

Unraveling African diversity from a cross-disciplinary perspective

1 | INTRODUCTION

The study of deep and more recent human history in Africa requires a cross-disciplinary perspective. To better understand the origin of our species and the complex human diversity of current-day populations from this continent, paleoanthropologists, archeologists, historical linguistics, anthropologists, and geneticists participated in the “Africa, the cradle of human diversity” international conference during May 22–25, 2019 (<https://africathecradleofhumandiversity.com>), at Uppsala University, Sweden (Figure 1). Leading researchers presented and discussed new results and multidisciplinary approaches to address long-standing questions about human evolutionary history and population dynamics in Africa and beyond. The conference covered an extensive time range in human evolution, starting with the evolution of early humans in Africa to the complex cultural and genetic diversity of modern-day African populations (Table 1).

The conference had broad geographic representation, with attendees from Sweden, the United States, South Africa, Nigeria, the United Kingdom, Germany, Zimbabwe, Canada, India, France, Italy,

Czech Republic, Uganda, Algeria, Tunisia, Turkey, Sudan, and Ethiopia (Figure 2). International participants were from a wide range of academic positions and had diverse academic backgrounds; 52% of attendees and 48% of invited speakers were female, and 31% were from underrepresented countries.

The scientific content of the conference included two keynote lectures, nine plenary sessions, two workshops, two poster sessions, and four short-talks by young researchers (Table 1). Plenary sessions varied in focus from largely theoretical to completely empirical studies, while focusing on human populations from different geographic regions and time periods in Africa. Two independently organized workshops, before and after the conference, respectively, focusing on more in-depth discussions of African linguistics and on quantitative methods for excavating the past from genomes, enriched scientific discussions.

The conference featured two keynote lectures by leading researchers. Marlize Lombard (University of Johannesburg, South Africa) presented a holistic approach to better understand the evolution of human cognition and hunting technologies in early humans, on the basis of the gene-culture co-evolution model,¹ and Lluís Quintana-Murci



FIGURE 1 Conference picture with invited speakers at the “Africa, the cradle of human diversity” conference [Color figure can be viewed at wileyonlinelibrary.com]

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TABLE 1 List of invited speakers, session, and titles of each lecture presented at the “Africa, the cradle of human diversity” conference

Speakers	Sessions and titles
Keynote lectures	
Marlize Lombard	<i>A holistic model for human origins and diversity research in Africa</i>
Lluís Quintana-Murci	<i>Understanding past demography and adaptation of African hunter-gatherers and farmers through genomics</i>
Early Humans in Africa	
Bernhard Zipfel	<i>Becoming human—Fossil hominins from Southern Africa</i>
Fidelis Masao	<i>Early modern human fossils from Eastern Africa—Recent investigation on the archaeology of the Ngoloba beds, Laetoli northern Tanzania</i>
Mark Thomas	<i>African structure: Moving beyond multiregional and simple out of Africa models of human evolution</i>
Cultural transitions in Stone Age and Iron Age in Africa	
Larry Barham	<i>Emergent behavioural diversity in the ‘Long’ Middle Pleistocene of Africa</i>
Gavin Whitelaw	<i>Sequence, homesteads, and marriage in the Iron Age of KwaZulu-Natal, South Africa</i>
Gilbert Collin Pwiti	<i>Costly signalling and the Zimbabwe culture</i>
Plan Shenjere-Nyabezi	<i>Great Zimbabwe, the Zimbabwe culture and the Nambya State, north-western Zimbabwe</i>
The first human divergences: Khoekhoe and San	
Brigitte Pakendorf	<i>Khoisan diversity from a linguistic, genetic and cultural perspective</i>
Mattias Jakobsson	<i>Ancient genomes from southern Africa push modern human emergence to 300,000 years ago</i>
Michael De Jongh	<i>Human Diversity—‘forgotten’ communities of the South African mosaic</i>
Biomedical research in Africa	
Michele Ramsay	<i>New insights from a pan-African genome-wide association study with lipid levels: an AWI-Gen sub-study</i>
Ananyo Choudhury	<i>Genomic data from >5000 South Africans reveal novel sub-structure reflecting the complex demographic history within South-Eastern Bantu speaker populations</i>
Himla Soodyall	<i>Nexus between genomics and society: a southern African perspective</i>
Western and West-Central African diversity	
Koen Bostoen	<i>The First Bantu Speakers South of the Central-African Rainforest: New Insights from Historical Linguistics and Archaeology</i>
Bernard Clist	<i>West-Central African diversity from the Stone Age to the Iron Age, continuities and transitions during the last 10,000 years</i>
Isabelle Ribot	<i>Shum Laka, a key site to explore ancient forager diversity in North-West Cameroon: new and ongoing research</i>
Hiba Babiker	<i>Genetic landscape of populations from Central Eastern Mali reveals the mystery of a language isolate and its speakers</i>
Eastern African diversity	
Paul Lane	<i>Beyond Ancestry and Migration: Other Ways of Exploring Diversity in Eastern Africa Through Integrated Multidisciplinary Research</i>
Anneli Ekblom	<i>Negotiating ethnicity and identity: the example of Baloï Southern Mozambique</i>
Nicole Boivin	<i>Settling Azania: The population history of coastal and island East Africa from the Late Pleistocene to the Late Holocene</i>
Southern African diversity	
Thembi Russell	<i>Grappling with diversity in livestock-related archaeology in southern Africa, from 2300 years ago</i>
Maryna Steyn	<i>A holistic approach towards understanding the past: the example of four women from Kwa-Zulu Natal (South Africa)</i>
Anne-Maria Fehn	<i>The Okavango River Basin as a contact zone—A linguistic perspective</i>
Jorge Rocha	<i>Tracing invisible footsteps: the genetic and linguistic legacy of pre-Bantu peoples in southwestern Angola</i>
Northern African diversity	
Isabelle Crevecoeur	<i>Late Pleistocene and Early Holocene human diversity from North-East Africa</i>
Rosa Fregel	<i>Paleogenomics of the Neolithic transition in North Africa</i>
Victor Černý and Estella Poloni	<i>Population structure and gene flow in the African Sahel/Savannah Belt</i>
African island diversity	
Paul Verdu	<i>From macro to micro genetic and linguistic evolution on the African shores of the transatlantic slave trade</i>
Chantal Radimilahy	<i>Human settlement in Madagascar: combination of genetic and anthropological approaches</i>
Denis Pierron	<i>Genomic landscape of human diversity across Madagascar</i>

(Continues)

TABLE 1 (Continued)

Speakers	Sessions and titles
	Short-talks by young researchers
Ezekia Mtetwa	<i>New light on Great Zimbabwe funerary landscapes and mortuary practices: Wider implications for genetic studies</i>
Ke Wang	<i>Investigating East African population structure through ancient genomes</i>
Francesca di Garbo	<i>Grammatical restructuring and population dynamics in Northwestern Bantu</i>
Mario Vicente	<i>Genetic affinities among southern Africa hunter-gatherers and the impact of admixing farmer and herder populations</i>

**FIGURE 2** Conference picture with all participants at the “Africa, the cradle of human diversity” conference [Color figure can be viewed at wileyonlinelibrary.com]

(Pasteur Institute, France) gave a comprehensive overview of recent genomic and epigenomic studies focused on the demographic history in Africa and human adaptations to new environments.^{2,3} Keynote lectures were followed by plenary sessions (Table 1) where talks explored a variety of topics, new methodological approaches, and recent studies of human diversity in Africa.

2 | PALEOANTHROPOLOGICAL AND ARCHAEOGENOMIC PERSPECTIVES OF EARLY HUMANS AND FIRST SOCIETIES IN AFRICA

The first plenary lectures presented a closer look at the fossil record of archaic hominins and early humans from different locations, their lithic technologies, and cultural transitions from the Stone Age to the Iron Age in Africa. These discussions highlighted that the roots of human diversity are very deep in Africa. During the Stone Age,

regional patterning of early humans emerged with difference decision-making sequence and social conventions across small groups.⁴ One of the technological revolutions was the efficiency of hafted hand axes.⁵

Current views from paleoanthropological, archeological, and genetic research support a complex meta-population model for the origin of anatomically modern humans within different regions of Africa long before the out-of-Africa migration.⁶ From 300,000 years ago onwards,⁷ our species evolved within genetically structured populations with region identities that varied spatially and temporally, connected to each other by gene flow.^{6,8,9}

Cross-disciplinary research of the highly diverse and divergent click-speaking hunter-gatherer groups from southern Africa, known as the Khoe-San, will help to elucidate deep human history, admixture patterns, and human adaptation.⁹ These groups have until recently led a hunter-gathering way of life; however, other means of subsistence occur as well, for example, the cattle and sheep pastoralism found among the Khoekhoe¹⁰ or the “peripatetic” lifestyle of the Damara.¹¹ The Khoe-San have high linguistic, cultural, and genetic diversity, and some groups still

preserve their hunter-gatherer lifestyle in remote and isolated areas.^{12,13}

Presentations also brought insights into on-going anthropological and genetic endeavors to encourage investigations of descendants of the earliest southern Africans who are still essentially “forgotten” by the authorities and the scientific community.¹⁴

The conference also reexamined ancient urban assemblages and complex spatial and sociopolitical organization at Great Zimbabwe and other Iron Age archeological sites in Africa.^{15,16} Great Zimbabwe represented a major ancient civilization that flourished in southern Africa between the 12th and 18th centuries AD.¹⁷ Archeologists highlighted the important need of collaborative research to better understand the demographic history and migrations of populations with different subsistence practices and technological innovations.^{18,19}

3 | NEW INSIGHTS TO STUDY PAST AND RECENT HISTORY IN AFRICA

The Bantu expansion is the most important linguistic, cultural, and demographic process in Late Holocene Africa.²⁰ It started in west-central Africa 5,000–3,000 years ago, and evolutionary genetics demonstrated that mass human migration was the main underlying force of this expansion.^{21,22} New cross-disciplinary research projects²³ will elucidate long-distant spread of farming practices and the interaction of migrating farmers with autochthonous groups, to shed additional light of when, where, and how early Bantu-speaking populations settled in wider regions from central, eastern, and southern Africa.⁹

An ongoing cross-disciplinary research project, BantuFirst (<http://www.bantufirst.ugent.be>), aims at gaining a better understanding of when, where, and how early Bantu speech communities settled in the wider Lower Congo region of central Africa between ca. 3,000 and 1,000 BP and how these newcomers interacted with autochthonous hunter-gatherers.²⁴ The BantuFirst project team includes archeologists and historical linguists who carry out research together with geneticists on the first Bantu speech communities south of the equatorial rainforest in parts of the Democratic Republic of Congo. This area of research will unravel long-standing questions about the routes and dynamics of the Bantu expansion in central Africa.

In eastern Africa, novel research of archeological, biomolecular, and ancient genomic data sets have begun to shed more light on the arrival of food producing populations and their integration with autochthonous foragers during the Bantu expansion.²⁵ Other research projects are studying environmental and social consequences of intensive agriculture over the last 500 years to investigate the extent of human-induced environmental changes in eastern African landscapes.²⁶

The Sahel/Savannah belt separates north Africa from sub-Saharan Africa, acting as a corridor of human migration between eastern and western Africa. This area is inhabited by nomadic pastoralists and sedentary farmers. Paleogenomic and population genetic studies on ancient DNA and contemporary populations have started to reveal new insights into population continuity and incoming gene flow in this region of Africa.^{27–29}

On both sides of the African continent, recent mass migrations contributed to one of the humanity's darkest chapters, the slave trade. Along the west African coast, the transatlantic slave trade impacted the demographic history of numerous populations,^{22,30} for example, the population history of Cape Verdean Kriolu speakers.³¹ The Indian Ocean slave trade network, along the east African coast, mainly impacted African islands from southeastern Africa, for example, the genetic landscape of the Malagasy population.^{32,33}

4 | ENGAGEMENT OF GENOMIC RESEARCH IN AFRICA

One of the sessions featured only African-based researchers from the Human Heredity and Health in Africa (H3Africa) Consortium, an international collaborative research consortium led by African researchers aimed at notably increasing large-scale genomic studies and genome-wide association studies (GWASs) in Africa.³⁴ This consortium also encourages the formation of intracontinental collaborations and development of training programs and facilities necessary to lead high-quality genomics and biomedical research in Africa.³⁵

One of the H3Africa projects, the AWI-Gen study, was designed to determine genetic and environmental contributions to cardiometabolic diseases and related traits in African groups. In this large-scale GWAS study, association and fine-mapping analyses have been conducted to discover novel genetic associations of lipid traits with genes that have only been observed to be polymorphic in African populations.³⁶

5 | CONCLUDING REMARKS AND FUTURE DIRECTIONS

In the “Africa, the cradle of human diversity” international conference, speakers presented and discussed current knowledge and ongoing research in Africa, using state-of-the-art approaches and a multi-disciplinary perspective. The event started by focusing on the biological and behavioral evolution of our species and finished with the demographic history and historical migrations of modern populations in continental Africa and African islands. This event set the ground for cross-disciplinary conversations between leading researchers from different scientific fields to investigate African human diversity. These conversations will continue after the conference, in ongoing research projects and future scientific meetings.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

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