THE MATTER OF PREHISTORY: PAPERS IN HONOR OF ANTONIO GILMAN GUILLÉN

Edited by

Pedro Díaz-del-Río
Katina Lillios
Inés Sastre

CONSEJO SUPERIOR DE INVESTIGACIONES CIENTÍFICAS
Madrid, 2020

Catálogo de publicaciones de la Administración General del Estado:
https://cpage.mpr.gob.es

EDITORIAL CSIC: *http://editorial.csic.es* (correo: *publ@csic.es*)

GOBIERNO DE ESPAÑA
MINISTERIO DE CIENCIA E INNOVACIÓN
CSIC
CONSEJO SUPERIOR DE INVESTIGACIONES CIENTÍFICAS
EDITORIAL CSIC

FSC MIXTO Papel FSC® C016626

ISBN: 978-84-00-10721-5
e-ISBN: 978-84-00-10722-2
NIPO: 833-20-189-7
e-NIPO: 833-20-190-X
Depósito Legal: M-30504-2020

Maquetación, impresión y encuadernación: Estudios Gráficos Europeos S.A.
Impreso en España. *Printed in Spain*

En esta edición se ha utilizado papel ecológico sometido a un proceso de blanqueado ECF, cuya fibra procede de bosques gestionados de forma sostenible.

V.

PERSPECTIVES ON THE BIOGEOGRAPHIC AND CULTURAL ADAPTATIONS OF EARLY HUMANS DURING THE FIRST INTERCONTINENTAL DISPERSALS

Ignacio de la Torre / Alfonso Benito-Calvo / Faysal Bibi / Jackson Njau / Shuwen Pei / Florent Rivals
Haowen Tong / Kevin Uno / Sara Varela / Xiujie Wu

Abstract

Our understanding of the emergence and dispersal of the earliest tool-making hominins has been revolutionised in the last decade, with sites in eastern Africa and China pushing records of both events several hundred thousand years earlier than previously thought. In recent years, climate and environmental factors have been considered by many as primary drivers of these evolutionary events in human history. However, models linking Earth's dynamics with biological speciation, cultural innovation and migration events with climate require further testing, and recent discoveries suggest that the picture of the earliest human colonization across the Old World is far more complex, demanding new approaches to the biogeography and adaptive behaviours of early humans. In this paper, we argue for a broader geographic approach to the study of early human occupation dynamics comparing long archaeological sequences from eastern Africa and China. We thus review major research questions involved in the investigation of the earliest human migrations and propose a route map to better understand the alternative evolutionary trajectories adopted by hominins that shared an overarching biological and cultural background, but that faced different climatic and biogeographic challenges and opportunities.

Keywords: early stone tool makers, hominin migrations, early Pleistocene in China and Africa.

Resumen

La comprensión de la aparición y dispersión de los primeros homininos que usaron herramientas ha experimentado una revolución en la última década, con yacimientos en África oriental y China que retrotraen ambos eventos varios cientos de miles de años antes de lo que se pensaba. A menudo, los factores climáticos y medioambientales se han considerado como los actores principales que guiaron la mayoría de los eventos evolutivos en nuestra especie. Sin embargo, los modelos que vinculan dinámicas terrestres climáticas con especiación biológica, innovación cultural y eventos migratorios requieren una validación más sólida, y necesitan de nuevas aproximaciones a la biogeografía y conductas adaptativas de los primeros humanos. En el presente artículo proponemos la necesidad de adoptar una aproximación geográfica amplia al estudio de las dinámicas de ocupación de los primeros humanos, basada en la comparación de África oriental y China, regiones que contienen dos de las secuencias más largas de primeros yacimientos arqueológicos en todo el mundo. Repasamos así los temas de investigación principales relacionados con el estudio de las primeras migraciones humanas, y proponemos una hoja de ruta para la comprensión de las trayectorias evolutivas alternativas adoptadas por homininos que, aun compartiendo un fondo biológico y cultural común, se enfrentaron a retos y oportunidades climáticas y biográficas diferentes.

Palabras clave: primeros talladores, migraciones humanas, Pleistoceno inferior en China y África.

5.1. INTRODUCTION

Timing of the emergence of the earliest techno-complexes (De la Torre 2011) and the first hominin dispersals from Africa into Europe (Roebroeks 2006) and Asia (Dennell and Roebroeks 2005) are regularly pushed back. This pace has accelerated in the last decade, when our views have changed radically with the earliest artefacts reported at 3.3 million years ago (Ma) in Africa (Harmand et al. 2015), 1.85 Ma in Georgia (Ferring et al. 2011), 1.2 Ma in Southwestern Europe (Carbonell et al. 2008), and potentially at 2.1 Ma in China (Zhu et al. 2018). While the importance of such discoveries cannot be overstated, it is also true that the field is dominated by a 'joining-up-the-dots' perspective (Dennell 2017) focused on first appearance data, which is by default provisional and is proving to be unreliable as an explanatory device for human biological and cultural adaptations.

Pliny's motto "ex Africa semper aliquid novi" drives a paradigm in which this continent saw the emergence of consecutive species of Early Pleistocene (Antón and Swisher 2004) and Middle Pleistocene (Lahr and Foley 2001) premodern humans and *Homo sapiens* (Stringer and Galway-Witham 2018), who then colonised the Old World. Despite the problems of this paradigm (Dennell and Roebroeks 2005), Africa is generally seen as the only region in the world with continuous human occupation throughout the entire Early and Middle Pleistocene (Dennell 2003). Massive chronological gaps between the earliest human evidence in eastern latitudes of Europe (Ferring et al. 2011) and in the western Mediterranean (Carbonell et al. 2008; Toro-Moyano et al. 2013) may suggest failed initial migrations and more than one "Out of Africa" event, while the fragmentary evidence in northern Europe could be linked to intermittent human occupation only during interglacial periods (Roebroeks 2005). An even more complicated picture emerges from Asia, where new discoveries (Zhu et al. 2018) suggesting human presence at 2.1 Ma would necessarily imply that *Homo ergaster/erectus* was not the first colonizer of Eurasia, as often thought (e.g., Antón 2003), and where the Early and Middle Pleistocene archaeological record is so sparse that a 'source-and-sink model' (Martinón-Torres et al. 2018) has been invoked to interpret a discontinuous pattern of occupation for the continent during this time.

A compendium of the 21st century grand challenges for archaeology (Kintigh et al. 2014) recognises, however, that key questions of the discipline are no longer concerned with the earliest, the longest, or the otherwise unique. If anything, the ever-increasing age depth for the emergence and dispersal of the first human cultures only exacerbates the complexities of the early archaeological record; as the gaps between known sites become wider in time and space, it becomes crucial to go beyond first-appearance discussions and focus on the broader biogeographic and cultural patterns involved. In addition, research on the premodern human occupation of the Old World can no longer be compartmentalised regionally, and any comprehensive study should be based on a comparative analysis of the alternative evolutionary and cultural pathways observed in each area. The need for drawing similarities and differences between the earliest archaeological sequences – those of Africa and Asia – has been recognised in recent years, but efforts have focused on either general literature reviews of the evidence in each region (Schick 1994; Dennell and Roebroeks 2006; Norton and Braun 2010), or comparisons of particular attributes of some stone tools (Norton and Bae 2008; Petraglia and Shipton 2008; Lycett and Bae 2010).

In the discipline of archaeology as a whole, substantial fieldwork efforts in the last few decades have produced extensive datasets, and the time is ripe for large-scale synthetic research (Kintigh et al. 2014). The archaeology of premodern humans is no exception to this trend, particularly in the two regions concerning this paper; triggered by the discoveries at Olduvai Gorge, fieldwork in eastern Africa since the 1960s has produced an unparalleled dataset of Early Stone Age sites. Similarly, the exponential growth of scientific research in China since the 1990s has multiplied the number of archaeological sites and revolutionised our understanding of human evolution in Asia.

The synthetic perspective advocated by Kintigh et al. (2014) for archaeology – also identified as one of the grand challenges in the study of cultural evolution as a whole (Brewer et al. 2017) – has indeed been substantiated in Antonio Gilman's career, in which a comparative approach has proved to be a highly productive research strategy (e.g., Gilman 1991). Such perspective is now possible and greatly needed to properly understand the ecological and cultural patterns of early humans. Nonetheless, such research should be based on the systematic analysis of quantitative datasets (thus superseding the current stage of superficial literature review comparisons) and include computational modelling – also identified as a general priority for the advance of the discipline (Kintigh et al. 2014). Given the lack of systematic comparisons between the eastern African and Chinese sites, metadata research must also be accompanied by a direct analysis of archaeological assemblages.

In summary, the confirmation of eastern Africa and China as the regions with the longest record of early archaeological sequences and the substantial datasets produced in recent years, present a unique opportunity to examine the be-

havioural ecology of premodern humans during the earliest colonization of the Old World, but also a challenge due to the disparity of archives, research traditions and the lack of systematic intra and inter-regional comparisons. Such exceptional challenges and opportunities should constitute the basis of new research programmes to compare early human cultural and ecological adaptations in what some would consider the source of most hominin species (eastern Africa) and in the recipient area for the first human migration/s (namely eastern Asia). Stemming from this all-embracing objective to understand the alternative evolutionary trajectories adopted by hominins that shared an overarching biological and cultural background (i.e., they were premodern humans using Early Stone Age technological solutions), research questions that deserve special attention include: how can we identify migration waves, and how many were there in the Early and Middle Pleistocene, between the two regions? How continuous is human occupation in the supposed evolutionary centre in eastern Africa as opposed to the discontinuous record of China? To what extent do biotic versus abiotic evolutionary factors dictate divergent trajectories in the colonization of Africa and Asia? Can risks and challenges faced by early humans in each region explain variations in hominin adaptations? Such questions are crucial to our understanding of Early Stone Age behavioural ecology, and structure the following themes.

5.2. EARLY HUMAN EXPANSION DYNAMICS ACROSS THE OLD WORLD – THE PREMISES

5.2.1. The role of the Red Queen and the Court Jester in early human dispersals and faunal turnovers in East Africa and China

According to Benton (2009), paleoecologists typically contrast evolutionary events through a 'Court Jester' perspective (one where extrinsic, abiotic factors such as tectonic episodes or climate change are responsible for extinction and speciation), whereas biologists – who normally are less concerned with time depth – often privilege the classic Darwinian theory (nowadays summarised in the 'Red Queen' hypothesis) that invokes intrinsic factors of species competition (see also Van Valen 1973; Barnosky 2001). While both perspectives coexist in human evolutionary studies, there is an overwhelming preference for abiotic explanations, from models that highlight the role of geographic features in shaping speciation (Bailey, Reynolds and King 2011) to those that see species turnovers in the context of climate change (Vrba 1996). These climatic hypotheses have used the eastern Africa record to link aridification events (De Menocal 2011), lake pulses (Trauth et al. 2005) or increasing environmental variability (Potts 1996) with species turnover and migration.

In the northern latitudes of Eurasia hominin speciation events might not been as recurrent as in Africa, but climatic variations must have played a fundamental role in shaping human biogeographic ranges, due to the constraints imposed by the advance of glaciers during stadial stages. This process is relatively well understood in Europe for modern human occupation during the Last Glacial Maximum (Tallavaara et al. 2015; Burke et al. 2017), the local extinctions of Neanderthals in northern latitudes (Hublin and Roebroeks 2009) and across the continent (Tzedakis et al. 2007), and the punctuated nature of Early Pleistocene hominin colonization (Hosfield and Cole 2018). A similar latitudinal expansion and contraction of hominin populations dictated by climatic fluctuations is considered for Asia (Dennell 2003, 2017a), although here the model requires testing due to the nearly complete absence of environmental proxies from archaeological contexts.

While the influence of abiotic mechanisms in biogeographic distributions both in eastern Africa and in China is evident, they do not satisfactorily explain patterns observed in the archaeological and paleontological record. In eastern Africa, Bibi and Kiessling (2015) emphasized the importance of continuous (and likely biotic) factors in modulating faunal change across the Pliocene and Pleistocene, whereas comparison of a tightly-constrained part of the Early Pleistocene sequence at Olduvai detected no changes in the faunal community despite intervening climatic fluctuations (Bibi et al. 2018). This suggests that mammal communities might be more robust than expected and that their foodwebs remained relatively stable (Nenzén, Montoya and Varela 2014).

In the case of China, the biogeographic division of modern faunal communities (Xie, MacKinnon and Li 2004) is broadly reproduced in the Pleistocene (Tong 2006) and there is paleontological evidence for shifts following climatic oscillations (Jablonski et al. 2000; Norton et al. 2010), so it is assumed that hominin ranges also fluctuated accordingly (Dennell 2013). Despite the appeal of this model, the archaeological evidence does not entirely follow predictions. For example, Zhoukoudien is the only site where human presence is recurrently recorded throughout the Middle Pleistocene (Shen, Gao and Granger 2009), and yet is located at quite a high altitude. In addition, the lack of environmental proxies to

test if the occupation of northern latitudes was indeed limited to interstadials is accompanied by a strikingly low density of human presence in the central and southern parts of China through the entire Pleistocene. While it has been proposed that premodern humans were ill-adapted to the subtropical forests of southern China (e.g., Ciochon and Bettis 2009), low density of hominin occupation in the central regions – which would be expected to act as refugia during colder periods (Dennell 2017b) – cannot be attributed only to sampling and/or taphonomic bias, given that paleontological assemblages in this area are reasonably abundant. Therefore, we argue that climatic factors alone do not explain hominin biogeographic dynamics. We hypothesize that biotic interactions (e.g., competition), which are known to be essential in shaping biodiversity and biogeographic patterns (Araujo and Rozenfeld 2014), may have played a fundamental role in hominin occupation dynamics, and therefore need to be properly addressed. This is particularly relevant when considering that early *Homo* had recently encroached on the carnivore guild (Pobiner and Blumenschine 2003), and therefore ecological competition with resident carnivore species may have been significant.

5.2.2. Cultural and biological connectivity between two continents?

The first appearance datum of hominins in China has steadily been pushed back from ~1 Ma (Schick and Toth 2000) to 1.36 Ma (Zhu et al. 2001), 1.66 Ma (Zhu et al. 2004) and now to potentially 2.1 Ma (Zhu et al. 2018). The discussion of human fossils has played an essential role in framing both the ecomorphological potential of early *Homo* to colonize new regions (Antón, Leonard and Robertson 2002) and in ascertaining the evolutionary links between the African and Asian premodern human demes (Antón 2003; Kaifu 2017), although they have often reached opposite conclusions (e.g., Martinón-Torres et al. 2007; Rightmire 2008).

If paleoanthropological discussions are inconclusive regarding the timing and extent of gene flow between the two continents, the interpretation of archaeological patterns is no less challenging. This essentially revolves around the controversial 'Movius Line', which arguably separates assemblages without handaxes to the east of India from those with handaxes in the rest of the Old-World Lower Palaeolithic (Schick 1994). Given the ever-increasing age of the earliest sites in China, it is now accepted that early *Homo* arrived in East Asia equipped with an Oldowan technology, and before the emergence of the Acheulean in eastern Africa. No handaxes have yet been indisputably reported in the Early Pleistocene of China, so it is also assumed that the founding *Homo* populations in East Asia remained isolated from cultural and genetic flows operating in the rest of the Old World. There is, however, no archaeological evidence that conclusively supports (or falsifies, for that matter) this hypothesis. Pei et al. (2017) have highlighted how little we know about the technological strategies ruling artefact production in the earliest Chinese sites, which makes it even more pertinent to consider these in relation to eastern African 'handaxe-free assemblages' (cf. De la Torre 2009) of a similar age. Equally important is the gap in our knowledge of mammal taxa other than hominins; while comparative anatomy of African and Asian early human fossils has received substantial attention (Antón 2003; Rightmire 2008), attempts to insert earliest human dispersal waves into the context of wider mammal migrations are limited (O'Regan et al. 2011; Tong et al. 2011) and have not involved direct comparisons of the faunal assemblages.

The archaeological evidence of the Middle Pleistocene is also contentious. Evidence for a new dispersal of Acheulean hominins from Africa is reported at ~0.8 Ma (Goren-Inbar et al. 2000), but there is no agreement whether it reached eastern Asia. In recent years, handaxe-bearing archaeological sequences have been discovered in central China (see a review in Li, Kuman and Li 2018), thus forcing a reconsideration of the meaning of the Movius Line. For some, eastern Asian handaxes are the result of independent innovations and technological convergence with the West (Corvinus 2004; Lycett and Bae 2010). Alternatively, other authors emphasize similarities with the African and western Asian Acheulean (Petraglia and Shipton, 2008; Li, Kuman and Li 2018), implying the existence of Middle Pleistocene cultural interactions across the entire Old World. Most of the discussion, however, has revolved around the comparison of handaxe metrics from published sources, with no consideration of handaxe technical features or the rest of the elements of the reduction sequences. These latter lines of inquiry, based on a first-hand comparison of materials from Africa and China, may be more effective in deciphering the overarching knapping schemes (De la Torre and Mora 2009), could facilitate a more solid assessment of homologies, technological convergences or shared technological principles, and could provide a methodology to evaluate the extent of continental interactions. Additionally, and although the recently discovered handaxe sequences have rarely yielded fossils, many other Middle Pleistocene sites in China contain abundant bone assemblages (Tong 2006), which so far have played no role in a revaluation of the Movius Line.

5.2.3. Centre and periphery in the Early and Middle Pleistocene? Continuities and discontinuities of the early archaeological record

Eastern Africa may have acted as a source area in which hominins – and many other mammal lineages – emerged and evolved. During the Early Pleistocene, eastern Africa is often considered as the main source area for technological innovations and dispersals into Eurasia. The translation of Wallerstein's (1974) concepts into Prehistoric research (Rowlands et al. 1987) has also been applied to the early archaeological record by Dennell (2003), who portrays eastern Africa as the only part of the Old World with continuous human occupation throughout the entire Pleistocene. In contrast, most of Eurasia remained unoccupied – or only sporadically inhabited – by premodern humans, with ephemeral colonization conditioned by latitudinal variations in of ecosystems between glacial and interglacial periods (ibid.; Roebroeks 2006). Recent genetic studies estimate that effective human population size in the entire Old World before 1.2 Ma was under 26,000 people (Huff et al. 2010), which suggests hominins would have been an exceedingly rare proportion of the mammal communities in Eurasia (Dennell 2017b), and provides further support to the notion of essentially deserted landscapes throughout the Early Pleistocene.

Populations may have not been much larger in the Middle Pleistocene, particularly in the case of Asia, where low demographic density has been used to explain the Movius Line (Lycett and Bae 2010; Lycett and Norton 2010). Since the loss of cultural traits and a lack of innovation transmission occur when small demographic levels (Shennan 2000) and local extinctions (Premo and Kuhn 2010) predominate, low hominin density and weakness of social networks could have precluded cultural transmission of innovations in Asia, whereas higher interconnectedness in Africa enabled the spread of the Acheulean (Lycett and Norton 2010). But alternative views are also possible, in which Africa too could have been the scenario of independent emergence and disappearance of early technologies where cultural transmission was minimal (Tennie et al. 2017), and therefore where a continuity of the archaeological record is not a prerequisite.

Once again, these models remain mostly theoretical, but the dramatic time depth gained by the earliest archaeological record both in Africa and China in the last few years, and the significant number of archaeological sites now reported in both regions – many of them in stratigraphic succession in various sedimentary basins – offers new opportunities for testing such hypotheses. In the current context where archaeology as a historic discipline is setting an agenda to evaluate the impact of discontinuities in the evolution of past societies (Barberena et al. 2017), an in-depth analysis of the *tempo* and *modo* of African and Asian Early and Middle Pleistocene sequences is essential to test their roles as centre and periphery during the age of premodern humans.

5.2.4. Risks and early human resilience in challenging environments

Early *Homo* (sensu Antón, Potts and Aiello 2014) and Middle Pleistocene premodern humans – who may include more than one deme (Antón 2003; Rightmire 2008; Kaifu 2017) – show a trend towards increased body and brain size, developmental plasticity and dietary expansion. Yet as an African lineage, early *Homo* would have encountered thermoregulatory challenges in the northern latitudes of Eurasia (Ruff 1993), challenges that would have needed to be met with cultural insulation solutions (Hosfield 2016). The largest concentration of Asian Early Pleistocene sites is found in the Nihewan basin, where today (i.e., an interstadial period) winter temperatures drop below -10°C. Given the rare evidence of fire use before the end of the Middle Pleistocene (Roebroeks and Villa 2011), it is plausible to depict the settlement of the northern latitudes of China as episodic (only during interstadials) and seasonal – during the warm months of the year (Dennell 2013). This model, however, remains entirely hypothetical, which is unfortunate given that we now know Early Pleistocene hominins did occupy northern European latitudes during cold periods (Parfitt et al. 2010), and arguments exist in favour of year-round (rather than seasonal) occupation (Hosfield 2016). Nonetheless, the archaeological evidence in Europe is too sparse, and a proper assessment of early human resilience to extreme environments should include the richer record of northeast China.

Early *Homo*'s encroachment on the carnivore guild (Pobiner and Blumenschine 2003) represented an adaptive opportunity with paramount evolutionary implications (Aiello and Wheeler 1995), but it may have also presented significant risks. If australopithecines regularly faced predation by African carnivores (Brain 1981) before hominins began to compete for meat resources, once early *Homo* became part of the carnivore guild at ~2.5 Ma, risks were unlikely to have decreased (Van Valkenburgh 2001). Njau and Blumenschine (2012) showed that early *Homo* faced high predation risk from predators and competition with carnivores (Pante et al. 2018). Still, carnivore paleoguilds of Africa show a clear acceleration of extinctions after 1.5 Ma, which has been correlated with the progressively higher

position of *Homo* in trophic chains (Lewis 1997; Werdelin and Lewis 2013).

While a similar pattern of hominin-induced extinction of carnivores may have occurred in Europe (Croitor and Brugal 2010; Meloro and Clauss 2012), the evidence in Asia is ambiguous, and there is a pressing need for dedicated taphonomic studies of Early Pleistocene sites (Pei et al. 2017). Additionally, a significant number of Chinese Middle Pleistocene caves have yielded hominin fossils alongside remains of other animals, but no (or very few) artefacts (Bakken 1997; Liu, Zhang and Wu 2005; Wu et al. 2019). Even the richest Middle Pleistocene archaeological assemblage in China, Zhoukoudian, could be a palimpsest of hyaena-den accumulations (Binford and Ho 1985), where >60% of human fossils bear tooth marks (Boaz et al. 2004). All of this leads us to hypothesize that many cave deposits in Middle Pleistocene China were formed by carnivores, rather than hominins. This may be pointing at a very different pattern of carnivore-hominin interactions from that observed in Africa and Europe, but needs validation via first-hand analysis of the evidence.

5.3. DISCUSSION – A ROADMAP TO THE INVESTIGATION OF BIOGEOGRAPHIC AND CULTURAL PATTERNS DURING THE EARLIEST HUMAN DISPERSALS

Competing hypotheses on the character and influence of climatic fluctuations in East African and Chinese mammal communities require validation through acquisition of new empirical evidence from environmental proxies but also through computational modeling, to produce Early and Middle Pleistocene climate models for both regions. Nonetheless, considering that the impact of Pleistocene climatic changes on long-term mammalian community structure appears to have been minimal in some regions (e.g. Bibi and Kiessling 2015), other factors may induce community collapse. For instance, the impact of early humans in local extinctions is suspected (Petraglia 2017), particularly during the colonization of new territories (Dennell 2017), but is yet to be properly investigated. Given the existence of long paleontological records before and after the emergence of stone tool technology in Africa and the arrival of humans in China, modeling the impact of hominin encroachment on mammal species biogeography and turnover is feasible and should be a priority of future research, particularly by analysing changes at a local scale using faunal assemblages from African and Chinese fossil sites, and by running experiments on the reconstructed foodwebs to model hominin impact on the fossil mammal communities. Ground-truthing of these models, however, should be tested with first-hand analyses; taxonomic systematics of selected geographic regions across wide temporal spans can be used, for example to portray changes in community structure before and after stone-tool making emerged and hominins encroached on the carnivore guild.

Early archaeological sites in China are secularly branded as Oldowan-like or Mode I (see recent reviews in Pei et al. 2017, 2019), thus emphasizing their technological affinities with the African Oldowan, but no direct, systematic comparisons of assemblages have ever been conducted. Therefore, it is unclear what their shared features are, apart from being core-and-flake technologies, and thus the alleged close cultural phylogeny is an assumption rather than a proof that the earliest colonization of China was made by Oldowan hominins. First-hand comparison of stone tool collections from African Oldowan sites and those with a similar age in China (particularly the rich Nihewan archaeological sequence) is therefore essential to establish a systematic set of defining features for both continents. In a similar vein, the Movius Line controversy has only recently prompted a quantitative approach, but the debate is still based on published material and grounded on metrical attributes that are not necessarily informative of similarities and differences between East and West handaxes. Again, first-hand comparisons between African and Chinese Middle Pleistocene sites are vital, and new studies should go beyond formal comparisons of metrical features and focus on the technological principles governing artefact production. Nonetheless, comparisons should not be limited exclusively to stone artefacts; the lack of comparative analysis between African and Chinese faunas has severely limited our understanding of mammalian biogeography throughout the Pleistocene. Much primary work – in the form of direct comparative taxonomic analysis – is needed to test the alleged biogeographic isolation of China during the Early and Middle Pleistocene, and to understand whether human dispersals took place within a broader context of faunal dispersals.

Concerning the explanatory potential of the centre and periphery concepts to depict earliest human dispersals, the main assumption to be tested is that discontinuities in the archaeological record of local sequences are linked to increased aridity (eastern Africa) and cold conditions (China), and that the opposite will be true during benign periods. However, despite the considerable intensity of research in eastern Africa, and the growing record in China, no comprehensive database yet exists of all the Early-Middle Pleistocene sequences and the archaeological proxies therein, so that they can be contrasted with the paleoenvironmental record.

An assessment of the succession of archaeological sites *within* each sequence and an evaluation of density peaks, troughs and gaps is also due, and is now feasible thanks to the relatively detailed availability of published reports.

Finally, the study of abiotic and biotic risks faced by early humans requires the formulation of new conceptual premises but also the application of new analytical techniques. As for the latter, speculative characterization of extreme environments conditioning human occupation should be tested through direct paleoecological analyses of relevant sites. Regarding biotic risks and inter-species competition, after three decades the hunting-scavenging debate of early *Homo* in Africa shows signs of having reached a conceptual and methodological impasse (Sahle, El Zaatari and White 2017). We thus advocate for a shift of focus where comparative analysis of bone surface modifications is coupled with a systematic assessment of community structures through time and space (e.g., Patterson et al. 2017). Zooarchaeological analysis of assemblages from different periods using the same protocols would guarantee the application of standardized analytical methods (e.g., Njau and Gilbert 2016), and therefore that results are comparable (i.e., that hominin/carnivore involvement in the formation of each faunal assemblage can be assessed *relatively* to one another). More importantly, by adding a community structure dimension to studies, changes in the diversity, abundance, size and ecological preferences of potential prey and predator competitors can provide insights about human-carnivore interactions (e.g., Blumenschine et al. 2012).

5.4. CONCLUSIONS

Regionalization of the archaeological record from the Middle Palaeolithic / Middle Stone Age onwards requires a careful consideration of biological and cultural local trajectories to assess variability in a global context. In contrast, the Lower Palaeolithic / Early Stone Age (and particularly its earlier stages) shares some essential characteristics – e.g., it is a hand-held stone tool technology produced by premodern humans – that may promote searching for global patterns during the first hominin dispersals across the Old Word. Significant efforts have been made earlier in the discipline (Movius 1948; Clark 1969) and in recent years (e.g., Petraglia and Korisettar 1998; Dennell 2003) to decipher global patterns of Early Stone Age occupation, but clearly more work can be done, particularly now, when the hard evidence – especially in China – is increasing exponentially.

We have argued in this paper that such work requires new and unconventional approaches to decipher archaeological patterns, which should go beyond paleoanthropological considerations and evaluate the role of natural phenomena in shaping our understanding of Pleistocene data. New perspectives should also be adopted in the selection of units and scales of analysis, in order to embrace a myriad of temporal and geographical resolutions comprising both metadata and primary sources, and analyses ranging from macro to micro scales. This kind of approach should be based on international collaborations where new data sets are produced, compared and synthesised, and be grounded in multidisciplinary perspectives that combine standard archaeological approaches with expertise ranging from geochemistry to computational modelling. The application of new analytical techniques to both legacy data and primary sources and their consolidation into models linking archaeological and paleoclimatic data, alongside the consideration of archaeological patterns in their biotic and abiotic context, will enable validation of previous theories and formulation of novel hypotheses on the *tempo* and *modo* of earliest human occupation in the Old Word, and particularly of its longest sequences in East Africa and China.

ACKNOWLEDGEMENTS

We thank Pedro Díaz-del-Río, Inés Sastre and Katina Lillios for inviting us to participate in this volume, and we are honoured to be part of this festschrift to Antonio Gilman, who has contributed so importantly to comparative research in prehistory. This project has received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (BICAEHFID, grant agreement No. 832980).

REFERENCES

AIELLO, L., and WHEELER, P. (1995): "The Expensive-Tissue Hypothesis. The Brain and the Digestive System in Human and Primate Evolution", *Current Anthropology,* 36, 199–221.

ANTÓN, S. C. (2003): "Natural History of Homo erectus", *Yearbook of Physical Anthropology,* 46: 126–70.

ANTÓN, S. C.; LEONARD, W. R., and ROBERTSON, M. L. (2002): "An Ecomorphological Model of the Initial Hominid Dispersal from Africa", *Journal of Human Evolution,* 43: 773–85.

ANTÓN, S. C.; POTTS, R., and AIELLO, L. C. (2014): "Evolution of Early Homo: An Integrated Biological Perspective", *Science,* 345: 1236828.

ANTÓN, S. C., and SWISHER III, C. C. (2004): "Early Dispersals of Homo from Africa", *Annual Review of Anthropology,* 33: 271–96.

ARAÚJO, M. B., and ROZENFELD, A. (2014): "The Geographic Scaling of Biotic Interactions", *Ecography,* 37: 406–15.

BAILEY, G. N.; REYNOLDS, S. C., and KING, G. C. P. (2011): "Landscapes of Human Evolution: Models and Methods of Tectonic Geomorphology and the Reconstruction of Hominin Landscapes", *Journal of Human Evolution,* 60: 257–80.

BAKKEN, D. A. (1997): "Taphonomic Parameters of Pleistocene Hominid Sites in China", in P. Bellwood and D. Tillotson (eds.), *Indo-Pacific Prehistory: The Chiang Mai Papers. Volume 3. Proceedings of the 15th Congress of the Indo-Pacific Prehistory Association* Chiang Mai, Thailand 5 to 12 January 1994. Australian National University, Canberra: 13–26.

BARBERENA, R.; MCDONALD, J.; MITCHELL, P. J., and VETH, P. (2017): "Archaeological Discontinuities in the Southern Hemisphere: A Working Agenda", *Journal of Anthropological Archaeology,* 46: 1–11.

BARNOSKY, A. D. (2001): "Distinguishing the Effects of the Red Queen and Court Jester on Miocene Mammal Evolution in the Northern Rocky Mountains", *Journal of Vertebrate Paleontology,* 21: 172–85.

BENTON, M. J. (2009): "The Red Queen and the Court Jester: Species Diversity and the Role of Biotic and Abiotic Factors Through Time", *Science,* 323: 728–32.

BIBI, F., and KIESSLING, W. (2015): "Continuous Evolutionary Change in Plio-Pleistocene Mammals of Eastern Africa", *Proceedings of the National Academy of Sciences,* 112: 10623–28.

BIBI, F.; PANTE, M.; SOURON, A.; STEWART, K.; VARELA, S.; WERDELIN, L.;... and TORRE, I. DE LA (2018): "Paleoecology of the Serengeti during the Oldowan-Acheulean Transition at Olduvai Gorge, Tanzania: The Mammal and Fish Evidence", *Journal of Human Evolution,* 120: 48–75.

BINFORD, L. R., and HO, C. K. (1985): "Taphonomy at a Distance: Zhoukoudian, 'The Cave Home of Beijing Man'?", *Current Anthropology,* 26: 413–42.

BLUMENSCHINE, R. J.; MASAO, F. T.; STOLLHOFEN, H.; STANISTREET, I. G.; BAMFORD, M. K.; ALBERT, R. M.;... and PRASSACK, K. A. (2012): "Landscape Distribution of Oldowan Stone Artifact Assemblages across the Fault Compartments of the Eastern Olduvai Lake Basin during Early Lowermost Bed II Times", *Journal of Human Evolution,* 63: 384–94.

BOAZ, N. T.; CIOCHON, R.; XU, Q., and LIU, J. (2004): "Mapping and Taphonomic Analysis of the Homo erectus Loci at Locality 1 Zhoukoudian, China", *Journal of Human Evolution,* 46: 519–49.

BRAIN, C. K. (1981): *The Hunters or the Hunted? An Introducion to African Cave Taphonomy.* The University of Chicago Press, Chicago.

BREWER, J.; GELFAND, M.; JACKSON, J. C.; MACDONALD, I. F.; PEREGRINE, P. N.; RICHERSON, P. J.;... and WILSON, D. S. (2017): "Grand Challenges for the Study of Cultural Evolution", *Nature Ecology & Evolution,* 1: 0070.

BURKE, A.; KAGEYAMA, M.; LATOMBE, G.; FASEL, M.; VRAC, M.; RAMSTEIN, G., and JAMES, P. M. A. (2017): "Risky Business: The Impact of Climate and Climate Variability on Human Population Dynamics in Western Europe during the Last Glacial Maximum", *Quaternary Science Reviews,* 164: 217–29.

CARBONELL, E.; BERMÚDEZ DE CASTRO, J. M.; PARÉS, J. M.; PÉREZ-GONZÁLEZ, A.; CUENCA-BESCÓS, G.; OLLÉ, A.;... and ARSUAGA, J. L. (2008): "The First Hominid of Europe", *Nature,* 452: 465–69.

CIOCHON, R. L., and BETTIS, E. A. (2009): "Asian Homo erectus Converges in Time", *Nature,* 458: 153–54.

CLARK, J. G. D. (1969): *World Prehistory: A New Outline.* 2nd edition. Cambridge University Press, Cambridge.

CORVINUS, G. (2004): "Homo erectus in East and Southeast Asia, and the Questions of the Age of the Species and Its Association with Stone Artifacts, with Special Attention to Handaxe-Like Tools", *Quaternary International,* 117: 141–51.

CROITOR, R., and BRUGAL, J.-P. (2010): "Ecological and Evolutionary Dynamics of the Carnivore Community in Europe during the Last 3 Million Years", *Quaternary International,* 212: 98–108.

DE MENOCAL, P. B. (2011): "Climate and Human Evolution", *Science,* 331: 540–42.

DENNELL, R. (2003): "Dispersal and Colonisation, Long and Short Chronologies: How Continuous Is the Early Pleistocene Record for Hominins outside East Africa?", *Journal of Human Evolution,* 45: 421–40.

— (2013): "The Nihewan Basin of North China in the Early Pleistocene: Continuous and flourishing, or discontinuous, infrequent and ephemeral occupation?", *Quaternary International,* 295: 223–36.

— (2017a): "Pleistocene Hominin Dispersals, Naïve Faunas and Social Networks", in M. Petraglia, N. Boivin and R. Crassard (eds.), *Human Dispersal and Species Movement: From Prehistory to the Present.* Cambridge University Press, Cambridge: 62–89.

— (2017b): "Human Colonization of Asia in the Late Pleistocene: The History of an Invasive Species", *Current Anthropology,* 58: S383–S396.

DENNELL, R., and ROEBROEKS, W. (2005): "An Asian perspective on early human dispersal from Africa", *Nature,* 438: 1099–104.

FERRING, R.; OMS, O.; AGUSTÍ, J.; BERNA, F.; NIORADZE, M.; SHELIA, T.;... and LORDKIPANIDZE, D. (2011): "Earliest human occupations at Dmanisi (Georgian Caucasus) dated to 1.85–1.78 Ma", *Proceedings of the National Academy of Sciences,* 108: 10432–36.

GILMAN, A. (1991): "Trajectories towards social complexity in the later prehistory of the Mediterranean", in T. K. Earle (ed.), *Chiefdoms: Power, Economy, and Ideology.* Cambridge University Press, Cambridge: 146–68.

GOREN-INBAR, N.; FEIBEL, C.S.; VEROSUB, K. L.; MELAMED, Y.; KISLEV, M. E.; TCHERNOV, E., and SARAGUSTI, I. (2000): "Pleistocene Milestones on the Out-of-Africa Corridor at Gesher Benot Ya'aqov, Israel", *Science,* 289: 944–47.

HARMAND, S.; LEWIS, J. E.; FEIBEL, C. S.; LEPRE, C. J.; PRAT, S.; LENOBLE, A.;... and ; ROCHE, H. (2015): "3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya", *Nature,* 521: 310–15.

HOSFIELD, R. (2016): "Walking in a Winter Wonderland? Strategies for Early and Middle Pleistocene Survival in Midlatitude Europe", *Current Anthropology,* 57: 653–82.

HOSFIELD, R., and COLE, J. (2018): "Early hominins in north-west Europe: A punctuated long chronology?", *Quaternary Science Reviews,* 190: 148–60.

HUBLIN, J.-J., and ROEBROEKS, W. (2009): "Ebb and flow or regional extinctions? On the character of Neandertal occupation of northern environments", *Comptes Rendus Palevol,* 8: 503–9.

HUFF, C. D.; XING, J.; ROGERS, A. R.; WITHERSPOON, D., and JORDE, L. B. (2010): "Mobile Elements Reveal Small Population Size in the Ancient Ancestors of Homo sapiens", *Proceedings of the National Academy of Sciences,* 107: 2147–52.

JABLONSKI, N. G.; WHITFORT, M. J.; ROBERTS-SMITH, N., and QINQI, X. (2000): "The Influence of Life History and Diet on the Distribution of Catarrhine Primates during the Pleistocene in Eastern Asia", *Journal of Human Evolution,* 39: 131–57.

KAIFU, Y. (2017): "Archaic Hominin Populations in Asia before the Arrival of Modern Humans: Their Phylogeny and Implications for the 'Southern Denisovans", *Current Anthropology,* 58: S418–S433.

KINTIGH, K. W.; ALTSCHUL, J. H.; BEAUDRY, M. C.; DRENNAN, R. D.; KINZIG, A. P.; KOHLER, T. A.;... and ZEDER, M. A. (2014): "Grand Challenges for Archaeology", *Proceedings of the National Academy of Sciences,* 111: 879–80.

LAHR, M. M., and FOLEY, R. (2001): "Mode 3, Homo Helmei and the Pattern of Human Evolution in the Middle Pleistocene", in L. Barham and K. Robson-Brown (eds.), *Human Roots. Africa and Asia in the Middle Pleistocene.* Western Academic & Specialist Press Limited, Bristol: 23–39.

LEWIS, M. E. (1997): "Carnivoran Paleoguilds of Africa: Implications for Hominid Food Procurement Strategies", *Journal of Human Evolution,* 32: 257–88.

LI, H.; KUMAN, K., and LI, C. (2018): "What Is Currently (Un)known about the Chinese Acheulean, with Implications for Hypotheses on the Earlier Dispersal of Hominins", *Comptes Rendus Palevol,* 17: 120–130.

LIU, W.; ZHANG, Y. Y., and WU, X. Z. W. (2005): "Middle Pleistocene Human Cranium from Tangshan (Nanjing), Southeast China: A New Reconstruction and Comparisons with Homo erectus From Eurasia and Africa", *American Journal of Physical Anthropology,* 127: 253–62.

LYCETT, S. J., and BAE, C. J. (2010): "The Movius Line Controversy: The State of the Debate", *World Archaeology,* 42: 521–44.

LYCETT, S. J., and NORTON, C. J. (2010): "A Demographic Model for Palaeolithic Technological Evolution: The Case of East Asia and the Movius Line", *Quaternary International,* 211: 55–65.

MARTINÓN-TORRES, M.; BERMÚDEZ DE CASTRO, J. M.; GÓMEZ-ROBLES, A.; ARSUAGA, J. L.; CARBONELL, E.; LORDKIPANIDZE, D.;... and MARGVELASHVILI, A. (2007): "Dental Evidence on the Hominin Dispersals during the Pleistocene", *Proceedings of the National Academy of Sciences,* 104: 13279–82.

MARTINÓN-TORRES, M.; XING, S.; LIU, W., and BERMÚDEZ DE CASTRO, J. M. (2018): "A 'Source and Sink' Model for East Asia? Preliminary Approach through the Dental Evidence", *Comptes Rendus Palevol,*17: 33–43.

MELORO, C., and CLAUSS, M. (2012): "Predator-Prey Biomass Fluctuations in the Plio-Pleistocene", *Palaios,* 27: 90–96.

MOVIUS, H. L. (1948): "The Lower Paleolithic Cultures of Southern and Eastern Asia", *Transactions American Philosophical Society (New Series),* 38: 329–420.

NENZÉN, H. K.; MONTOYA, D., and VARELA, S. (2014): "The Impact of 850,000 Years of Climate Changes on the Structure and Dynamics of Mammal Food Webs", *PLoS ONE,* 9: e106651.

NJAU, J. K., and BLUMENSCHINE, R. J. (2012): "Crocodylian and Mammalian Carnivore Feeding Traces on Hominid Fossils from FLK 22 and FLK NN 3, Plio-Pleistocene, Olduvai Gorge, Tanzania", *Journal of Human Evolution,* 63: 408–17.

NJAU, J. K., and GILBERT, W. H. (2016): "Standardizing Terms for Crocodile-Induced Bite Marks on Bone Surfaces in Light of the Frequent Bone Modification Equifinality Found to Result from Crocodile Feeding Behavior, Stone Tool Modification, and Trampling", *FOROST (Forensic Osteology),* 3: 1–13.

NORTON, C. J., and BRAUN, D. R. (eds.) (2010): *Asian Paleoanthropology: From Africa to China and Beyond.* Springer, Heidelberg.

NORTON, C. J.; JIN, C.; WANG, Y., and ZHANG, Y. (2010): "Rethinking the Palearctic-Oriental Biogeographic Boundary in Quaternary China", in C. J. Norton and D. R. Braun (eds.), *Asian Paleoanthropology: From Africa to China and Beyond.* Springer, Heidelberg: 81–100.

O'REGAN, H. J.; TURNER, A.; BISHOP, L. C.; ELTON, S., and LAMB, A. L. (2011): "Hominins without Fellow Travellers? First Appearances and Inferred Dispersals of Afro-Eurasian Large-Mammals in the Plio-Pleistocene", *Quaternary Science Reviews,* 30: 1343–52.

PANTE, M. C.; NJAU, J. K.; HENSLEY-MARSCHAND, B.; KEEVIL, T. L.; MARTÍN-RAMOS, C.; PETERS, R. F., and TORRE, I. DE LA (2018): "The Carnivorous Feeding Behavior of Early Homo at HWK EE, Bed II, Olduvai Gorge, Tanzania", *Journal of Human Evolution,* 120: 215–35.

PARFITT, S. A.; ASHTON, N. M.; LEWIS, S. G.; ABEL, R. L.; COOPE, G. R.; FIELD, M. H.;... and STRINGER, C. B. (2010): "Early Pleistocene Human Occupation at the Edge of the Boreal Zone in Northwest Europe", *Nature,* 466: 229–33.

PATTERSON, D. B.; BRAUN, D. R.; BEHRENSMEYER, A. K.; MERRITT, S.; ŽLIOBAITĖ, I.;... and BOBE, R. (2017): "Ecosystem Evolution and Hominin Paleobiology at East Turkana, Northern Kenya between 2.0 and 1.4 Ma", *Palaeogeography, Palaeoclimatology, Palaeoecology,* 481 (1): 1–13.

PEI, S.; DENG, C.; TORRE, I. DE LA; JIA, Z.; MA, D.; LI, X., and WANG, X. (2019): "Magnetostrati Graphic and Archaeological Records at the Early Pleistocene Site Complex of Madigou (Nihewan Basin): Implications for Human Adaptations in North China", *Palaeogeography, Palaeoclimatology, Palaeoecology,* 530: 176–89.

PEI, S.; XIE, F.; DENG, C.; JIA, Z.; WANG, X.; GUAN, Y.;... and TORRE, I. DE LA (2017): "Early Pleistocene Archaeological Occurrences at the Feiliang Site, and the Archaeology of Human Origins in the Nihewan Basin, North China", *PLoS ONE,* 12: e0187251.

PETRAGLIA, M. (2017): "Hominins on the Move: An Assessment of Anthropogenic Shaping of Environments in the Palaeolithic", in M. Petraglia, N. Boivin and R. Crassard (eds.): *Human Dispersal and Species Movement: From Prehistory to the Present.* Cambridge University Press, Cambridge: 90–118.

PETRAGLIA, M. D., and KORISETTAR, R. (eds.) (1998): *Early Human Behavior in Global Context. Rise and Diversity of the Lower Paleolithic Record.* Routledge, London.

PETRAGLIA, M. D., and SHIPTON, C. (2008): "Large Cutting Tool Variation West and East of the Movius Line", *Journal of Human Evolution,* 55: 962–66.

POBINER, B. L., and BLUMENSCHINE, R. J. (2003): "A Taphonomic Perspective on Oldowan Hominid Encroachment on the Carnivoran Paleoguild", *Journal of Taphonomy,* 1: 115–41.

POTTS, R. (1996): *Humanity's Descent. The Consequences of Ecological Instability.* Morrow, New York.

PREMO, L. S., and KUHN, S. L. (2010): "Modeling Effects of Local Extinctions on Culture Change and Diversity in the Paleolithic", *PLoS ONE,* 5: e15582.

RIGHTMIRE, G. P. (2008): "Homo in the Middle Pleistocene: Hypodigms, Variation, and Species Recognition", *Evolutionary Anthropology,* 17: 8–21.

ROEBROEKS, W. (2005): "Life on the Costa del Cromer", *Nature,* 438: 921–22.

— (2006): "The Human Colonisation of Europe: Where Are We?", *Journal of Quaternary Science,* 21: 425–35.

ROEBROEKS, W., and VILLA, P. (2011): "On the Earliest Evidence for Habitual Use of Fire in Europe", *Proceedings of the National Academy of Sciences,* 108: 5209–14.

ROWLANDS, M.; LARSEN, M., and KRISTIANSEN, K. (1987): *Centre and Periphery in the Ancient World.* Cambridge University Press, Cambridge.

RUFF, C. B. (1993): "Climatic Adaptation and Hominid Evolution: The Thermoregulatory Imperative", *Evolutionary Anthropology,* 2: 53–60.

SAHLE, Y.; EL ZAATARI, S., and WHITE, T. D. (2017). «Hominid Butchers and Biting Crocodiles in the African Plio–Pleistocene», *Proceedings of the National Academy of Sciences,* 114: 13164–69.

SCHICK, K., and TOTH, N. (2000): "Origin and Development of Tool-Making Behavior in Africa and Asia", *Human Evolution,* 15: 121–28.

SCHICK, K. D. (1994): "The Movius Line Reconsidered: Perspectives on the Earlier Paleolithic of Eastern Asia", in R. Corruccini and R. Ciochon (eds.), *Integrative Paths to the Past: Paleoanthropological Advances in Honor of F. Clark Howell.* Prentice Hall, Englewood Cliffs: 569–96.

SHEN, G.; GAO, X., and GRANGER, D. E. (2009): "Age of Zhoukoudian Homo erectus Determined with 26Al/10Be Burial Dating", *Nature,* 458: 198–200.

SHENNAN, S. (2000): "Population, Culture History, and the Dynamics of Culture Change", *Current Anthropology,* 41: 811–35.

STRINGER, C., and GALWAY-WITHAM, J. (2018): "When Did Modern Humans Leave Africa?", *Science,* 359: 389–90.

TALLAVAARA, M.; LUOTO, M.; KORHONEN, N.; JÄRVINEN, H., and SEPPÄ, H. (2015): "Human Population Dynamics in Europe over the Last Glacial Maximum", *Proceedings of the National Academy of Sciences,* 112: 8232–37.

TENNIE, C.; PREMO, L. S.; BRAUN, D. R., and MCPHERRON, S. P. (2017): "Early Stone Tools and Cultural Transmission: Resetting the Null Hypothesis", *Current Anthropology,* 58: 652–72.

TONG, H. (2006): "Composition des faunes de mammifères quaternaires en Chine selon un gradient Nord-Sud", *L'Anthropologie,* 110: 870–87.

TONG, H.; HU, N.; LIU, J., and CLARKE, R. (2011): "Inter-Regional Comparisons on the Quaternary Large Mammalian Faunas between China and Sub-Saharan Africa", *Acta Geologica Sinica,* 85: 91–106.

TORO-MOYANO, I.; MARTÍNEZ-NAVARRO, B.; AGUSTÍ, J.; SOUDAY, C.; BERMÚDEZ DE CASTRO, J. M.; MARTINÓN-TORRES, M.;... and PALMQVIST, P. (2013): "The Oldest Human Fossil in Europe, from Orce (Spain)", *Journal of Human Evolution,* 65: 1–9.

TORRE, I. DE LA (2009): "Technological Strategies in the Lower Pleistocene at Peninj (West of Lake Natron, Tanzania)", in K. Schick and N. Toth (eds.), *The Cutting Edge: New Approaches to the Archaeology of Human Origins.* Stone Age Institute Press, Bloomington: 93–113.

— (2011): "The Origins of Stone Tool Technology in Africa: A Historical Perspective", *Philosophical Transactions of the Royal Society B: Biological Sciences,* 366: 1028–37.

TORRE, I. DE LA, and MORA, R. (2009): "Remarks on the Current Theoretical and Methodological Approaches to the Study of Early Technological Strategies in Eastern Africa", in E. Hovers and D. R. Braun (eds.), *Interdisciplinary Approaches to the Oldowan.* Springer, Dordrecht: 15–24.

TRAUTH, M. H.; MASLIN, M. A.; DEINO, A., and STRECKER, M. R. (2005): "Late Cenozoic Moisture History of East Africa", *Science,* 309: 2051–53.

TZEDAKIS, P. C.; HUGHEN, K. A., and HARVATI, K. (2007): "Placing Late Neanderthals in a Climatic Context", *Nature,* 449: 206–8.

VAN VALEN, L. (1973): "A New Evolutionary Law", *Evolutionary Theory,* 1: 1–30.

VAN VALKENBURGH, B. (2001): "The Dog-Eat-Dog World of Carnivores. A Review of Past and Present Carnivore Community Dynamics", in C. B. Stanford and H. T. Bunn (eds.), *Meat-Eating & Human Evolution.* Oxford University Press, Oxford: 101–21.

VRBA, E. (1996): "Climate, Heterochrony and Human Evolution", *Journal of Anthropological Research,* 52: 1–29.

WALLERSTEIN, I. (1974). *The Modern World-System,* vol. I: *Capitalist Agriculture and the Origins of the European World-Economy in the Sixteenth Century.* Academic Press, New York.

WERDELIN, L., and LEWIS, M. E. (2013). "Temporal Change in Functional Richness and Evenness in the Eastern African Plio-Pleistocene Carnivoran Guild", *PLoS ONE,* 8: e57944.

WU, X. J.; PEI, S. W.; CAI, Y. J.; TONG, H. W.; LI, Q.; DONG, Z.;... and LIU, W. (2019): "Archaic Human Remains from Hualongdong, China, and Middle Pleistocene Human Continuity and Variation", *Proceedings of the National Academy of Sciences,* 116: 9820–24.

XIE, Y.; MACKINNON, J., and LI, D. (2004): "Study on Biogeographical Divisions of China", *Biodiversity & Conservation,* 13: 1391–1417.

ZHU, R. X.; HOFFMAN, K. A.; POTTS, R.; DENG, C. L.; PAN, Y. X.; GUO, B.;... and HUANG, W. W. (2001): "Earliest Presence of Humans in Northeast Asia", *Nature,* 413: 413–17.

ZHU, R. X.; POTTS, R.; XIE, F.; HOFFMAN, K. A.; DENG, C. L.; SHI, C. D.;... and WU, N. Q. (2004): "New Evidence on the Earliest Human Presence at High Northern Latitudes in Northeast Asia", *Nature,* 431: 559–62.

ZHU, Z.; DENNELL, R.; HUANG, W.; WU, Y.; QIU, S.; YANG, S.;... and OUYANG, T. (2018): "Hominin Occupation of the Chinese Loess Plateau since about 2.1 Million Years Ago", *Nature,* 559: 608–12.