Letter to the Editor

Am. J. Hum. Genet. 75:524–526, 2004

Reply to Bortolini et al.

To the Editor:

The availability of new mtDNA data from central Africa has allowed Bortolini et al. (2004 [in this issue]) to evaluate two alternative scenarios, formulated by Salas et al. (2004), regarding the source of the L3g mtDNAs carried from Africa to America by the Atlantic slave trade. Bortolini et al. proposed that the American L3g haplotypes have an Atlantic African provenance, rather than a direct eastern African origin, and that their most likely source was Cameroon or the neighboring regions.

On the basis of the extensive amount of new data that can be added to the L3g phylogeny (fig. 1), we are wholeheartedly in favor of this scenario. Of particular interest are three mtDNA sequences belonging to the L3g1 haplogroup that we observed in southwestern Africa (Angola and Cabinda), this region being the second most important source for the Atlantic slave trade (Thomas 1997), with an important demographic impact in Brazil. Overall, L3g1 appears to reflect the contribution of southwestern Africa—and probably central Africa also—to America (66% of the American L3g sequences), whereas the American L3g2 mtDNAs might be of predominantly central African origin. Because L3g3 is present in central and southwestern Africa, it might be expected that L3g3 sequences will also be found in future surveys of American populations of recent African descent. Thus, Brazilian types (which occur within L3g1 and L3g2) can be of either central or southwestern African origin.

We can now briefly reconstruct a plausible history of L3g (fig. 1). Both the phylogeography and the time depth (TMRCA, 61,800 years ago ± 17,700 years) of L3g clearly testify to its eastern African origin. Indeed, the root type (16223-16293T-16311-16355-16362-16399) is found in Sudan, Uganda, and Tanzania, and L3g displays the highest divergence in Tanzania, Uganda, Kenya, and Ethiopia (with a strong founder event distinguishing the click-language isolate of the Hadza) (fig. 1). Diversity on the Atlantic coast of Africa is, by contrast, restricted to a few mtDNAs at the tips of the network. This may have been the result of interactions established after contact between southerly dispersing western and eastern Bantu speakers who spread from the Cameroon region and the Great Lakes, respectively (Phillipson 1993). In the wake of this interaction, some L3g lineages may have been diffused towards the Atlantic west coast (Cameroon, Gabon, and Angola). The recent arrival of L3g on the Atlantic coast (during or subsequent to the initial Bantu dispersals) likely explains its low diversity in this region, in contrast with the high diversity in eastern Africa (e.g., a single L3g2 type accounts for most [~57%] of the central African L3g mtDNAs). Long-term networks established between central and southwestern Africa after the initial long, gradual, and intermittent western Bantu expansion (Vansina 1995) would have contributed to its subsequent diffusion. The Bantu expansion would also explain the distribution of other central African haplogroups (e.g., L1c) and the lack of strong genetic drift in southwestern Africa (which is detected in the southeast in some Bantu lineages [Salas et al. 2002]). More recently, these haplogroups would have been carried to America during the slave-trade period.

From this view, we can safely rule out the Atlantic coast of western Africa as an important source for American L3g, since this haplogroup has not been detected at present in a large sample (>1,200 mtDNAs) that includes individuals from, among other places, Cabo Verde, Senegal, Sierra Leone, and Nigeria. Some diffusion into northern Africa (Egypt, with signatures in Sudan and Nubia) as well as into the Middle East (Syria, Israel, and Palestine) has been detected, probably reflecting the haplogroup's greater antiquity in eastern Africa.

In conclusion, we can now extend the putative area of origin of the American L3g to the Atlantic fringe that runs from Cameroon to Angola and can probably rule out a direct eastern African origin. The latter surmise also agrees with historical documentation. Important regions, however, remain uncharacterized, such as the Congo basin and the Central African Republic.

Acknowledgments

We would like to thank Giovanni Destro-Bisol, Valentina Coia, and Gabriella Spedini (Laboratory of Molecular Anthropology, Department of Animal and Human Biology, Uni-

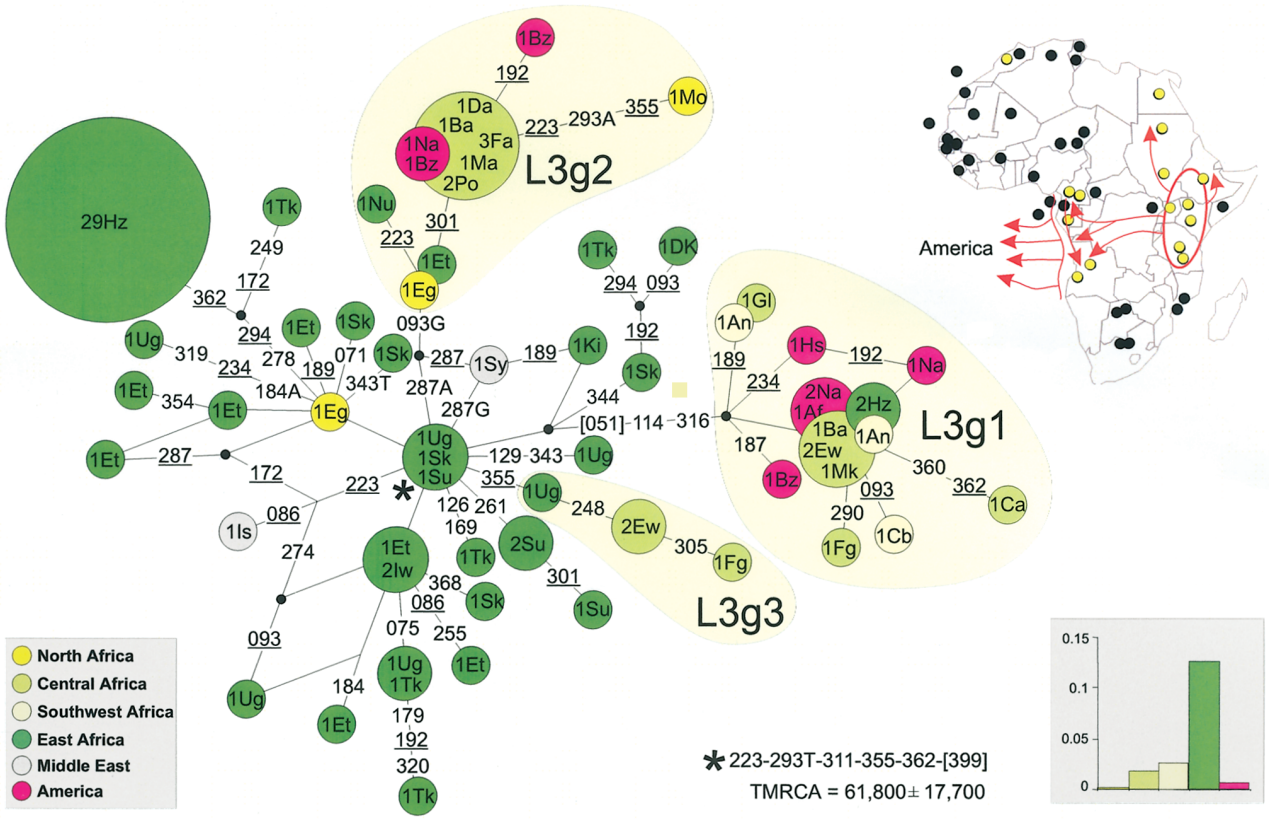

Figure 1 Median-joining network (Bandelt et al. 1999) of L3g mtDNAs. The circle sizes are proportional to the haplotype frequency in the sample. Positions are indicated as variants from the revised Cambridge reference sequence, minus 16,000; a letter next to the position indicates a transversion. Parallel mutations are underlined and diagnostic positions outside of the common mtDNA segment analyzed (from 16060 to 16362) are in brackets. We here define three sublineages of L3g: L3g1, characterized by 16051-16114-16189-16316; L3g2, characterized by 16093G-16287A; and L3g3, which lacks transition 16355 from the root. The histogram (*bottom right*) illustrates the frequency of L3g in different African regions and in America, and the map (*top right*) shows the diffusion pattern of L3g within Africa. A yellow dot indicates the presence of L3g in the population sample, whereas a black dot indicates its absence. Time estimates are computed as in Salas et al. 2002. Note that the Colombian mtDNA included in Bortolini et al.'s (2004 [in this issue]) network has been excluded from this phylogeny, whereas the Cameroonese data is included here. Eastern Africa: Tz = Tanzania, Hz = Hadza (Tanzania), Dk = Dakota (Tanzania), Sk = Sukuma (Tanzania), Iw = Iraqw (Tanzania), Ki = Kikuyu (Kenya), Tk = Turkana (Kenya), Ug = Uganda, Et = Ethiopia, Su = Sudan, Nu = Nubia (Sudan/Egypt). Northern Africa: Eg = Egypt, Mo = Berber (Morocco). Central Africa: Ew = Ewondo (Cameroon), Ba = Bakaka (Cameroon), Da = Daba (Cameroon), Fa = Falis (Cameroon), Ma = Mandara (Cameroon), Po = Podowkos (Cameroon), Ca = Cameroon, Fg = Fang (Gabon), Mk = Makina (Gabon), Gl = Galoa (Gabon). Southwestern Africa: Cb = Cabinda, An = Angola. America: Bz = Brazil, Hs = "Hispanic" (North America), Na = North America. Middle East: Sy = Syria, Is = Israel. TMRCA = time to the most common recent ancestor. Details of the L3g sequences will be supplied by the corresponding author on request.

versity of Rome "La Sapienza") and Sandra Beleza, Leonor Gusmão, and Antonio Amorim (Instituto de Patologia e Imunologia Molecular da Universidade do Porto, Portugal), for allowing us the use of their unpublished and valuable data.

ANTONIO SALAS,[1] ANTONIO TORRONI,[2] MARTIN RICHARDS,[3] LLUIS QUINTANA-MURCI,[4] CATHERINE HILL,[5] VINCENT MACAULAY,[6] AND ÁNGEL CARRACEDO[1]

[1]*Unidad de Genética, Instituto de Medicina Legal, Universidad de Santiago de Compostela, A Coruña, Galicia, Spain;* [2]*Dipartimento di Genetica e Microbiologia, Università di Pavia, Pavia, Italy;* [3]*School of Biology, University of Leeds, Leeds, United Kingdom;* [4]*Centre National de la Recherche Scientifique, Institut Pasteur, Paris;* [5]*Department of Chemical and Biological Sciences, University of*

Huddersfield, Huddersfield, United Kingdom; and [6]*Department of Statistics, University of Glasgow, Glasgow, United Kingdom*

References

Bandelt H-J, Forster P, Röhl A (1999) Median-joining networks for inferring intraspecific phylogenies. Mol Biol Evol 16:37–48

Bortolini MC, Da Silva WA Jr, Zago MA, Elion J, Krishnamoorthy R, Gonçalves VF, Pena SDJ (2004) The phylogeography of mitochondrial DNA haplogroup L3g in Africa and the Atlantic slave trade. Am J Hum Genet 75:523–524 (in this issue)

Phillipson DW (1993) African archaeology. Cambridge University Press, Cambridge

Salas A, Richards M, De la Fe T, Lareu M-V, Sobrino B, Sánchez-Diz P, Macaulay V, Carracedo Á (2002) The making of the African mtDNA landscape. Am J Hum Genet 71: 1082–1111

Salas A, Richards M, Lareu M-V, Scozzari R, Coppa A, Torroni A, Macaulay V, Carracedo Á (2004) The African diaspora: mitochondrial DNA and the Atlantic slave trade. Am J Hum Genet 74:454–465

Thomas H (1997) The slave trade: the history of the Atlantic slave trade, 1440–1870. Macmillan, London

Vansina J (1995) New linguistic evidence and the "Bantu expansion." J Afr Hist 36:173–195

Address for correspondence and reprints: Dr. Antonio Salas, Unidad de Genética Forense, Universidad de Santiago de Compostela, Galicia, Spain. E-mail: apimlase@usc.es

0002-9297/2004/7503-0022$15.00