection (Itan *et al.* 2010). It is also the predominant LP allele in the Fulbe populations tested (Mali—Lokki *et al.* 2011; Cameroon—Ingram *et al.* 2009; Fig. 16). How did this allele with an otherwise European/Eurasian distribution end up in Fulbe genomes?

One possibility is that it was acquired through relatively recent interactions ($\leq 2,000$ ya) with Berber and/or Arab populations, who also carry this allele. With additional genetic data from northern and northeastern African populations, especially Fulbe and neighboring populations from Mauritania and Senegal, we could use the patterns of variation in microsatellite markers (Coelho *et al.* 2005) and linkage disequilibrium in the region surrounding the 13910*T allele to test whether contemporary Berber and Arab populations have higher levels of microsatellite variation and smaller regions of linkage disequilibrium relative to the Fulbe. If they do, it would indicate that they have carried the 13910*T allele longer than the Fulbe have and could have been the source.

Fig. 15 Lactase gene variants. Lactase (LCT) and MCM6 are two genes located side by side on chromosome 2. The four SNPs that have been shown to impact the gene expression of LCT are located between the 12th and 13th exons (coding regions) of MCM6. These SNPs are labeled and the geographic regions where the persistence allele is thought to have arisen are listed. *Dashed lines* indicate larger distances between the SNP and exon locations within MCM6 (data reviewed in Ingram *et al.* 2009)

Alternatively, populations ancestral to the Fulbe could have acquired the –13910*T allele much earlier while in north central or northeast Africa (possible source areas for those “distinctive” AAC’s). Both of these areas are early centers of cattle pastoralism from at least 6000 BCE. In the Central Saharan massifs of the Tadrart Acacus, Tassili, Ennedi, Hoggar, and Aïr, rock art testifies to a flourishing pastoral era, first dominated by cattle and later dominated by ovicaprids. The recent identification of dairy fat residues in pottery from a Pastoralist Period rock shelter site in southwest Libya places the beginnings of milking at around 5000 BCE, since dairy fats were not detected in pottery from earlier hunting/gathering and Pastoralist phases at the site (Dunne *et al.* 2012).

With increasing aridity, groups of cattle herders are well documented between 4000 and 2500 cal BCE to the south and west, in the Teneré (Gifford-Gonzalez 2008), the Azawagh Valley of Niger (Paris 1996, 2000), and the Tilemsi Valley in Mali (Smith 1979; Manning 2011). Some or all were presumably using milk. Between 2500 and 2000 BCE, millet was domesticated, and agropastoral economies spread widely in the Sahel from 2000 cal BCE, although there is definite evidence for pastoral economies without millet continuing in some areas (Breunig & Neumann 2002). It appears that cattle-herders (with or without millet) arrived in the *dhar* region of Mauritania at about this time. Did they milk? And if so, what LP allele(s) did they carry?

The fact that all North Atlantic speakers (Fulbe, Wolof, and Serer) have high frequencies (50–100 %—Itan 2010) of lactase persistence (Fig. 17) suggests a considerable history of dairying in the region. Of these, only the Wolof have been genotyped for lactase persistence alleles, and, intriguingly, they carry none of the four alleles identified to date (Global Lactase Persistence Database: <http://www.ucl.ac.uk/>

Fig. 16 Frequency of the $-13910T$ lactase persistence allele in Africa and Eurasia (data reviewed in Ingram *et al.* 2009 and supplemented with data from Lokki *et al.* 2011)

[mace-lab/resources/glad](#)). This suggests that we still have much to discover about the history and convergent evolution of lactase persistence in Africa. This point is reinforced by the fact that the four known alleles do not explain the full extent to which lactase persistence is present in many African populations (*e.g.*, Tishkoff *et al.* 2007). Therefore, the identification and genotyping of these alleles in Western and Central Africa with corresponding microsatellite and linkage disequilibrium data would provide additional information regarding the spread of dairying peoples in general and past movements of populations ancestral to North Atlantic speakers in particular.

Fig. 17 Frequency of lactase persistence in Africa and Eurasia (data reviewed in Ingram *et al.* 2009)

However fine the resolution that may be achieved regarding modern genetic variation, direct evidence for past population variability and its geographic distribution remains a yawning gap. For the questions we are interested in—*e.g.*, the distributions and interactions of various North African, Eurasian and sub-Saharan populations at various points during the Holocene, the distribution of genetic variation with regard to different hunting/collecting/fishing and pastoral groups that lived in the Sahara during the Holocene—the study of ancient DNA offers a potential route to relevant data. Although human skeletal remains are abundant in the Sahara and Sahel, the unfortunate fact is that DNA is a fragile molecule that degrades in relation to temperature and other factors, with preservation predicted to be lowest in hot,

humid climates (Brown & Brown 2011; Ottoni 2008). Attempts to extract ancient DNA from cattle bones from two archaeological sites in the Sahelian zone of Senegal and Mali had a 25 % success rate (Edwards *et al.* 2004). Of over a dozen human remains analyzed from Libyan pastoralist sites, only one yielded mtDNA that could be characterized as to haplogroup (Babalini *et al.* 2002; Ottoni 2008). However, the apparent success in retrieving ancient DNA from 34 of 50 burials in a Roman cemetery in Dakhleh Oasis (Graver *et al.* 2001) and from a dozen 12,000-year-old skeletons from Taforalt cave in Morocco (Kefi *et al.* 2005) provides a reason for cautious hope. Unfortunately, the many human remains previously collected by Saharan and Sahelian expeditions are unlikely to be suitable candidates, as scrupulous collection and processing protocols must be followed to avoid contamination with modern DNA. Future research projects that recover human remains should do so under the conditions that would make testing for ancient DNA feasible.

As a final research methodology that is useful for investigating population differences that may signal the arrival of immigrant groups or the mixing of phenotypically distinctive groups, bioarchaeology must be mentioned. Human skeletal material has been one of the most underutilized sources of information about the West African past. Many archaeological sites in the Sahel and Sahara have burials that have been exposed by erosion or deflation. Hundreds have been excavated in the last three decades, but most have been studied only briefly to estimate sex and age at death (Dutour 1989 and Petit-Maire 1979 are notable exceptions). This overlooks the potential of this material for biodistance or biological affinity analysis with other populations. Measurements on the neurocranium and the facial skeleton have long been used to assess the degree of biological relatedness among living and past populations. While the human bones from West African sites are often too fragmentary for metric studies, teeth are usually better preserved, and the study of dental non-metric traits (Scott and Turner 1997) can provide evidence on population affinities and changes in the biological composition of groups due to migration (*e.g.*, Irish 1998, 2000, 2005). Development of a database of dental non-metrics for the many excavated remains from throughout West Africa and the Sahara should be a priority, a project that C. Stojanowski (personal communication) has already initiated. Teeth can often be analyzed for the incidence of caries and indicators of childhood stress and disease, such as enamel hypoplasias, even when bones are too degraded for identification of other hard tissue pathologies. Isotopic analysis of teeth is another powerful analytical tool. Particularly for studies of pastoralism, microsampling of growth increments of tooth enamel, and analysis of various isotopes such as strontium, lead, and oxygen can reveal seasonal mobility as well as migration (Balasse *et al.* 2002; Brown & Brown 2011, pp. 85–87; Smith 2012).

Conclusion

Genetic analysis and archaeology have partnered productively in investigating the early expansion of Austronesian speakers from Southeast Asia into Near Oceania and western Polynesia. Several factors have made it possible for archaeological and genetic studies to converge at comparable levels of chronological and temporal resolution. On the genetics side, these include:

- A steady increase over the past decade in numbers of Oceanic and Southeast Asian populations sampled for genetic analysis
- Increased use of genome-wide analysis accompanied by improvements in demographic modeling and computational methods to infer finer-grained population structure in Melanesian and Polynesian population samples
- Enhanced precision in dating the emergence of the “Polynesian motif” in Melanesia using whole mtDNA sequence data (Soares *et al.* 2011).

On the archaeological side, there is the requisite critical mass of local, regional, and extra-regional site documentation, including:

- Well-described and dated archaeological sequences on a wide variety of the islands of Near and Remote Oceania
- Precise dates for the Lapita horizon, identified at some 200 sites
- Documentation for pre-Lapita assemblages in Near Oceania and Island Southeast Asia and late and post-Lapita assemblages more widely (Spriggs 2011).

The outcome of this convergence is the recognition that the early Austronesian expansion did not emanate from a single source (Taiwan or Melanesia) and transmit a Neolithic “package” of new plants, animals, artifacts types, and technologies. The process was more complex, involving gene flow from multiple areas and local cultural patterns of hybridity and innovation (Spriggs 2011; Green 1991). Better sampling and improved methods in both archaeology and genetics have thus enabled the consideration of social process at the mesoscale level of the *conjecture*. Our Pacific case study demonstrates that the oft-lamented incommensurability of the temporal and spatial frameworks employed for archaeological and genetic data can be surmounted.

The research conditions that enable this desirable convergence are lacking in our West African example, however. Available genetic data are of limited utility because the North Atlantic language populations of greatest interest—Wolof, Serer, Tukolor, and Senegalese Fulbe—along with neighboring groups in southern Mauritania and eastern Senegal/Western Mali, are all among the most poorly sampled in West Africa. One sure path to higher resolution inferences on population structure is assembling “dense sample sets of known and detailed provenance” within a historically informed research program (Veeramah *et al.* 2010). Increased use of genome-wide genetic analysis is another. In addition, we have outlined a particular focus on studies of the lactase gene and microsatellites in its surrounding region as a possible method for inferring the antiquity of interactions of dairying groups and non-dairying groups in different areas. Historical linguistic analysis of Fulfulde and other North Atlantic languages might reveal loan words for herding and/or milking that help reconstruct interactions that introduced new cultural practices. To date, this has not been investigated (R. Blench, personal communication).

An even more pressing need is the establishment of a basic archaeological database for the regions mentioned above, comprising well-dated information from closed excavation contexts on material culture, subsistence economy, exotics, technology, and settlement layout. Currently, this is available for certain chronological periods since 2500 BP in only a handful of areas along the Senegal

River (Delta: Mbow 1997; Middle Valley: Bocoum 2000; Chavane 1985; Deme 2003; Deme & McIntosh 2006; McIntosh & Bocoum 2000; McIntosh *et al.* 2012; Upper Senegal: Gokee 2012; Thiaw 1999), and is rare to nonexistent elsewhere in Senegal and in much of southernmost Mauritania. Further afield, the larger picture of pastoralism's spread is still painted with very broad strokes for much of West Africa; we need many more projects designed to illuminate the chronology, local context, and development of economies with herding components (*e.g.*, Breunig and Neumann 2002; Garcea 2012; Gifford-Gonzalez 2008; MacDonald 1994; Manning 2008). In addition, incorporating a well-designed bioarchaeology focus into research projects will help clarify to what extent the spread of pastoralism involved the migration of pastoralists (demic expansion) or the adoption of livestock and herding practices by local hunting/collecting groups. In the case of the Fulbe, biometric data and dental non-metric data can be used to investigate affinities with archaeological populations and to study the emergence of a distinctive Fulbe morphology, providing a complementary dataset to that provided by genetic analysis. Using this kind of multidisciplinary approach, we can move beyond the macroscale interpretations that have largely characterized efforts to integrate African genetic, archaeological, and linguistic data to date and better focus on the economic and climatic factors, the regional and local interactions, and social dynamics implicated in culture change and ethnogenesis.

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