Linguistic, cultural and genetic perspectives on human diversity in west-central Africa

A JOINT ESF EUROCORES PROJECT

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Acknowledgments

- ESF
- The organisers of the final OMLL conference
- All funding organisms (CNRS, MEC, DFG)
- All collaborators (Africa, Europe, ...)
- All individuals who accepted to be sampled

Outline

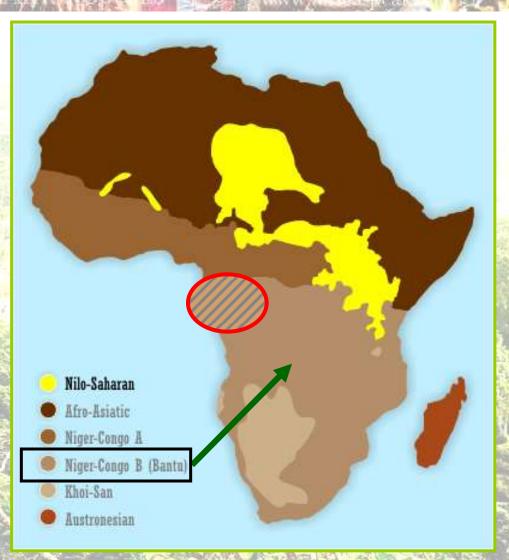
- Linguistic and cultural diversity
- Objectives of project
 Colke Van der Veen (Lyon)
- Results mtDNA variation analysis
 Lluis Quintana-Murci (Paris)
- Results Y-chromosome variation analysis
- Conclusions and ongoing work
 David Comas (Barcelona)

The Bantu languages

Language family comprising some 500 languages spread over most of sub-Saharan Africa

One of the many branches of the Niger-Congo phylum

Focus on the Northwest

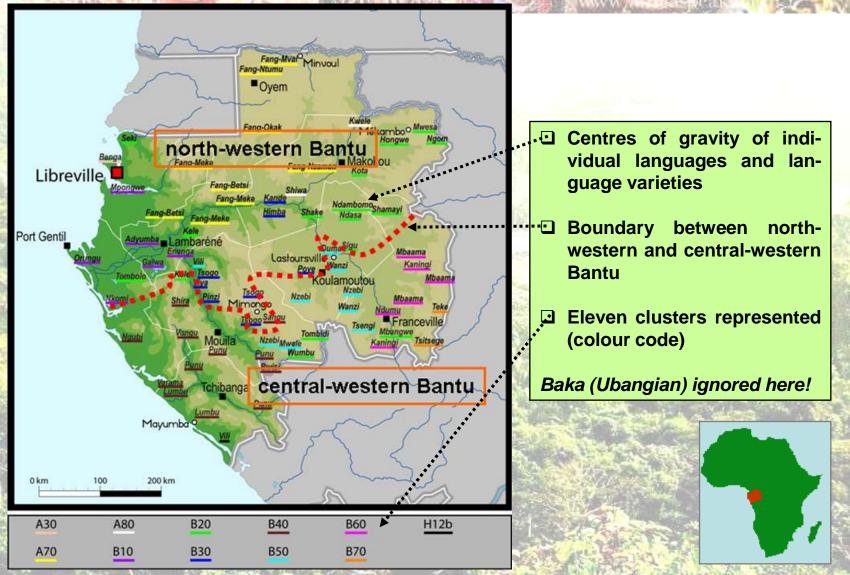


Linguistic and cultural diversity

PATTERNS

- Taking Gabon as a representative example:
 - High degree of linguistic and cultural diversity (at regional level)
 - Some 50⁺ ethno-linguistic communities
 - Varieties belonging to 11 higher-level linguistic clusters
 - Farming villagers vs. hunter-gathering (semi-)nomads
 - Hunter-gathering groups: all, except one (i.e. Baka), are Bantu-speaking communities
 - Major linguistic boundary: north-western vs. centralwestern Bantu
 - Cf. (i.a.) Bastin et al. 1999 ; Holden and Gray 2006
 - More or less widespread convergence phenomena due to cohabitation and contact

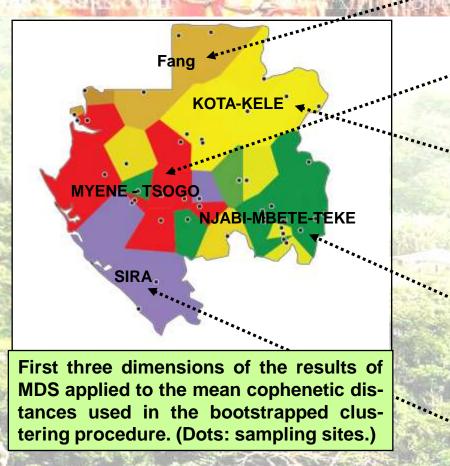
Linguistic diversity and major linguistic boundary



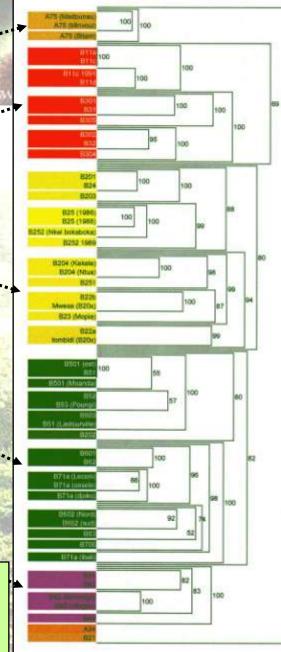
Linguistic and cultural diversity

- Ongoing fieldwork improves understanding of the often complex linguistic relations
- Recent advances in classification: Alewijnse et al. (2007)
 - Computational approach (J. Nerbonne, RUG, Netherlands)
 - ALGAB database (DDL, Lyon): 53 sampling sites, phonetic data points for 160 glosses
 - Overall, results corroborate previous views
 - Some innovative results
 - KOTA-KELE (B20) emerging as a unified group in spite of clear signs of admixture
 - Link between MYENE-TSOGO (B10-B30), but less solid as previously thought (due to convergence?)
 - Special position of Benga (A34) and Seki (B21)

Alewijnse et al. (2007)



Consensus dendrogram. Labels coloured as in map. Numbers associated with the groups indicate how reliably that group emerged, from a total of 100 runs.



Linguistic and cultural diversity

Cultural traits



- Overall, cultural traits and clusters of such traits reinforce the linguistic subdivisions, at different levels
 - Mating patterns (exogamy, endogamy)
 - Descent systems (patrilineal, matrilineal)
 - Artefacts (masks, reliquaries, etc.)
 - Traditional technological traits (ironwork, hunting, fishing, travelling by pirogue, weaving, sculpture, etc.)
 - Initiation rituals
 - Dances, songs and music (types, styles, etc.)
 - Taboos (food, sex, naming predators, etc.)
 - Toponymy (manners of naming places)
- The Ogooué river as some (relative) natural barrier

Gabon: masks as an example of cultural diversity



Linguistic and cultural diversity

Peopling of the area

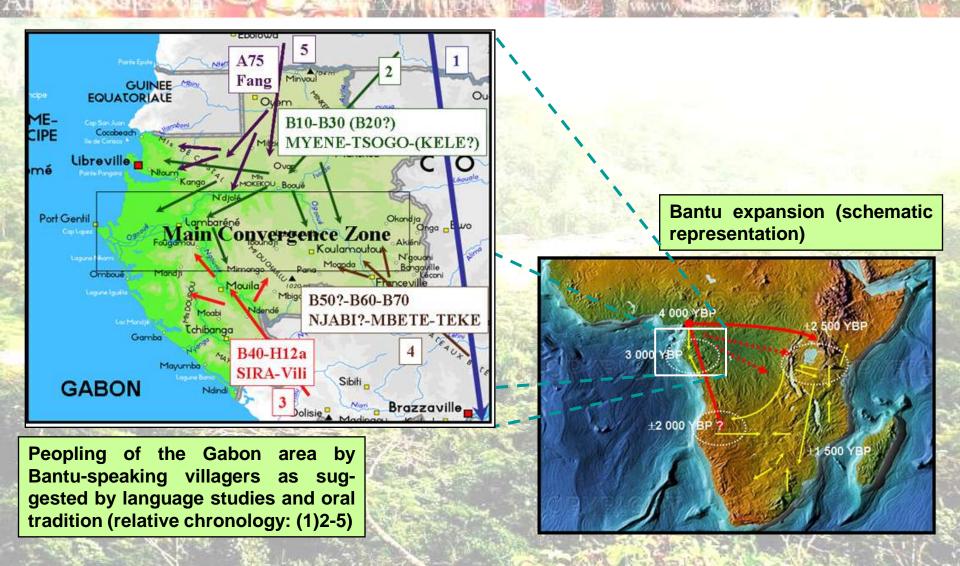


 Hypotheses based on extensive language studies and oral tradition, and (indirectly) on recent archaeological findings

Demic western Bantu expansion

- Three millennia of progressive peopling
- Small groups of hunter-gatherers already in situ!
- Bantu-speaking villagers practising some more or less developed form of agriculture
 - Successive waves
 - Relatively small groups
 - Different time depths
 - Cf. Recent arrival of Fang in the Estuary and centre (19-20th c. AD)
 - High rate of between-group interaction
- Some extent of interaction with the hunter-gathering communities

Peopling of Gabon area and western Bantu expansion



Objectives of the project

- Improve understanding of human diversity in westcentral Africa on basis of uniparental markers (*mtDNA and Y-chromosome variation*)
 - Test the hypothesis of a demic Bantu expansion
 - Look for possible correlations between languages and genes for Bantu-speaking populations (test case with a limited time depth (4000 YBP)!)
 - Determine, if possible, the pre-Bantu gene pool
 - Determine differences between agriculturalists (villagers) and hunter-gatherers (semi-nomads)
 - Impact of lifestyle!
 - Look for evidence of exchanges between populations
 - Look for possible sexual asymmetries in migratory patterns
 - Examine the odd 'Out-of-Egypt' hypothesis for the Bantuspeaking Fang population (Gabon, Cameroon)

Objectives of project

Rigorous sampling with well-defined criteria:

- Generally, 2 populations per major linguistic cluster
- 50 individuals per sampled population
- Sampling in the field with individuals' consent
- Both parents of subject belonging to same ethno-linguistic group
- As a rule, male subjects of 35 years and older
- Use of an ethno-linguistic questionnaire for detailed study of the affiliation through lineages (over 4 generations) and the relations between these lineages (*clans*) and the villages over time

Objectives of project





Populations and numbers of individuals sampled in Gabon Total: 960 samples from 21 populations (1 non Bantu-speaking pop.)

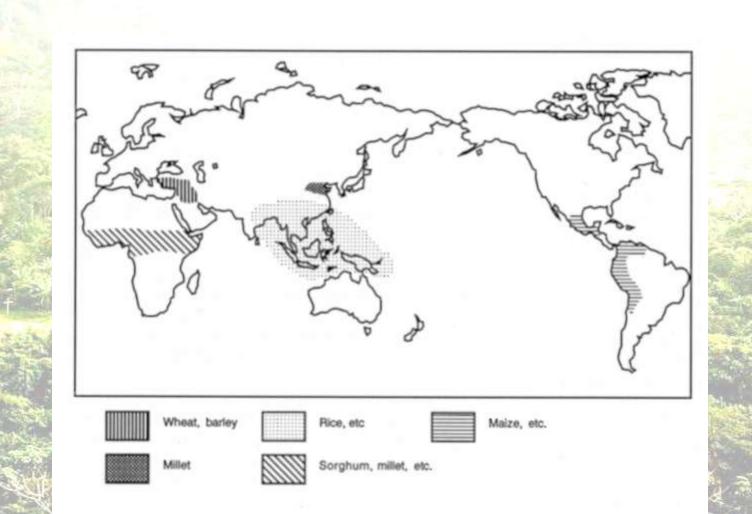
Objectives of project

- Additional samples (440) from previous and more recent projects taken into account (west-central Africa)
 E.g. project coordinated by E. Heyer and S. Bahuchet
- Total of some 1400 individuals
 - Some 980 agriculturalists (20 populations)
 - Some 420 hunter-gatherers (9 populations)
- Central Africa: at present, one of the best documented areas of Africa, from the genetic point of view!
 - Major progress since Salas et al. (2002): "very poorly represented"

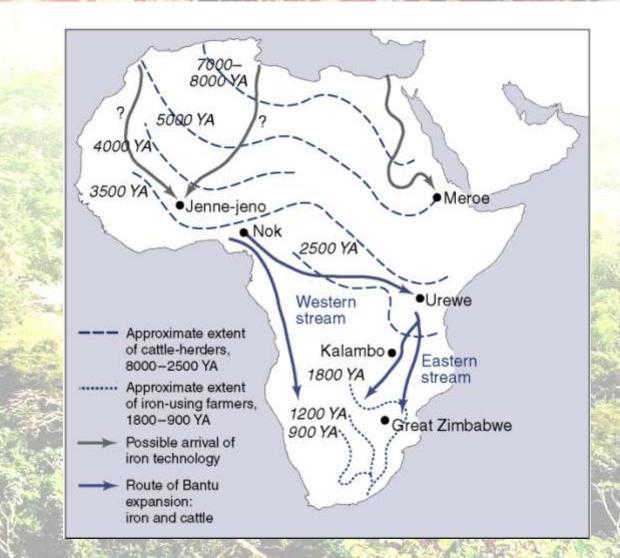
Maternal DNA variation of Bantu-speaking agriculturalists and Pygmy huntergatherers from central-west Africa

- Institut Pasteur, Paris: Helene Quach, Francesca Luca, Etienne Patin, Blandine Massonnet
- Institut de Sciences de l'Homme (Lyon): Lolke van der Veen, Jean-Marie Hombert, Patrick Mouguiama-Daouda
- Musée de l'Homme, Paris: Paul Verdu, Evelyne Heyer, Serge Bahuchet, Alain Froment
- Universitat Pompeu Fabra, Barcelona: Jaume Bertranpetit, David Comas
- Other collaborators: Doron Behar, Antonio Salas, Ken Kidd, Lucas Sica, etc
- Funding: CNRS, ESF, French Ministry of Research (Prosodie) ESF Eurocores, OMLL Final Conference, Rome, December 12-14 2007

The first major change in human history: Transition from hunter-gathering to agriculture



In Africa

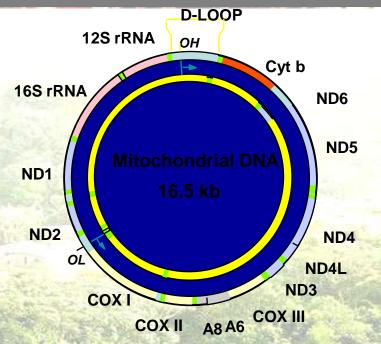


The transition from hunter-gathering to agriculturalism

- Increase of population densities:
 - More resources available
 - Higher reproductive capacities:
 - Longer lifespan
 - Earlier reproductive age
- Change in lifestyle: from nomadism to sedentarism
- Different relation with pathogens:
 - Higher densities: higher transmision
 - Sedentary lifestyle: higher contamination
 - Pastoralism: zoonosis

mtDNA genome



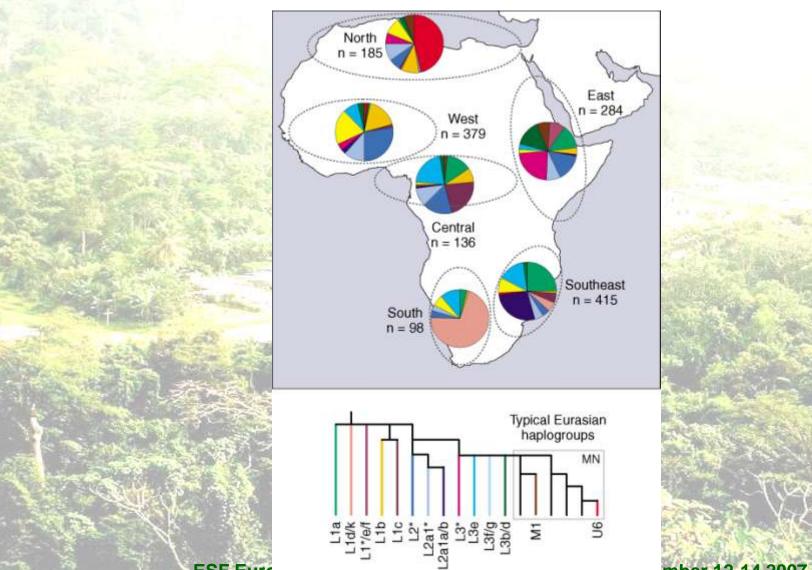


- 1981 Human mitochondrial genome was sequenced
- Strict maternal inheritance
- No recombination
- High mutation rate

Central African questions

- Get a mtDNA panorama of central African populations
- Better understand the maternal gene pool of population located near the initial Bantu-expansions
- Evaluate the genetic exchange between agriculturalists
 and hunter-gatherers
- Get insights into the gene pool of Pygmy populations: unique origin? Different origins? Common initial gene pool with agriculturalists?

mtDNA African landscape



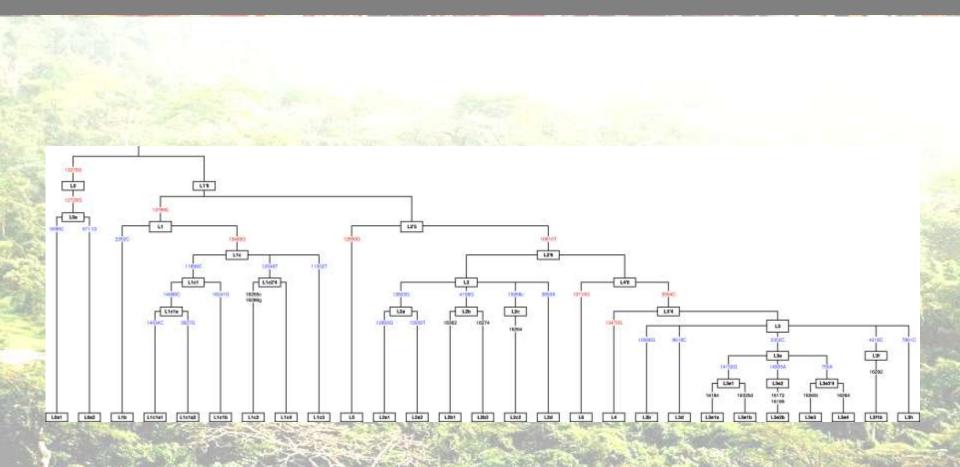
State of the collection: final samples sizes analyzed

POP CODE	POPULATION	COUNTRY	LIFES TYLE	Ν
BEN	BENGA	GABON	AGR	50
DUM	DUMA	GABON	AGR	47
EVI	EVIYA	GABON	AGR	38
EWD	EWONDO	CAMEROON	AGR	25
FAN-CM	FANG	CAMEROON	AGR	39
FAN-GB	FANG	GABON	AGR	66
GAL	GALOA	GABON	AGR	51
GIS	ESHIRA	GABON	AGR	40
KEL	AKELE	GABON	AGR	48
КОТ	КОТА	GABON	AGR	56
MAK	MAKINA	GABON	AGR	45
NDU	NDUMU	GABON	AGR	39
NGU	NGUMBA	CAMEROON	AGR	88
NZE	NZEBI	GABON	AGR	63
OBA	OBAMBA	GABON	AGR	47
ORU	ORUNGU	GABON	AGR	20
PUN	PUNU	GABON	AGR	52
SHA	SHAKE	GABON	AGR	51
TEK	ATEKE	GABON	AGR	54
TSO	MITSOGO	GABON	AGR	64
BAB	PYGMY-BABONGO	GABON	HG	45
BAK-CC	PYGMY-BAKA	CAMEROON-CENTRE	HG	30
BAK-CW	PYGMY-BAKA	CAMEROON-WEST	HG	58
BAK-GB	PYGMY-BAKA	GABON	HG	39
BAKO	PYGMY-BAKOLA	CAMEROON	HG	88
BEZ	PYGMY-TIKAR	CAMEROON	HG	35
BIA	PYGMY-BIAKA	C.A.R.	HG	56
BKY	PYGMY-BAKOYA	GABON	HG	31
MBU	PYGMY-MBUTI	D.R.C.	HG	39

-a total of 1404 individuals
-20 Bantu-speaking
agriculturalists populations
(983 individuals)
-9 Pygmy hunter-gatherer
populations (421 individuals)



Genotyping strategy based on complete mtDNA sequences



Our analyses

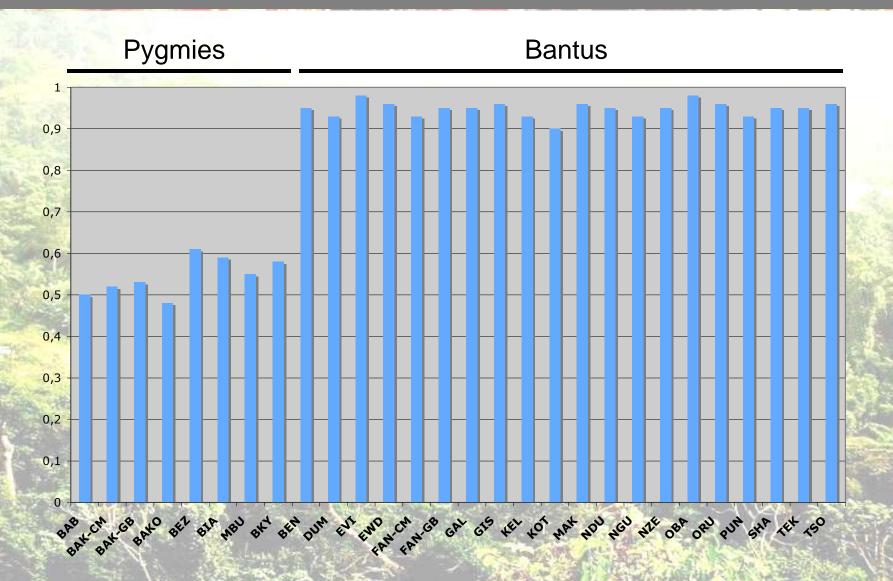
Coding-regions SNPs:

33 coding-region SNP analyses taking into consideration previous phylogenies AND complete mtDNA sequence data phylogenies: coding-regions SNPs provide information about the main lineages in the mtDNA tree

Sequence of HVS-I region:

the hyper-variable region can provide information about the timedepth of the different mtDNA lineages

Population diversity



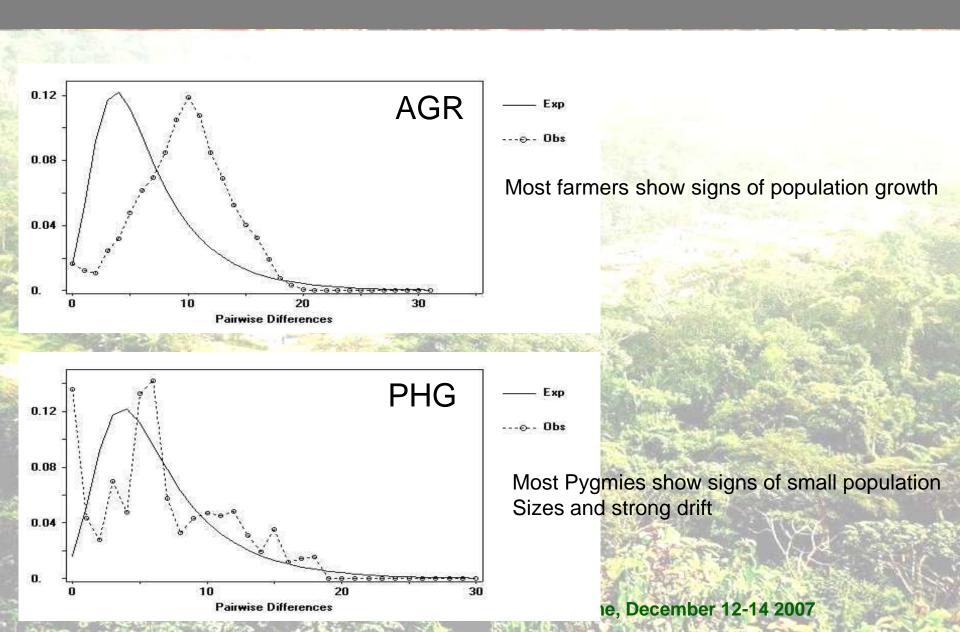
Population diversity and demographic regimes

Table 1. General diversity indices and neutrality tests for the different agriculturalist and hunter-gatherer populations here studied.

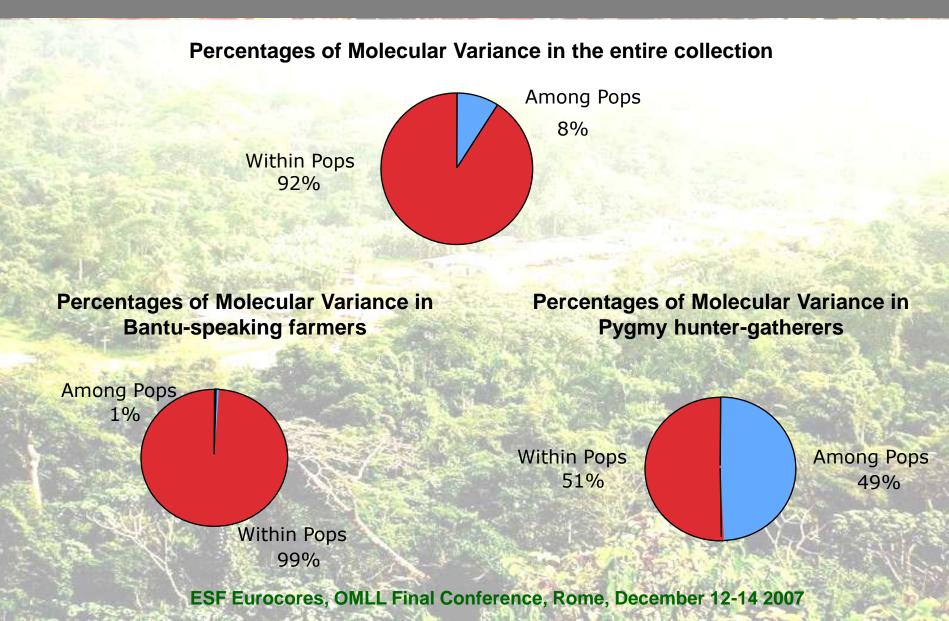
Population	Location	n *	Hg D (SE)	Ht D (SE)ª	Pi (SE) [≞]	Tajima's <i>D</i> (<i>P</i>) ⁱ	Fu's <i>F</i> s (<i>P</i>) [:]
Bantu-speaking						,	
agriculturalists							
Akele	Gabon-West	48	.925 (.022)	.985 (.008)	9.811 (4.571)	-0.70 (.262)	-16,76
Ateke	Gabon-Southeast	54	.945 (.012)	.985 (.007)	9.088 (4.248)	-0.76 (.231)	-21,96
Benga	Gabon-Northwest	50	.931 (.016)	.952 (.015)	9.922 (4.616)	-0.67 (.307)	-4.53 (.101)
Duma	Gabon-East	47	.925 (.016)	.973 (.010)	9.258 (4.332)	-0.92 (.193)	-9,09
Eshira	Gabon-West	40	.939 (.016)	.971 (.012)	10.077 (4.703)	-0.68 (.293)	-5.84 (.060)
Eviya	Gabon-Centre	38	.898 (.023)	.932 (.018)	9.135 (4.297)	-0.52 (.299)	-0.08 (.539)
Ewondo	Cameroon-West	25	.900 (.023)	.933 (.023)	9.933 (4.702)	0.05 (.571)	0.95 (.692)
Fang-CM	Cameroon-South	39	.880 (.028)	.970 (.014)	9.333 (4.381)	-0.44 (.402)	-9,46
Fang-GB	Gabon-North	66	.930 (.012)	.971 (.009)	8.849 (4.132)	-0.78 (.235)	-12,99
Galoa	Gabon-West	51	.925 (.019)	.965 (.011)	9.002 (4.214)	-0.96 (.172)	-6.13 (.047)
Kota	Gabon-East	56	.900 (.023)	.967 (.010)	10.562 (4.885)	-0.61 (.283)	-8.28 (.021)
Makina	Gabon-Centre	45	.928 (.017)	.962 (.016)	9.306 (4.356)	-0.71 (.269)	-7.28 (.027)
Mitsogo	Gabon-Centre	64	.898 (.025)	.961 (.011)	9.058 (4.224)	-0.84 (.219)	-9.50
Ndumu	Gabon-Southeast	39	.953 (.013)	.973 (.013)	9.417 (4.418)	-0.92 (.178)	-8,01
Ngumba	Cameroon-West	88	.932 (.010)	.969 (.007)	10.090 (4.655)	-0.35 (.435)	-14.10
Nzebi	Gabon-Southeast	63	.949 (.010)	.976 (.010)	8.955 (4.181)	-1.16 (.110)	-22,92
Obamba	Gabon-Southeast	47	.942 (.016)	.988 (.007)	9.741 (4.542)	-1.13 (.108)	-17,49
Orungu	Gabon-West	20	.905 (.041)	.974 (.025)	10.895 (5.173)	-0.13 (.508)	-3.53 (.090)
Punu	Gabon-Southwest	52	.946 (.014)	.982 (.007)	9.124 (4.266)	-1.24 (.096)	-15,94
Shake	Gabon-East	51	.899 (.022)	.973 (.011)	10.195 (4.733)	-0.68 (.275)	-13,01
Eastern Pygmy	the state of the state of the	13.00	1 1.1.1	and all a	Contract (2 Contractor	
Mbuti	D.R.C	39	.710 (.041)	.823 (.034)	6.877 (3.307)	1.05 (.886)	2.69 (.851)
Western Pygmy	R S			St. State	Contraction of the second		ALC: NO POINT
Babongo	Gabon-Southeast	45	.721 (.052)	.749 (.058)	6.945 (3.327)	-0.27 (.493)	1.75 (.799)
Baka-CC	Cameroon-Centre	30	.540 (.080)	.830 (.035)	5.425 (2.688)	0.26 (.655)	3.34 (.899)
Baka-CW	Cameroon-Southwest	58	.654 (.040)	.786 (.037)	5.667 (2.757)	-0.75 (.256)	1.52 (.766)
Baka-GB	Gabon-Northeast	39	.533 (.034)	.757 (.052)	4.124 (2.098)	0.08 (.569)	2.76 (.886)
Bakola	Cameroon-West	88	.455 (.033)	.722 (.024)	3.509 (1.805)	2.01 (.971)	5.05 (.942)
Bakoya	Gabon-Northeast	31	.333 (.096)	.548 (.087)	3.011 (1.614)	-0.99 (.190)	4.26 (.954)
Biaka	C.A.R	56	.724 (.030)	.823 (.030)	6.006 (2.906)	0.05 (.632)	2.42 (.857)
Tikar	Cameroon-North	35	.464 (.054)	.703 (.027)	2.911 (1.565)	1.46 (.923)	4.38 (.955)
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* Sample size; Gene diversity based on haplogroup profiles (Hg D) and standard error (SE); ^aGene diversity based on HVS -I sequence-based haplotypes (Ht D); ^bAverage number of pairwise differences (Pi); ^bAll *P* values are < .05 (for Tajim aÕs*D*) and <.02 (for FuÕ *F*_S), except where noted.

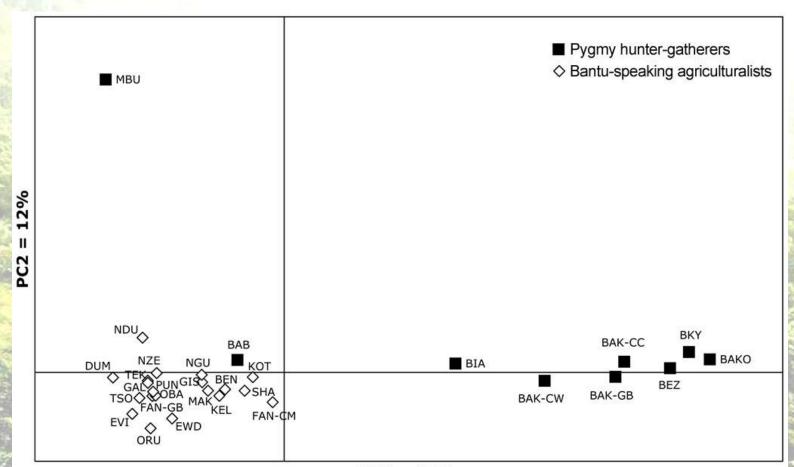
Mismatch HVS-I distributions



Analysis of MOlecular Variance (AMOVA)



Population relationships: entire collection



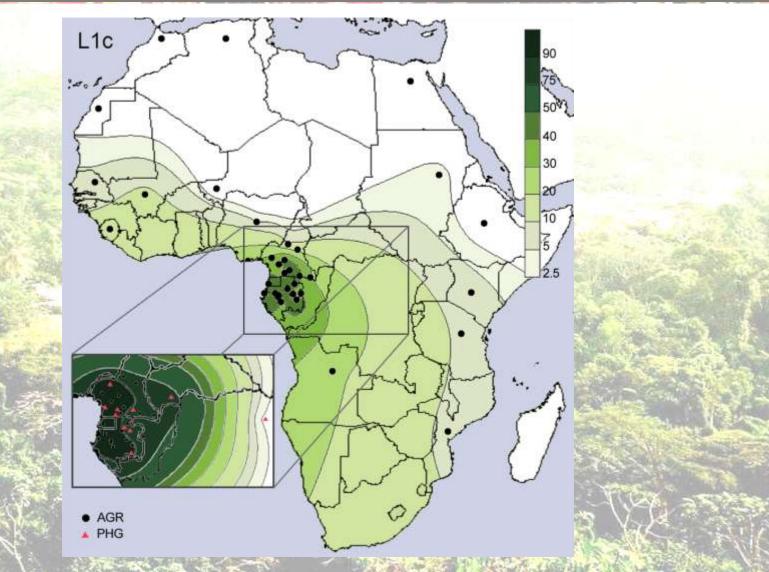
PC1 = 67%

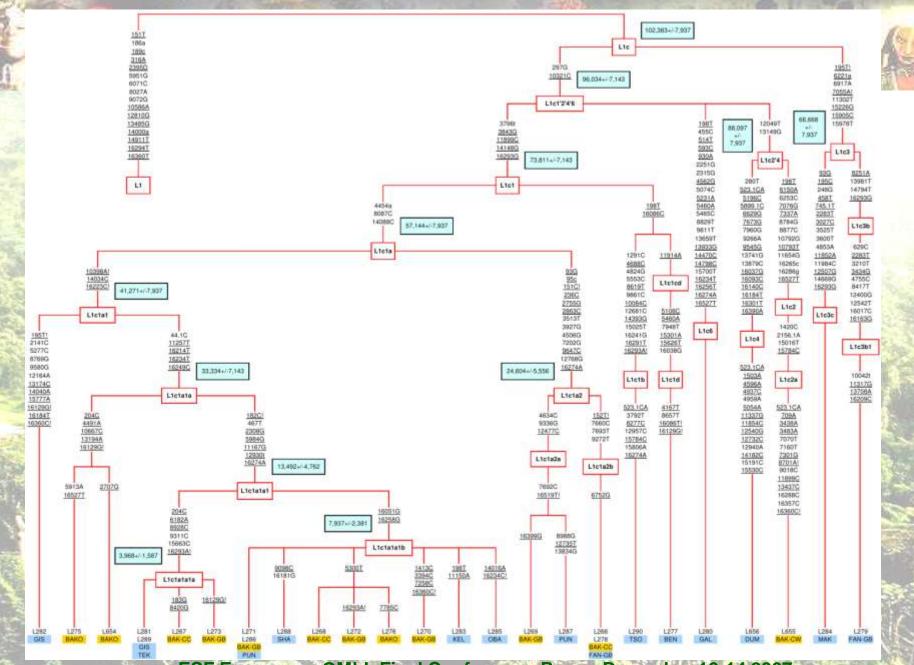
Hg profiles

	2	AGR		tern PHG	Eastern PHG	
Haplogroup	N	%	Ν	%	N	%
L0a1	64	6.5%	3	0.8%	0	0.0%
L0a2	26	2.6%	7	1.8%	10	25.6%
L1b	63	6.4%	0	0.0%	0	0.0%
L1c*	5	0.5%	0	0.0%	0	0.0%
L1c1	14	1.4%	1	0.3%	0	0.0%
L1c1a1	113	11.5%	204	53.4%	0	0.0%
L1c1a2	87	8.9%	115	30.1%	0	0.0%
L1c1b	27	2.7%	21	5.5%	0	0.0%
L1c2	28	2.8%	5	1.3%	0	0.0%
L1c3	44	4.5%	0	0.0%	0	0.0%
L1c4	33	3.4%	13	3.4%	0	0.0%
L2*	3	0.3%	2	0.5%	0	0.0%
L2a*	1	0.1%	0	0.0%	8	20.5%
L2a1	131	13.3%	0	0.0%	0	0.0%
L2a2	4	0.4%	0	0.0%	17	43.6%
L2b1	13	1.3%	0	0.0%	0	0.0%
L2b2	2	0.2%	0	0.0%	0	0.0%
L2c2	16	1.6%	0	0.0%	0	0.0%
L2d	12	1.2%	1	0.3%	0	0.0%
L3*	8	0.8%	0	0.0%	0	0.0%
L3b	30	3.1%	0	0.0%	0	0.0%
L3d	38	3.9%	2	0.5%	0	0.0%
L3e1*	23	2.3%	2	0.5%	0	0.0%
L3e1a	28	2.8%	0	0.0%	0	0.0%
L3e1b	5	0.5%	0	0.0%	0	0.0%
L3e2*	17	1.7%	0	0.0%	0	0.0%
L3e2b	40	4.1%	0	0.0%	0	0.0%
L3e3	29	3.0%	0	0.0%	0	0.0%
L3e4	7	0.7%	0	0.0%	0	0.0%
L3f1b	56	5.7%	6	1.6%	0	0.0%
L3h	8	0.8%	0	0.0%	0	0.0%
L4	8	0.8%	0	0.0%	0	0.0%
L5	0	0.0%	0	0.0%	4	10.3%

L1 clades accounts for by 37% of agriculturalists and 95% of western Pygmies

A likely central African origin of L1c





A central African origin of L1c1a

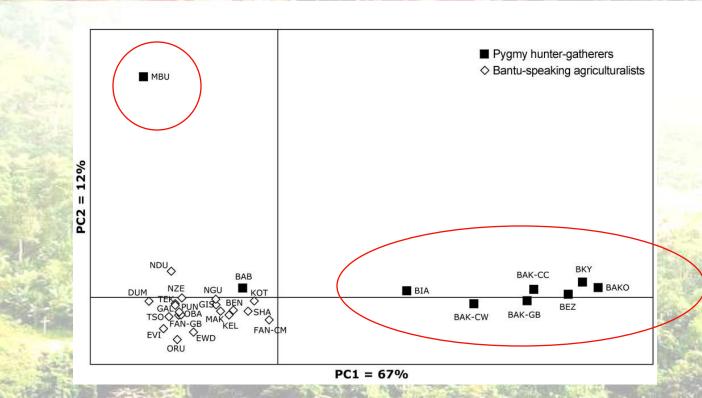
- SNP typing of the whole collection for the internal SNPs within L1c
- L1c1a is present in 20.3% of AGR populations and 83.5% in PHG populations
- L1c1a is restricted to central Africa, presenting a coalescent time of ~57,100 YBP
- Our analyses show a central African origin of this lineage, suggesting that the ancestral population giving rise to both proto-farmers and Pygmies was mainly composed of this lineage
 ESF Eurocores, OMLL Final Conference, Rome, December 12-14 2007

- The maternal gene pool of AGR is homogeneous (PC plot, AMOVA and 60% of FST are not significant)

- L1c1a (20.3%), L2a1 (13.3%), L0a1 (6.5%), L1b (6.4%), L3e2 (5.8%), L3e1 (5.7%) and L3f1b (5.7%)

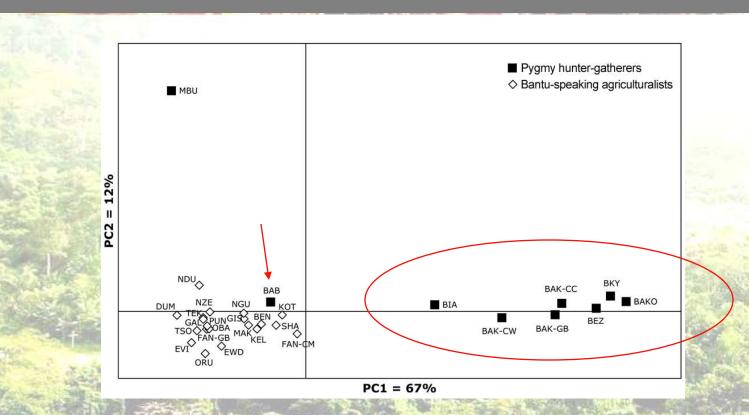
- The coalescence time of L1c1a (57,000 YBP) is 25,000 years older than the remaining Hgs, suggesting and initial central African gene pool dominated by L1c and later enriched by the arrival/or expansion of the carriers of other Hgs.

The maternal gene pool of Pygmy hunter-gatherers



-All Fst are significant involving Mbuti -Phylogeographically, no hgs shared, completely different genetic background -Clear lack of common maternal ancestry -Real lack of common ancestry? Convergence?

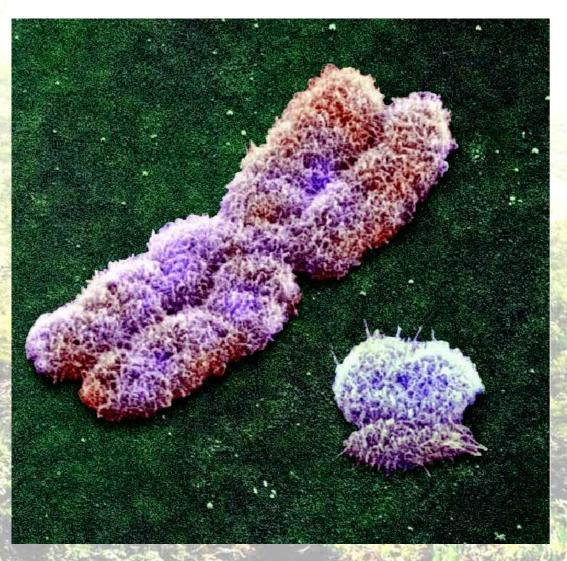
Western Pygmies

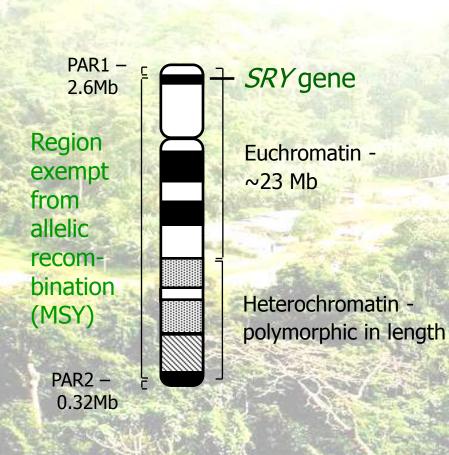


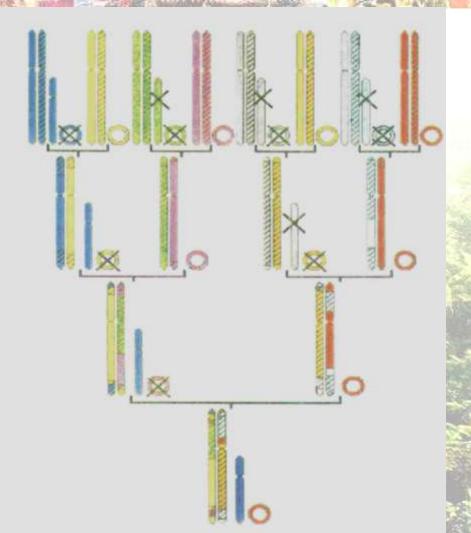
More heterogeneous (12% of inter-pop) than the group of agriculturalists
Babongo? Gene flow? Inter-cultural marriages are more common
~83.5% of contemporary western PHG share a single maternal ancestor in the form of the autochthonous Central African Hg L1c1a (in the form of the two sister clades L1c1a1 and L1c1a2).

Conclusions

- initial divergence of the ancestors of contemporary Pygmies from an ancestral Central African population starting not earlier than ~70,000 years ago (their last common ancestor)
- a period of isolation between the two groups needed to explain their phenotypic differences
- long-standing and asymmetrical maternal gene flow from Pygmies to agriculturalists, starting not earlier than ~40,000 years ago (the time when the two shared lineages appeared) and persisting until the last few thousands of years (sharing of recently appeared lineages between the two groups)
- enrichment of the proto-agriculturalist maternal gene pool by the arrival and/or posterior demographic expansion of L0a, L2 and L3 carriers.





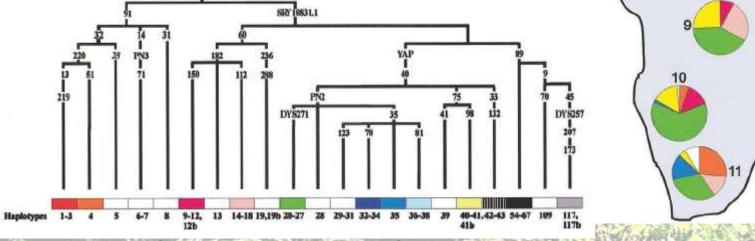


Specific lineages in Pygmy

Eurasian lineage in Northern Cameroon: back migration from Asia ?

Northern Cameroon

Southern Cameroon



Modified from Cruciani et al. 2002

Eastern Pygmies



Central/West African collection:

~900 samples from Gabon and Cameroon

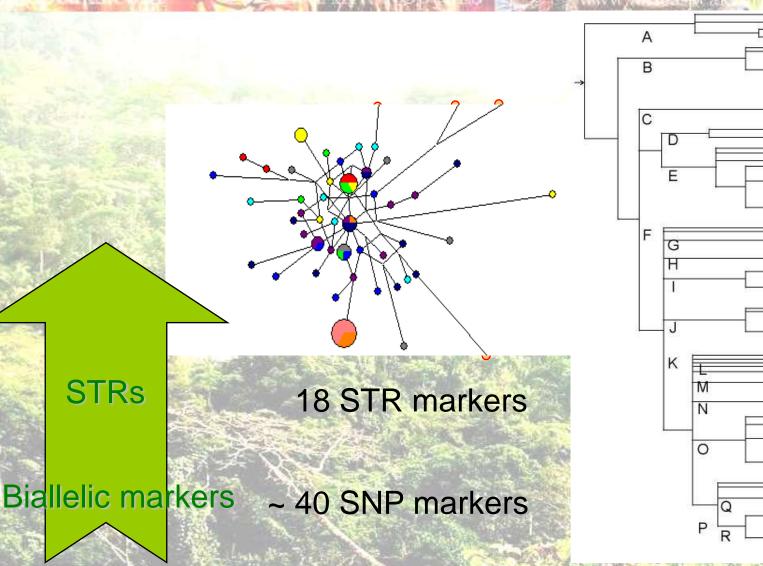
- 3 Pygmy samples
- 20 Bantu-speaking agriculturalists

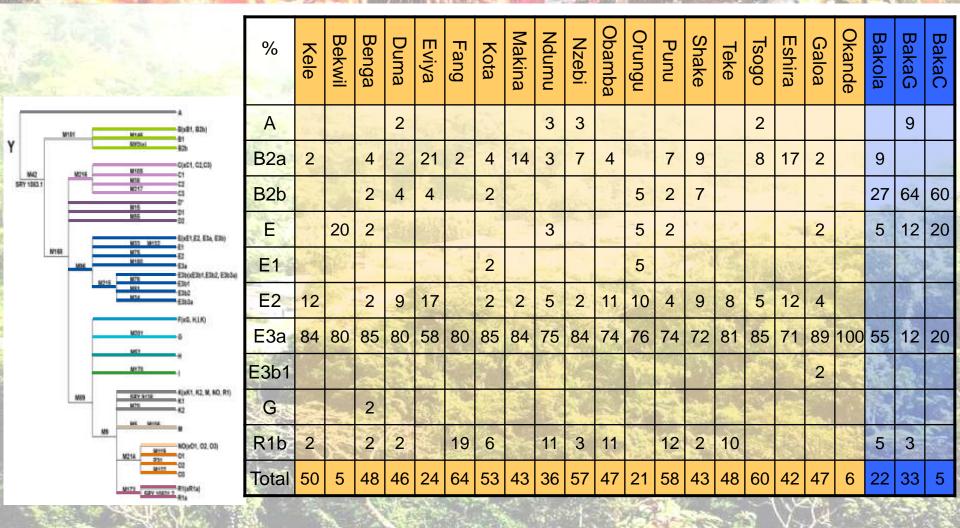
- 20 Bantu-speaking agriculturalists pops:

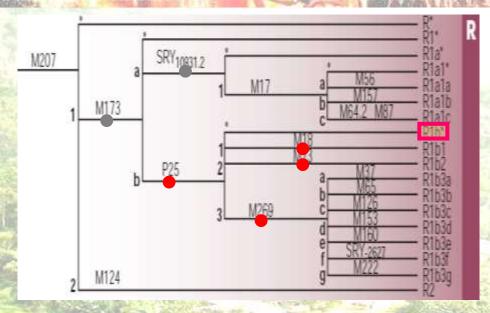
Gabon: Benga, Duma, Eviya, Fang, Galoa, Eshira, Kele, Kota, Makina, Ndumu, Nzebi, Obamba, Orungu, Punu, Shake, Teke, Tsogo, Bekwil, Ngumba, Okande

- 3 Pygmy populations:

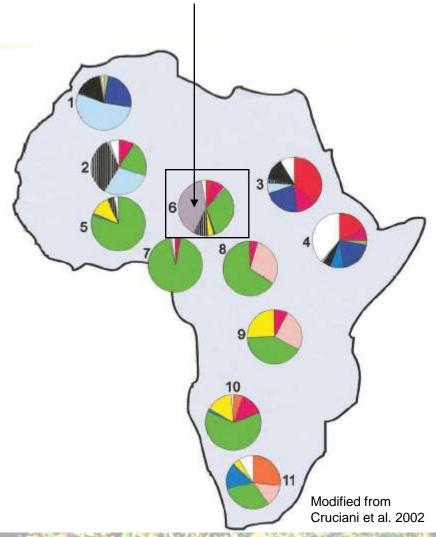
- 1 Baka population from Central/East Cameroon
- 1 Baka population from Gabon
- 1 Bakola population from Cameroon



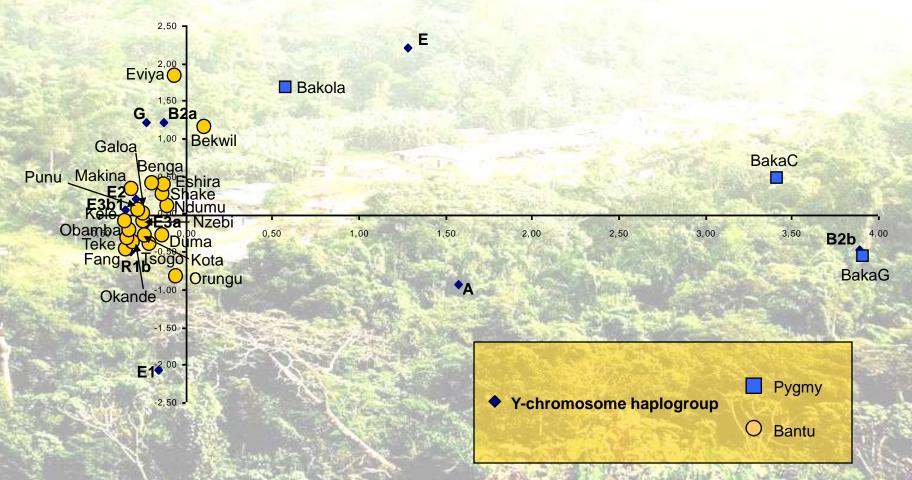




Haplogroup R1b* North Africa Middle East Haplogroup R1b*



Correspondence analysis: haplogroup composition First two dimension plot (75.6% genetic variance)

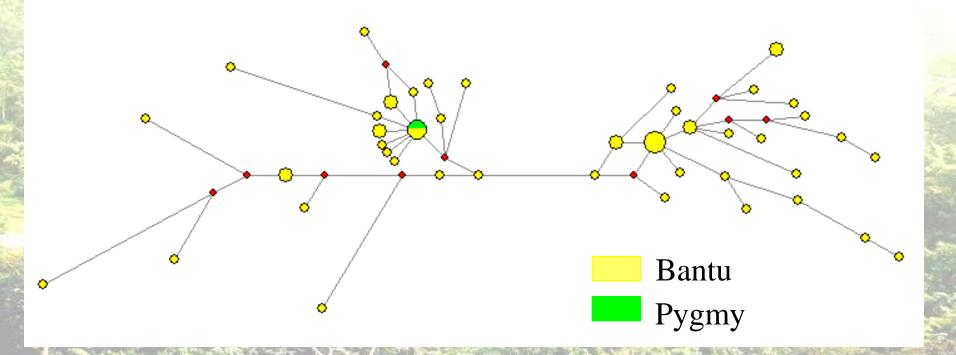


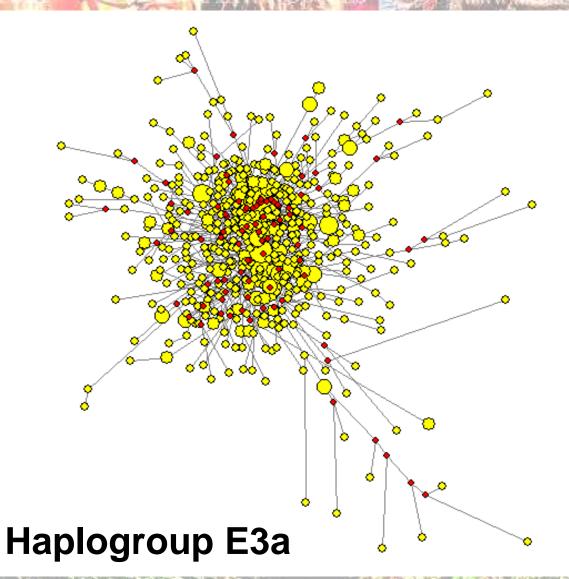
Analysis of MOlecular VAriance (AMOVA): haplogroup composition

HAPLOGROUPS	Between groups	Among populations	Within Populations
All populations		12%	88%
Bantu agriculturalist	Anti-A	2%	98%
Pygmy		25%	75%
Bantu versus Pygmy	34%	3%	63%

All values are significant (p<0.001)

Haplogroup B2a





Founder Bantu Haplotype (Thomas et al. 2000)

HAPLOGROUP E3a

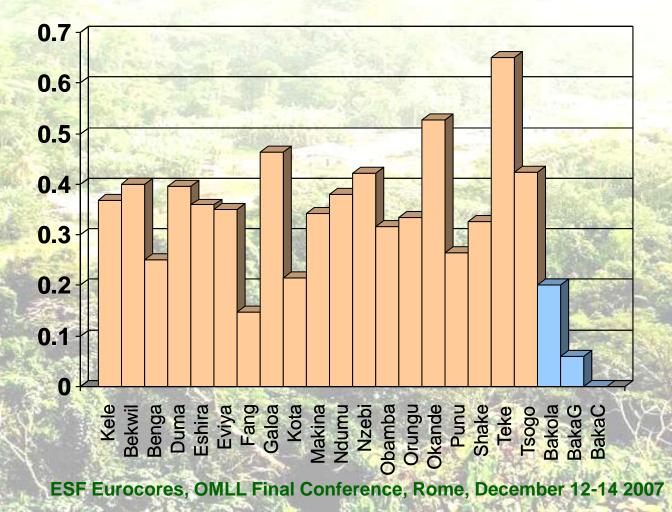
DYS 391 - DYS 390 - DYS 393 - DYS 392 - DYS 19

10 - 21 - 13 - 11 - 15

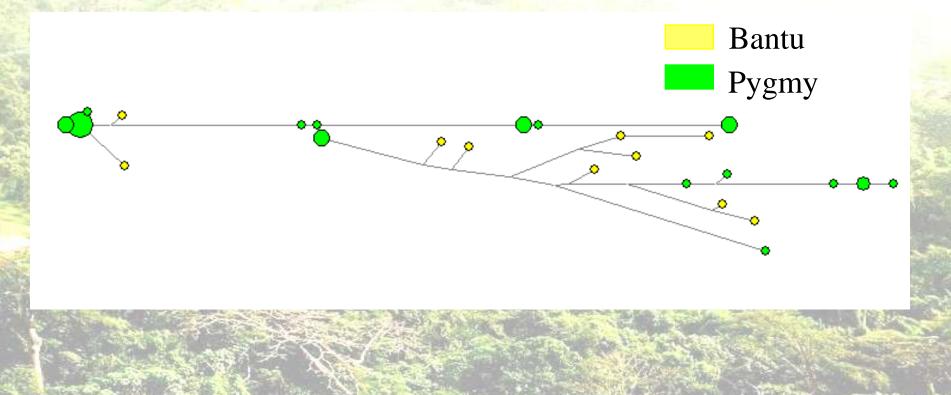
One step-neighbours:

11 - 21 - 13 - 11 - 15 10 - 22 - 13 - 11 - 15 10 - 21 - 12 - 11 - 15 10 - 21 - 14 - 11 - 15 10 - 21 - 13 - 10 - 15 10 - 21 - 13 - 12 - 15 10 - 21 - 13 - 11 - 1410 - 21 - 13 - 11 - 16

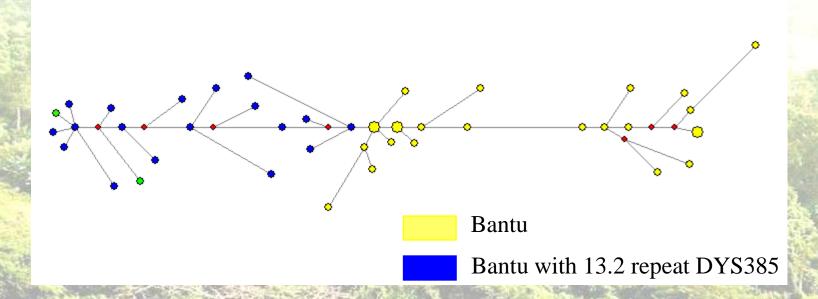
Founder "Bantu haplotype" frequencies

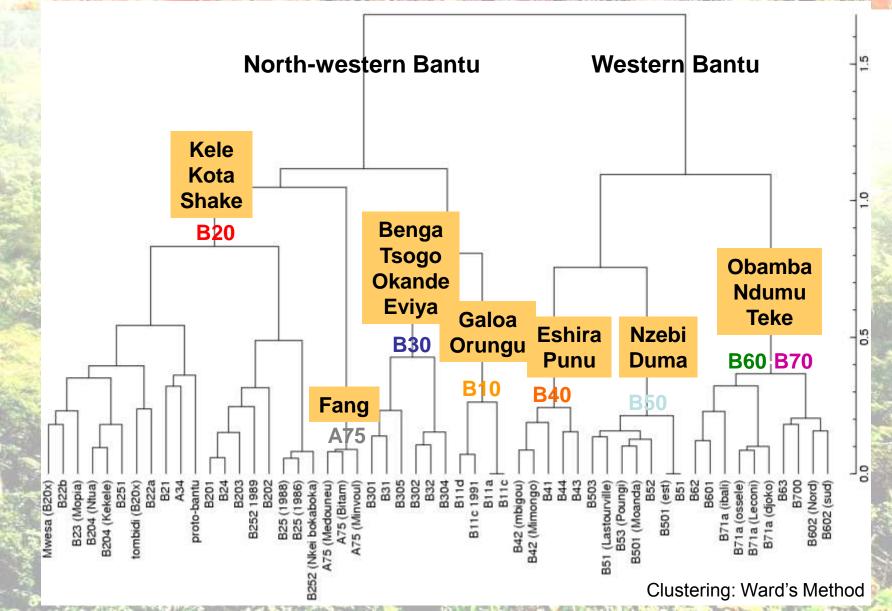


Haplogroup B2b



Haplogroup R1b*





- Genetic differentiation between Bantu/Pygmies: common ancestry, differentiation and contacts
- Bantu agriculturalist homogeneity/Pygmy heterogeneity: Bantu expansion and Pygmy isolation
- Sexual asymmetry: Bantu Y lineages into Pygmy
- Presence of non-African haplogroup in Bantu (R1b): contact with northern populations

Conclusions and perspectives

- Description of W-C African genetic landscape
- Differentiation between agriculturalists and Pygmies:
 - Common ancestors, isolation and gene flow
- Asymmetrical gene flow:
 - Maternal gene flow from Pygmy to Bantu agriculturalists
 - Paternal gene flow from Bantu agriculturalist to Pygmy
 - The offspring can be assimilated in both groups
- Homogeneity within agriculturalists: common and recent origin: Bantu expansion.
- Lack of correlation between genes and languages
- Ethnic groups or populations socially constructed

Thank you for your attention!