

Modern human origins and dispersal: current state of knowledge and future directions

Accumulating evidence from various fields of study has substantially advanced our understanding of modern human origins and dispersal. Fossil evidence in hand supports the African origin of our species, although its sparseness leaves many questions unanswered. Similarly, genetic studies provide unprecedented insights into the evolutionary history of our species, lending further support to its African origin and Late Pleistocene dispersal beyond the continent. On the other hand, inferring the origin and dispersal of a given hominin species based on archeological evidence is more difficult because Paleolithic technologies do not necessarily imply the taxonomic or genetic affinities of their makers. Perhaps most difficult of all is inferring the origin and evolution of behaviors, such as language, which leave hardly any trace in the Paleolithic record.

With funding from the German Research Foundation, the DFG Center for Advanced Studies was established at the University of Tübingen two years ago with the ambitious goal of transcending traditional divides between biological and cultural sciences relevant to the study of our species' evolution. At a symposium held November 3-4, 2017 in Tübingen, the Center brought together geneticists, paleontologists, archeologists, and linguists to assess the current state of knowledge and explore future research directions.

The symposium, which highlighted the theme of modern human origins and dispersal, particularly focused on novel multidisciplinary research from eastern Africa. Based on ongoing investigations by the Center's Junior Research Group (led by YS), as well as collaborative research by visiting fellows, the symposium envisioned a venue for discussing the biocultural evolution of modern humans.

Speakers at the symposium presented new and ongoing research using both field and laboratory work, starting with background talks on the biological and behavioral evolution of our species. Ensuing talks and discussions explored a variety of controversial topics and perspectives, as well as methodological and contextual issues surrounding the origins and dispersal of modern humans (Table 1).

1 | CURRENT STATE OF KNOWLEDGE

1.1 | Fossil and genomic evidence

Over the last decades, the debate on modern human origins has shifted from a simple model of monogenesis and a single dispersal out of Africa to one that focuses on admixing lineages and dynamic movement across geographical space since Pleistocene times. Whereas mitochondrial sequencing¹ once popularized a single-origin hypothesis and

challenged the multiregional model of human origins, genome-wide sequencing of extant and extinct individuals has now demonstrated the complex interactions among hominin populations in the past.² The current paradigm reflects the rapid advances of human genomics and ancient DNA alongside new fossil discoveries, with a general consensus by symposium participants that these advances have led to more complex scenarios to explain the diversity of our species. Still, questions remain unanswered: Was the process toward anatomically modern forms uniform across the vast African continent and, if so, was it slow or abrupt? How do ancient genomes more broadly inform this process and the history of the *Homo sapiens* lineages?

The period between ~250-350 ka was identified in this symposium as a crucial time frame. Stringer (Natural History Museum, London) posited that by this time at least three hominin lineages existed in the continent, raising questions about their possible admixture or isolation. Krause (Max Planck Institute-SHH, Jena) reported on mitochondrial gene flow from the *sapiens* lineage to Neanderthals in Europe, possibly due to a dispersal from Africa. The existence of an African-Eurasian connection in the Middle Pleistocene has long been posited on the basis of the human fossil record,³ but discoveries and dating calibrations of previously reported fossils require revisions. This was exemplified by Stringer's progress report on updating the chronometric date for the Kabwe fossil from Zambia. Gunz (Max Planck Institute-EVA, Leipzig) reported work on the newly dated Jebel Irhoud site, as well as comparative morphometric work on the facial form of fossil and recent humans. He proposed that the model of a *heidelbergensis* ancestor for our species will likely need to be revised, hypothesizing that facial form is a retention of an ancestral condition, while the globular form of the brain and neurocranium is a derived condition unique to modern humans. The presence of a modern facial form was reiterated by Schlebusch (Uppsala University), with reference to the Florisbad fossil and new genomic dates pushing back the estimate of modern human divergence up to ~350 ka.

Ambrose (University of Illinois) framed an early modern-human dispersal out of Africa within the context of a revised timeline for the eastern African megadroughts at >130 ka and the occupation of the Levant thereafter. Pagani (University of Padova) discussed evidence in extant Papuan genomes that supports the inference of an early dispersal around this time. Discussion centered on how an earlier Middle Pleistocene introgression could affect this inference. Also noted was the need for more fossils from secure stratigraphic contexts outside of Africa with reliable chronometric dates. Schlebusch reviewed how

TABLE 1 List of symposium presenters, sessions, and short titles of works presented.^{a,b}

Presenter	Session*	Title
Chris Stringer Johannes Krause Philipp Gunz Carina Schlebusch	1	The significance of Middle Pleistocene African diversity to MH origins and dispersal African Middle Pleistocene gene flow into Neanderthals The origins of <i>Homo sapiens</i> diversity The genetic history of Africa based on modern and ancient DNA
Manuel Will Alison Brooks Yonatan Sahle Marta Mirazón Lahr	2	Timing and trajectory of cultural change during the MSA of Africa Complexity & cultural transmission in the Middle-Late Pleistocene of eastern Africa New research on the Late Pleistocene archeology of Ethiopia Emerging complexity in late human evolution in East Africa: Insights from Turkana
Christian Tryon Stanley Ambrose Amanuel Beyin Patrick Roberts	3	The African equatorial Great Lakes region & Late Pleistocene human dispersals Climate isochrons and the archeology of MH dispersals from eastern Africa Western littoral of the Red Sea & its place in early human dispersals out of Africa Exploring diverse environmental contexts of Late Pleistocene human dispersals
Luca Pagani Pavel Duda Tom Güldemann	4	Out of Africa expansion(s): a genomic perspective MH dispersal within and outside of Africa revealed by the supertree approach The linguistic prehistory of eastern Africa
Isabelle Crevecoeur Hugo Reyes-Centeno Lamy Khalidi	5	Late Pleistocene & early Holocene human biological diversity in the Nile Valley The Mumba Rockshelter (Tanzania) and its relevance to modern human origins Human mobility, interaction and the first pastoralists in the Ethiopian Afar

*Session 1- The origins of MH: Fossils and genomes; 2- The origins of MH: Archaeology and fieldwork; 3- Climatic & ecological contexts of dispersal out of Africa; 4- Genomic & linguistic diversity in & out of Africa; 5- Eastern Africa from the Late Pleistocene to the Holocene.

^aModern humans" abbreviated here as MH.

^bFull titles of oral and poster presentations and abstracts available at <http://www.wordsandbones.uni-tuebingen.de/symposium2017/>

genomes of Holocene Africans are refining our understanding of the diversity of African populations before the Bantu expansion. Crevecoeur (University of Bordeaux), Mirazón Lahr (University of Cambridge), and Reyes-Centeno reiterated this point by emphasizing the great diversity in skeletal form of northeastern African populations from the terminal Pleistocene and early Holocene.

1.2 | Archeological evidence and approaches

Interest in what archeology can tell us about the origins and dispersal of modern humans has recently increased. Because of the ubiquity and durability of stone tools, they are often used in inquiries about when modern humans spread out of Africa. However, with *fossiles directeurs* dominating current inferences,⁴⁻⁶ the potential ability of archeological evidence to meaningfully expand knowledge on these topics must still be exhaustively explored. Major questions discussed at the symposium include how much archeology can contribute to our understanding of modern human origins and dispersal and what needs to be done in order for the archeology of critical regions like eastern Africa to meaningfully contribute to such discussions.

If a single most important point pertinent to archeology was highlighted at the symposium, it was the need for more Late Pleistocene archeological sites in eastern Africa and, in conjunction with them, better understanding of the dynamics of the first cultural and behavioral changes at the local level. Contrary to the South African record, which

was thoroughly reviewed by Will (University of Tübingen), eastern Africa lacks the long and well-dated Late Pleistocene sequences necessary for understanding behavioral, technological, social, demographic, and ecological contexts across the Late Pleistocene. Untangling which contexts drove the apparent peculiarities in the trajectories of cultural transitions and behavioral or technological innovations in eastern versus southern South Africa requires more sites and long-term research programs in the former. Tryon (Harvard University) argued that understanding the covariation of culture and environment at micro scales can help us recognize patterns that are consistent with the out-of-Africa dispersal.

Notwithstanding inherent drawbacks, can certain technologies and behaviors be proposed as quintessentially human? Some of the talks, such as those by Brooks (George Washington University) and Khalidi (University of Nice Sophia Antipolis), stressed the importance of complex social networks as seen in obsidian procurement and exchange patterns. Generally, "intangible culture moves faster and farther than genes," Brooks stressed, arguing for a deeper antiquity of cultural complexity. Similarly, Sahle reviewed the evolution of early complex projectiles at Aduma (Ethiopia). Together, these talks accentuated the need to closely explore behavioral and technological traits that were arguably decisive in modern humans' adaptation to new environments and their successful spread within and out of Africa.⁶⁻⁸ In agreement with this, Roberts (Max Planck Institute-SHH, Jena) proposed that early humans' adaptiveness and plasticity uniquely enabled them to

successfully expand into novel ecologies that previously were considered to be unattractive – deserts by 100 ka and rainforests by >45 ka.

Results from a new project in the Sudan, reported by Beyin (University of Louisville), suggest much older hominin coastal adaptation in the region, with implications for yet another alternative dispersal route along the western Red Sea littoral. Similarly, a rich archeological record from west Turkana, presented by Mirazón Lahr, revealed emerging complexity in the later prehistory of the region. Changing environments and limited resources were posited to have brought prehistoric groups together into restricted areas. It was also noted that such clustering may have fostered interactions, including violent ones. Could that have been the case among early Late Pleistocene populations?

1.3 | Linguistics as a tool to trace population history

Standard linguistic reconstruction via the comparative method, which involves harnessing regular sound-change patterns in cognates, currently reaches back to a maximum of ~6 ka for families such as the Indo-European, Uralic, and Austronesian.⁹ If similarities in morphological features are taken into account, this might be pushed to ~10 ka for the Afroasiatic macrofamily,⁹ which spans northern and eastern Africa as well as the Near East. Reconstruction of shared vocabulary can also provide insights into subsistence patterns and technological inventions.^{10,11} This currently is an under-explored avenue of research, particularly for lesser-known language families, with potential to complement archeological finds.

Automated computational methods designed to reconstruct language families based on word lists yield time-depths that are in rough agreement with archeological and historical evidence,¹² thus strengthening arguments for prehistoric population spreads as reflected, for instance, in the proposed Nostratic/Eurasian macro-family.¹³ A crucial topic for future research is, therefore, the agreement or disagreement between linguistic and genetic,¹⁴ as well as morphometric¹⁵ clustering.

Current research further suggests that linguistic “fossils,” such as “ultraconserved” words¹⁶ and typologically rare click sounds,¹⁷ might be stable over long evolutionary periods, in some cases even reflecting early branching events of *Homo sapiens* around 50 ka. Such studies are inevitably controversial, the reason being that they claim to reach far beyond the generally accepted comparative horizon, and are often based on conjectures that are not backed by more fine-grained linguistic evidence.¹⁸

2 | CONCLUDING REMARKS

The emerging evidence supports an African origin and out-of-Africa dispersal of modern humans. However, the details of these events are still largely unknown. Fossil and genetic evidence is converging on a consensus of deep roots for the *sapiens* lineage and a more recent evolution of populations with highly encephalized, globular crania, thus far first observed in the fossil record of eastern Africa. Determining how this hallmark anatomically modern trait is related to the demographic success of modern humans will require further work, but it seems that,

at least to some degree, it is associated with changes in behavior and culture.

Archeologically, a move away from literal interpretations of stone-tool forms and technologies, as well as nuanced assessment of the trajectories of cultural or behavioral changes in tandem with environmental and other variables, warrant better understanding. Pioneering and renewed research in cave or rockshelter contexts promises the long sequence, superior preservation, and fine-grained picture currently lacking in regions more proximal to the hypothesized modern-human dispersal routes, such as eastern Africa. Research on obsidian provenance along both sides of the southern Red Sea also has the potential to yield high-quality archeological data relevant to Late Pleistocene human migrations and exchange networks. Equally important, reassessment of previous collections housed in different museums across this region ensures greater knowledge.

In the coming years, one of the biggest challenges for computational linguistics will be to develop a generally accepted methodology for testing linguistic “fossils” and reconstructing deep linguistic history, complementing the comparative method. While often aiming for the deepest possible conjecture, interdisciplinary research at the interface of archeology, genetics, anthropology, and linguistics is most fruitful when meeting in historic time periods. After all, only solid converging evidence of human interaction in shallower time can open a window into deep population history.

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