

AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 140:454–464 (2009)

A Multi-Perspective View of Genetic Variation in Cameroon

V. Coia,^{1,2} F. Brisighelli,^{3,4} F. Donati,¹ V. Pascali,³ I. Boschi,³ D. Luiselli,⁵ C. Battaggia,¹ C. Batini,^{1,6} L. Taglioli,⁷ F. Cruciani,⁸ G. Paoli,⁷ C. Capelli,⁹ G. Spedini,^{1,10} and G. Destro-Bisol^{1,10*}

¹Dipartimento di Biologia Animale e dell’Uomo, Sapienza Università di Roma, Roma 00185, Italia

²Dipartimento di Filosofia, Storia e Beni Culturali, Università di Trento, Trento 38100, Italia

³Istituto di Medicina Legale, Università Cattolica di Roma, Roma 00168, Italia

⁴Unidade de Xenética, Instituto de Medicina Legal, Universidad de Santiago de Compostela, Santiago 15782, Spain

⁵Dipartimento di Biologia Evoluzionistica Sperimentale, Università di Bologna, Bologna 40126, Italia

⁶Departament de Ciències Experimentals i de la Salut, University “Pompeu Fabra”, Barcelona 08002, Spain

⁷Dipartimento di Biologia, Università di Pisa, Pisa 56126, Italia

⁸Dipartimento di Genetica e Biologia Molecolare, Sapienza Università di Roma, Roma 00185, Italia

⁹Department of Zoology, University of Oxford, Oxford, OX1 3PS, UK

¹⁰Istituto Italiano di Antropologia, Roma 00185, Italia

KEY WORDS microsatellites; autosomes; Y-chromosome; mtDNA; language; geography

ABSTRACT In this study, we report the genetic variation of autosomal and Y-chromosomal microsatellites in a large Cameroon population dataset (a total of 11 populations) and jointly analyze novel and previous genetic data (mitochondrial DNA and protein coding loci) taking geographic and cultural factors into consideration. The complex pattern of genetic variation of Cameroon can in part be described by contrasting two geographic areas (corresponding to the northern and southern part of the country), which differ substantially in environmental, biological, and cultural aspects. Northern Cameroon populations show a greater within- and among-group diversity, a finding that reflects the complex migratory patterns and the linguistic heterogeneity of this area. A striking reduction of Y-chromosomal genetic diversity was observed in some populations of the northern part of the country (Podokwo

and Uldeme), a result that seems to be related to their demographic history rather than to sampling issues. By exploring patterns of genetic, geographic, and linguistic variation, we detect a preferential correlation between genetics and geography for mtDNA. This finding could reflect a female matrimonial mobility that is less constrained by linguistic factors than in males. Finally, we apply the island model to mitochondrial and Y-chromosomal data and obtain a female-to-male migration Nv ratio that was more than double in the northern part of the country. The combined effect of the propensity to inter populational admixture of females, favored by cultural contacts, and of genetic drift acting on Y-chromosomal diversity could account for the peculiar genetic pattern observed in northern Cameroon. Am J Phys Anthropol 140:454–464, 2009. ©2009 Wiley-Liss, Inc.

□ Language, culture, history and genes: the case of “Afro-Asiatic” speakers in Cameroon, a review of aspects of “A Multiperspective View of Genetic Variation in Cameroon”,

Am. J. Phys. Anthropol. 140: 454 - 464 (Coia, 2009)

Shomarka O. Y. KEITA and Christopher EHRET

The use of data from multiple disciplines is now not uncommon in what might be called “historical” genetic studies which address the peopling of a region. Such studies are generally understood to offer valuable insights, but also to potentially have some shortcomings. For example, they may include invalid assumptions about ethno-historical continuity, or demonstrate the uneven use or under-appreciation of current ideas, data, or debates from the various fields needed to contextualize genetic data, or the misapplication of terms (see MacEachern, 2000, 2001; Pluciennik 2001). For example, it would be incorrect to use the term Bantu as the designation of a Mendelian population, since there are many Bantu speaking populations, or metonymically for Niger-Congo speakers or a particular craniometric pattern. In terms of interpretation there may also be the temptation to link data from one field to that of another in a causal explanatory fashion which is not defensible, or to justify one discipline’s hypothesis with another’s data when correlations are found, thus engaging in circular reasoning and violating Boas’ dictum that there is no intrinsic relationship between biology, language and culture (Boas, 1940). Ontologically and analytically the origin of a language phylum or family must not be conflated or confused with the origin of the biological profile of its most numerous current speakers.

This addendum addresses aspects of the valuable presentation of the analysis of Y chromosomal STR genetic variation in northern Cameroon by Coia et al. (2009), with the above caveats in mind. Coia et al. (2009: 454, 455) include linguistic and archaeological information in their presentation. Specifically of interest is their comment on Afro-Asiatic (Afrasian/Afrasan/Lisramic/’Hamito-Semitic’) speakers and the implications of this claim. Citing David (1981) they state (2009:454):

“The northern region was first populated around 8000 BP by groups belonging to the *original* Afro-Asiatic or Hamito-Semitic linguistic stock from the Near East.” (our emphasis).

The suggestion that northern Cameroon was first settled by a primary migration of Near Easterners speaking ‘original’, in other words, undifferentiated Afro-Asiatic, is problematic, and a different view will be shared here. This paper examines this issue by reviewing David’s work (1981), criteria for assessing population migration, the evidence on Afro-Asiatic’s geographical origins, and issues related to interpreting associations between biology and culture.

Historical linguistics

David (1981:93) does suggest, based on the greatest diversity principle, that Afroasiatic has been spoken in northern Cameroon longer than any other phylum. However, his specific reference is to the Chadic family within the Afro-Asiatic phylum (see Newman 1980), and not ‘original’ (undifferentiated) Afro-Asiatic. David also states that, given the “northeast African centre” of the coordinate branches of Afro-Asiatic and the climatic record, it is unlikely “any form of proto-Chadic” would have arrived before 5000 BC, indicating that Coia *et al.* (2009) have over-read his suggested date and missed his implications as to the origin area or urheimat of the phylum. In summary, David’s view is that proto-Chadic speakers arrived from within Africa, not from the Near East, and no earlier than 5000 BC, which is notably later than 8000 BP (approximately 6900 BC, using a standard calibration program with a confidence interval of 100 years).

The movement of ‘populations’, no matter how defined, has been of interest to anthropologists, and scholars have brought different kinds of evidence to bear in seeking to identify and understand migration. Also primary movements have to be distinguished from secondary and later migrations. Rouse (1986) suggests that the hypothesis of a major migration in “prehistory” (we prefer “early history”) is best supported if there is convincing parallel (and independent) evidence from language, culture/archaeology, and biology. In such an approach the evidence must meet the criteria of the respective disciplines in order to avoid circular reasoning. The suggestion by Coia *et al.* (2009) for a direct migration of undifferentiated Afroasiatic speakers to Cameroon from the Near East can be explored using Rouse’s criteria.

While the geographical origin of proto-Afroasiatic is sometimes debated—historically perhaps largely for non-linguistic reasons, which include an over-focus on Semitic (Bender 1997; Blench, 2006), the interpretation of linguistic evidence by most researchers who study the entire phylum, using standard approaches, best supports an African origin (e.g.s. Greenberg, 1973; Bender, 1975, 1982, 1997, 2003; Ehret, 1984, 1995, 2008; Blench, 1993; Nichols, 1997; Hodge, 2004; Ehret *et al.*, 2004; Diakonoff, 1965, 1981, 1988). Preconceptions about the phenotype of the original speakers of the members of the phylum, or its branches, or presumed notions of their biogeographical origin were also considered in the discussion, influenced by raciotypological concepts of human variation (see e.g.s. Newman, 1980; Ruhlen, 1987; Keita and Kittles, 1997). In other words ideas about “race” figured into what was to be considered as “possible” for Afroasiatic origins. Evolutionary approaches to human variation and more nuanced appreciations of biology and culture are clarifying. Fundamentally it is linguistic concepts and principles that are most important in the determination of the locale of origin and internal classification of a language family.

The “greatest diversity” principle implies an African origin, since five out of six of the generally recognized Afro-Asiatic families are restricted to Africa, with Semitic being the lone outlier in southwest Asia (Greenberg, 1963; Nichols, 1997; Bender, 1997; Ehret, 1984, 1995, 2008; Hodge, 2004). If Ongota is included as a new branch of Afroasiatic (Fleming, 2006) the number rises to six out of seven. The “fewest moves” principle requires a region in the northeast quadrant of Africa as the likely place of origin, perhaps in Ethiopia (Bender, 1975), although Nichols (1997) suggests that this impression of the “center of gravity” of the phylum may be due to migration and accretion, and that the Sahara is a more likely place of origin. Skinner (1984), based on animal names, also proposes the Sahara. Ehret (2006a), in part also using wild animal names, places the earliest Afroasiatic lands more specifically in areas stretching from the Red Sea hills to the northern Horn of Africa, a region which includes a part of the range of the common donkey’s wild ancestors, which

is restricted to Africa (Beja-Pereira et al., 2004). Significantly, a term for this wild progenitor can be reconstructed in proto-Afroasiatic.

Arguments from the patterning of lexical, phonological, morphological innovation strongly indicate, moreover, that the deepest branching in the Afroasiatic family is Omotic, and that Omotic forms one primary linguistic lineage coordinate with a sister lineage of which all the rest of the Afroasiatic branches are sublineages (Fleming, 1974; Ehret, 1980, 1995; Ehret et al., 2004). Modern Omotic languages are geographically restricted to southern Ethiopia, but there is also evidence that they may once have been spoken in parts of northern Ethiopia (Ehret, 1976). Ongota, which may be a still deeper branch, is also restricted to Ethiopia (Fleming, 2006). There are alternative schemes of the sub-classification of the branches of Afroasiatic, i.e. of the internal relationships of its families (see e.g.s. Blench, 1993, 2006; Ehret, 1995; Bender, 1975, 1997; Diakonoff, 1965, 1988). Taken as a set of viable alternatives, these independently derived taxonomic hypotheses collectively even more strongly place Afroasiatic's origin in Africa.

Afroasiatic is an old phylum. Reconstruction of its vocabulary indicates that the proto-Afroasiatic (or proto-Afrasian) people were most probably grain collectors, not food producers (Ehret et al., 2004). The immense linguistic diversity within the phylum and even within many of its extant African families (Omotic, Cushitic, Chadic) as compared to Indo-European is consistent with dating the proto-Afroasiatic period to as early as 15,000 or more years ago (Ehret, 1979, 2006a, 2008; Hodge, 2004; Fleming, personal communication). Hunter-gatherer cultures of overlapping dates with subsistence strategies consistent with the lexical evidence for proto-Afroasiatic existed in both northeastern Africa and an Asian area continuous with Africa (see comments in Diakonoff, 1998, and Ehret, 1984), but again in this case the overall evidence supports an African origin.

The time of the migration would not yield 'original' Afrasian speakers. In the Near East proto-Semitic was spoken by agriculturalists in the millennium BC, living between the transition from the epipaleolithic to the Bronze Age (Diakonoff, 1981, 1998). Levantine migrants of this period would have brought a Semitic (or a related extinct family), not Chadic, and the Chadic branch cannot be "derived" from Semitic. None of the internal taxonomies of Afroasiatic suggest a primary relationship between Chadic and Semitic (see Ehret, 1995; Diakonoff, 1988; Blench, 1993; 2006; Bender, 2003). Chadic is apparently older than Semitic, which would also complicate a migrationist claim temporally; "in fact, Semitic may be the youngest...branch of Afrasian..." (Bender, 997: 28). A recent Bayesian phylogenetic analysis places the speakers of a well-defined Common Semitic (versus its Neolithic ancestor) in the Syria-Lebanon-Palestine region at approximately 5750 BP (Kitchen et al., 2009), whereas proto-Chadic or at least its immediate ancestor probably dates on the order of 1000 years earlier (Ehret, 2006b). However, Semitic has been postulated to have been the language of some early agriculturalists in the Levant (Diakonoff, 1988) making them older than the Bronze Age. A primary migration of Near Eastern food producing settler colonists to northern Cameroon at either of these dates would have in theory left a demographically successful Semitic-speaking community, unless it was totally bioculturally assimilated by subsequent events which would have left some linguistic evidence. Blench (1999, 2006), based on a restricted linguistic analysis, suggests the non-standard view that Chadic may be closer to Cushitic, and may have completed differentiation en route from east Africa via the Sahel corridor. Leaving aside linguistic evidence, at the biopopulation level such a migration is consistent with the mitochondrial DNA data (Cerny et al., 2004, 2007), but not with Y chromosome findings, since Cushitic speaking populations to date, have a notably higher frequency of E group lineages than tested Chadic speakers (see Somali data in Flores et al. 2005, and summary

data in Keita, 2008), but this may be due to insufficient data. In any case Boas' dictum still holds and we have to be able to consider complex pathways in history that defy simplistic interpretations.

Archaeology

Archaeological data also are not supportive of Near Eastern settlement of northern Cameroon of the stated date. The earliest well documented settlements date to the second millennium BC although there are some earlier finds (David, 1981; Breunig et al., 1996), and the material culture is not consistent with colonization from the Near East (see discussion in Breunig et al., 1996; MacEachern, 2009). While some scholars argue for a connection between the central branch of living Chadic speakers to the “Sao” civilization of the first millennium BC and AD in the Chad Basin, the evidence suggests that this culture and people are of endogenous origin, and adopted some items ultimately, but not directly, from the Near East (e.g.s. sheep and goat) via the Sahara. This is not a rare phenomenon. For example, local early to mid-Holocene Maghreb and Nile Valley populations adopted Near Eastern domesticates as a part of their pre-existing subsistence strategies thereby gradually transforming them (Wetterstrom, 1993; Rahmani, 2003, 2004). They also likely assimilated some migrants. Similarly, in the same broad era gourds, melons, and castor beans, and likely cattle, which were domesticated by Nilo-Saharan speaking peoples based on linguistic evidence, became a part of the Egyptian subsistence strategy (Ehret, 2001, 2006a). The evidence from archaeology and linguistics do not suggest demic diffusion/massive foreign settler colonization replacing the local people in either case.

Genetics/Historical genetics

While Coia et al. (2009) do not explicitly state that the Uldeme and other neighboring Chadic-speaking groups are the early ‘original’ Afro-Asiatic-speaking settlers from the Near East, or even their lineal descendants, their presentation seems to have this implication because these groups have the highest frequencies in Africa of the R1*M173 [R1b1*(xR1b1b2)] lineage which presumably came from Asia. However, notable frequencies are also found in speakers of other African language phyla (Cruciani et al., 2002). Their findings of low STR variability may have some bearing on the time of migration. Assuming that STR variability can reliably be used as an accurate “clock” (see Bosch et al., 1999) this might indicate a less ancient migration or incorporation of males with this lineage. The lack of accompanying “Asian” mtDNA lineages is deemed problematic in a normative view which postulates whole communities as migrants. Hypotheses of “asymmetric gene flow” or “divergent drift” have both been used to explain these observations (Coia et al., 2005), and there is no consistent evidence at this time that Chadic speaking ethnic groups came from the Near East.

There seem to be three major possible scenarios for the genetic profile based on a synthesis of the evidence. Given that R1*M173 is likely of southwest Asian origin and that a notably high frequency (40%) is found in a Jordanian population (Flores et al 2005), and assuming that this frequency has always been high, it is possible that groups of Arab pastoralists who appeared in the central Sahara fairly recently are responsible for this lineage. Holl (1994, 2003) notes the appearance of Shuwa Arabs in this area in the century, who fanned out from the Nile Delta into the Sahara and then Chad basin in a distribution that strongly matches the lineage’s pattern. However, the Banu Hilal came centuries earlier and entered

the Maghreb and Sahara (Hourani, 1990; Nebel, 2002). A subgroup of either of these peoples may have had a high frequency of the R1*M173. Social change related to a range of factors may have contributed to the refugia of the Mandara mountains and nearby regions with various peoples settling there (see e.g. see review of local history by MacEachern (2009). A variant on this theme of migration and assimilation is the hypothesis that Near Eastern male migrants settled in the Chadian region among different peoples in the first millennium BC, but had a major impact by bequeathing major persisting identifiable constructs from Near Eastern culture (Lange, 2007). However, while such a migration could possibly explain the Y chromosome findings, this particular diffusionist interpretation of central Saharo-Sudanic history has not won wide acceptance among historians and archaeologists. It is also difficult to envision such a migration having this kind of cultural impact without evidence for communities having large numbers of women.

Another possibility is that this lineage came to Africa in the mid-Holocene, brought by pastoralists, who were assimilated into the oasis cultures of the Sahara (see e.g.s. McDonald, 1998; Kuper and Kropelin, 2006). Collectively these “communities” can be postulated to have formed a cultural interaction zone and biological met a population (Keita, 2005). In this scenario some Near Easterners would have merged with African pastoralists and sedentists speaking languages from multiple phyla—a process which still occurs today. If the changes over time in the green Sahara can be thought of altering the dimensions of a metapopulation with subsequent migration then an uneven random “shuffling” process involving persons of varying origins can be hypothesized which would have variably distributed this lineage (and others) in circum-Saharan populations with the increased aridity of the desert (Hassan, 1988). Current frequencies would reflect drift and founder events.

A third scenario is that R1*M173 in Africa is due to the migration of paleolithic hunters and gatherers (Cruciani, 2002) in a “back-to-Africa” migration of modern humans without any likely known/knowable language affiliation, and thus were a part of general early human history. This would place them in Africa before the onset of a moister Sahara, with migrations and gene flow spreading the lineage into small populations before and after the clear differentiation of various linguistic phyla, further modified by later population interactions. Again the green Sahara would play a role.

It is probably significant that R1*M173 is not found in other Near Eastern samples in similar high frequencies; those from other populations are notably lower: Jordan population (7.9%), Iraq (11.3%), Lebanon (4.8%), Syria (9.9%), and Palestine (8.4%) (see Flores et al., 2005), which is what one might expect if this lineage emerged within an early ancestral or Common Semitic speaking population as a “private” marker, or was a part of the genetic background of the population in which Common Semitic crystallized. It is important to recall that preproto-Semitic would have had an ancestor in Africa, spoken by biogeographical Africans. Lineages can be lost. However, its frequencies are distributed somewhat evenly geographically in the Near East among different populations of various linguistic phyla (Altaic, Indo-European, Semitic branch of Afroasiatic) (Flores et al., 2005). There is no evidence that it alone (see e.g. Luis, et al. 2004), composed the male paleolithic base population of Saharan/supra-Saharan Africa and was later “diluted” by A, B and E haplogroups—rather the reverse seems to have happened. Its distribution—Arabian Peninsula, Egypt, Cameroon, does roughly parallel some known Arab migrations as noted. As has been mentioned it is not found in high frequency in a Somali sample [Cushitic speakers] (Flores et al., 2005) or in summary data of the Egyptian region, Berber and non-Somali Cushitic speakers (Keita, 2008). However, Luis et al. (2004) do report a notable frequency in one sample from northern Egypt, which is geographically closer to Jordan.

Conclusion

The notion that Afroasiatic-speaking populations in Africa are “Eurasian” immigrants who brought Afroasiatic and horticulture to Africa (see e.g. Diamond 2005), is reminiscent of Seligman’s “Hamitic hypothesis” (Seligman, 1930; Sanders, 1969), which has been discredited conceptually by linguists, historians and biological anthropologists (e.g.s Greenberg, 1955, 1966; Sanders, 1969; Hiernaux, 1975). While the border regions of Africa were subject to influence by known historical actors such as the Vandals, Phoenicians, Arabs, Greeks, Romans, and did absorb earlier migrants, there is no Y chromosome or fossil evidence to suggest that these regions were devoid of indigenous people (a potentially problematic notion in any case). Evolutionary approaches to variation and an appreciation of language shift have more explanatory power in understanding African biocultural variation. African populations and regions are notably genealogically interconnected via the E haplogroup of the Y chromosome (Cruciani, 2002; Keita, 2005, 2008). Lineages presumably brought by ancient movements back to Africa by modern humans in the Pleistocene have been reworked by the new environment of their receiving populations and together now reflect an African biological history. Such migrations cannot be compared to those since 2000 BC of known groups. It is important to note also that a small amount of steady migration/gene flow per generation with all offspring remaining in a region or cultural-linguistically defined population (and assimilating) can substantially change gene frequencies in 1000 to 2000 years (Cavalli-Sforza, 1991) in the receiving group. Such migration could theoretically lead in time to genetic “replacement” without a massive distinct settler colonization event or change in identity. This process is not to be confused with events like the settling of Madagascar or Finland, or the settler colonization of southern Africa by Europeans.

In summary, the Y chromosome analysis of Coia *et al.* (2009) provides an important refinement of the biological profile of northern Cameroon in showing the low STR diversity, whose implications for migration deserve more examination, perhaps simulations including various scenarios. The suggestion that “original” [undifferentiated] Afro-Asiatic speakers from the Near East settled the region around 8000 BP and by implication brought R1*M173 is not supported by evidence, or required by their analysis. Archaeology indicates permanent settlement in the Chadian region in the second millennium BC, not earlier, with a local origin for the Sao culture now sometimes identified with some Chadic speakers.

Acknowledgments

The authors have nothing to declare.

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□ The authors

Professor Christopher Ehret, Ph.D., is Professor Emeritus of History at UCLA. He was a pioneer in the use of historical linguistics in the construction of historical narratives in Africa, thus making contributions to African historiography. His publication record includes numerous books and articles on historical linguistics and African history. Professor Ehret has encouraged and utilized the perspectives of examining the history of a range of peoples breaking with some paradigms in western historiography. He has presented evidence for the interconnections of African peoples are varying time depths and eschews concept of "prehistory" which he regards as problematic. Professor B.A. Ogot of Kenya has praised his work for its innovation. Professor Ehret has presented numerous lectures on African history and historiography, most recently the Huggins lecture, Harvard University.

Dr. S.O. Keita M.D., D.Phil., is a biological anthropologist and physician and currently research associate of the department of anthropology, Smithsonian Institution, and affiliated with the Center for Research on Genomics and Global Health, NIH. He is formerly senior research associate in the National Human Genome Center at Howard University. His interests include the history of ideas about human variation in Africa and persistent colonialist thought, the conceptualization of infraspecific variation in general and Africa particularly, genetics and African historiography and aspects of the skeletal biology of ancient Nile Valley and northwestern Maghreban populations. He has published in various journals and given lectures in various museums in consultation with exhibits, most recently with the Boston Museum of Fine Arts.