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Editorial

Paleofloras, paleovegetation and human evolution

This special issue is aimed at exploring the links between environmental changes and the patterns of biological and cultural evolution of hominins. Its conception arises from the relative imbalance between hominin fossil discoveries and knowledge about paleoenvironments associated with these findings. The collection includes both new records and empirical work, with emphasis on floristic and vegetation features, as their crucial role in shaping landscapes and habitat resources. Within an evolutionary framework, it is this focus that has attracted the interest of a number of scholars concerned with the postulation that selective pressures on Primates in favor of bipedalism could be related to the depletion of forests in eastern and central Africa and that in turn this was as a consequence of climatic changes after 6 Ma (Dart, 1925; Sockol et al., 2007). This postulation, so-called Savannah hypothesis, contends that mammalian evolution itself can be related to the spread of more open (C_4) grasslands in East Africa after about 10 Ma (Sage, 2004; Feakins et al., 2013; Uno et al., 2016). The evolution of Poaceae during the Paleogene and its ecological success at the biome scale during the Neogene (Carrión, 2003; Willis and McElwain, 2013) can be therefore interpreted as historical contingencies (ss. Gould, 1989, 2002) for human evolution (Fig. 1).

Cultural transitions are doubtlessly involved. The emergence of the Oldowan industry and the internal diversification of australopithecines took place within the context of increasing variability in climatic conditions after about 2.8 Ma (Bobe et al., 2002; deMenocal, 2004). The appearance of *Homo erectus* and the associated Acheulian industry in Africa was coeval with environmental variability changes after 1.8 Ma (deMenocal and Bloemendal, 1995; deMenocal, 2004). From a more paleogeographic perspective, the earliest expansions of *Homo* towards southern Africa and Asia seem synchronous with the extinction of *Paranthropus* and have been correlated to the climatic changes that provoked desertification within a large part of the savannah biome of the Rift Valley and the southern Africa highveld (Ségalen et al., 2004). In this scenario, the new discoverings of *H. erectus* in Shangchen, China, at 2.12 Ma (Zhu et al., 2018) must be now taken into account. Yet, the earliest dispersals from Africa of *Homo sapiens* have been interpreted as associated with dry spells (Scholz et al., 2007; deMenocal, 2008; Carto et al., 2008; Armitage et al., 2011; Lopez et al., 2016).

Technological innovation may possibly be connected with environmental variability (Anton et al., 2014). Considering Eurasia, Kahlke et al. (2011) indicated that the tendency of human fossil and archeological sites to occur preferentially in areas with a high diversity of habitats and resources, including large river systems. These characteristics are especially visible between 1.7 and 1.3 Ma, when humans spread westward through the Mediterranean region, and subsequently northwards during the early Middle Pleistocene interglacials. These authors argued that stable environmental conditions would be correlated with low-risk application of proven subsistence strategies, while innovation would have been prompted by high rates of environmental change, such as during the Upper Pleistocene when the western Palearctic experienced its most unfavorable conditions. For a more recent period, Finlayson and Carrión (2007), after examining the distribution of Middle to Upper Paleolithic transitional industries across Europe from 45 to 30 ka, found sharp physiographical boundaries between different types of archeological sites, suggesting that these industries, made by both Neanderthals and anatomically modern humans (AMHs), were independent responses to rapid climatic changes. These stresses, experienced by human populations across the Palearctic, would have created a platform for innovation that, in the Late Pleistocene, involved trends towards light, portable and projectile technology, portable over long distances thereby reducing risk in an unpredictable environment.

Fig. 1. The cover image of this special issue displays a Neanderthal skull and a grass (Poaceae) flower. It symbolizes the concept of historical contingency in evolution based on the fact that it is unlikely that hominins would have evolved to our species if the grasses had not originated previously. Evidence of fossil Poaceae dates from the late Cretaceous/early Paleogene. They radiated from the Eocene onwards and ecologically spread in savanna biomes ever since the Miocene. Today, grasses are probably the most important plant family on Earth, dominating several biomes and ecosystems, influencing global climates, providing food for humans, and covering nearly half of the terrestrial surface. Plant and human evolution cohered through two stories of evolutionary success. *Artwork: Gabriela Amorós Seller.*

The vegetation and other features of the physical environment have been regarded trigger points in the evolution, adaptation and/or

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dispersal of such hominin taxa as *Sahelanthropus tchadensis* at 7–6 Ma (Brunet et al., 2002, 2005; Lebatard et al., 2008), *Orrorin tugenensis* at 6.2–5.8 Ma (Pickford and Senut, 2001; Senut et al., 2001; Senut, 2006; Roche et al., 2013), *Ardipithecus ramidus* and *A. kaddaba* between 5.8 and 4.1 Ma (Haile-Selassie et al., 2004; Suwa and Ambrose, 2014), *Australopithecus anamensis* at 4.2–3.9 Ma (White, 2003), *A. afarensis* at 4–3 Ma (Radosevich et al., 1992; Bonnefille et al., 2004; Haile-Selassie et al., 2010), *A. bahrelghazali* at 3.4–3 Ma (Brunet et al., 1996), *Kenyanthropus platyops* at 3.5–3.2 Ma (Leakey et al., 2001), *Australopithecus garhi* at 2.5 Ma (Asfaw et al., 1999; de Heinzelin et al., 1999), *Homo habilis* at 2.4–2.3 Ma (deMenocal, 2004; Wood and Strait, 2004), *Paranthropus robustus* at 2–1.2 Ma (de Ruiter et al., 2009). In general, paleoecological research has suggested that arboreal environments were important habitats for the Miocene hominins and hominids (Elton, 2008), and that most *Australopithecus* lived in a more forested habitat than *Homo*, which became the first genus adapted to savannah-grassland, grassland and steppe (Jacobs, 2004).

It is pertinent here to cite Dennell and Roebroeks' (2005) savannahstan model that brought together the savanoid environments of the Eurasian and African continent during the Out-Of-Africa 1 event. These authors consider that the first dispersals could have taken place much earlier than the speciation of *H. ergaster-erectus* (e.g. at the time of *H. habilis*), or even that intra-Asian speciation could exist within an open environmental context, although undoubtedly with an important woody component. This model would reduce the emphasis on migration, in this regard it must be considered that there are always taxonomic assumptions behind paleoecological and evolutionary perspectives. In fact, Dennell and Roebroeks (2005) raised the dilemma that would have been brought into debate if *Homo georgicus* had been named *Australopithecus georgicus* and how this simple taxonomic transposition would have changed our perception of the Out-of-Africa 1. Certainly, there is no evidence that australopiths migrated out of Africa, but it cannot be discarded that their absence from the fossil record is not due to taphonomic circumstances (e.g. preservation issues), or lack of prospecting, or differences in the intensity of research. Taphonomic limitations are obvious, as Dennell et al., 2008; Dennell, 2009 pointed out, bearing in mind that the Pliocene savannah grasslands extended from western Africa to northern China.

Traditionally, the preferred interpretations have been habitat-centered, proposing that human morphologic and behavioral adaptations emerged with the African savannah, or were influenced by the environmental pressure of an expanding dry savannah. More recently, hypotheses involving variability selection have been formulated (e.g. Potts, 1998) and are gaining support (Bonnefille et al., 2004; Trauth et al., 2007; Potts and Faith, 2015; Winder et al., 2015). The emphasis here is an ability of hominins to adapt or to respond to environmental change, rather than selection within or due to a single type of environment. While coping with shifts in environmental conditions, resource to behavior versatility, phenotypic plasticity and gene polymorphism would have been of capital importance (Anton et al., 2014). This can be illustrated with *Ardipithecus ramidus*, which would have occupied both wooded areas and wooded grasslands with intensive grazing (WoldeGabriel et al., 2009), or with *Australopithecus anamensis* which has been found at Kanapoi and Allia Bay (Kenya) clearly associated with availability of vegetation mosaics like open savanna with low trees and shrubs, nearby grasslands and gallery forests (Cerling et al., 2013). Similarly, through the study of stable isotopes on pedogenic carbonates at the *Homo* Kanjera site, SW Kenya, Plummer et al. (2009) documented that these hominids moved through a vast mosaic of landscapes, including very open savannas, but also wooded savannas, riparian forest, and lake margin hygrophilous vegetation.

Apart from the aforementioned results, it is perhaps worth mentioning that the connections between hominin evolution and environmental changes have been largely established on the assumption that the main forcing come from some combination of high-latitude influences from glacial–interglacial climate cycles, and low-latitude insolation forcing of African monsoonal rainfall changes (e.g. deMenocal, 1995; Potts, 2013). These are also recorded in terms of vegetation and paleohydrological changes by $\delta^{13}C$ and $\delta^{18}O/\delta D$ measurements, respectively, of plant waxes (Feakins and deMenocal, 2010; Tierney et al., 2017) and paleosol carbonates (Levin, 2015). But environmental variability also exists at basinal and local scales and these may present distinct deviations from regional trends, such as it is explored by Barboni et al. (2019) documenting the importance of groundwater to the first hominin record in Africa. These authors provide new field data from spring sites in the Awash Valley, Ethiopia, and Lake Eyasi-Lake Manyara region, Tanzania, and re-evaluate published data from the *Ardipithecus*-bearing Aramis Member, Ethiopia. The results are important in terms of evolution, adaptation and dispersal. Due to its puzzling physiography, the arid regions of East Africa displayed during the study period a diversity of habitats such as groundwater-fed wetlands, *Hyphaene* palm woodlands, *Phoenix reclinata* palm woodlands, and structurally complex and species-rich forest patches. It bears emphasis that these habitats carry some characteristic pollen and phytolith signals that could be masked by the signal of surrounding grass-dominated shrublands and grasslands.

Barboni et al. (2019) show that the Aramis Member (Awash Valley, Ethiopia), which is so far the best documented paleo-groundwater ecosystem in the region, is just one of the >50 examples in Africa and the Middle East where evidence of groundwater systems co-exist with hominin and/or archeological remains. This paper emphasizes the importance of springs, which at the local scale, favor a distinctive vegetation, rich in species and structurally complex, while at the landscape scale, springs represent hydro-refugia favoring increased gathering of animals that allow migrations during dry periods. These authors show that there is a bias towards edaphically sustained woodlands in the literature dealing with the paleoecology of hominin-bearing sites, and hold the view that early species such as *Sahelanthropus tchadensis, Orrorin tugenensis*, and *Ardipithecus ramidus* lived in mosaic environments consisting of grasslands, mixed grasslands, woodlands, and forests, where wooded habitats were maintained by edaphic rather than regional (climatic) humidity. This is indeed thought-provoking particularity because these ecosystems may have been attractive for arboreal and pre-biped primates in a context of increasing aridity and expansion of grass-dominated open habitats during several episodes of the Miocene and Pliocene.

To improve our knowledge on the relationship between environmental change and hominin evolution as early as during the Late Miocene, Hopley et al. (2019) bring to this issue a new stable isotope and trace element record from a unique karstic system, the Hoogland Cave in the Schurveberg Mountain area of the Gauteng Province in South Africa. The analyzed speleothem is composed of thin layers of calcite interspersed with metastable aragonite, most of which has been diagenetically altered to secondary calcite. The speleothem material shows low $\delta^{13}C$ values which become a valuable proxy of past vegetation. Dated by uranium-lead and magnetostratigraphy between 7.25 and 5.33 Ma, this speleothem is the oldest known cave deposit from the Cradle of Humankind, and the first evidence of Miocene cave infill in this region. So far, the studied paleocave deposits of the Cradle of Humankind come from the Late Pliocene to Early Pleistocene (Herries et al., 2009; Pickering et al., 2011).

The main analytical results by Hopley et al. (2019) involve that a purely C_3 vegetation was present during the Messinian Salinity Crisis in the summer rainfall zone of South Africa millions of years after C_3 dominated vegetation disappeared from the present-day savannahs of eastern and northern Africa (Cerling et al., 2011). There is doubt whether it was a C_3 grassland or a C_3 woodland. However, given the indication of closed canopy forests during several stages of the southern African Plio-Pleistocene, including extremely low $\delta^{13}C$ values in some fossil herbivore teeth and fossil woods, the prevalence of woodlands seems highly probable. By showing that that the regional C_4 grass expansion was post-Messinian, and therefore occurred millions of years later in South Africa than it did in eastern Africa (Cerling et al., 1997), this paleoenvironmental record fits the quantum yield model of Ehleringer et al. (1997) that predicts a temperature/latitudinal control over C_3/C_4 plant distribution. Rainfall depletion (Dupont et al., 2013) and increased fire regimes (Hoetzel et al., 2013) may have also played a role in the arrival of C_4 plants to the region across the Pliocene. In the light of this post-Messinian shift of southern African vegetation, and taking into account the chronology of the main events of hominin evolutionary change in the region, Hopley et al. (2019) revisit the long-held assertion that the African paleovegetation record fails to support the savannah hypothesis of hominin origins (e.g. Domínguez-Rodrigo, 2014). The discussion about the influence of savannah expansion in hominin evolution has focused on eastern Africa (White et al., 2009), because of its continuous record of hominin fossil finds from 6.2 Ma onwards (Senut et al., 2001). The South African record has a rather restricted temporal range of about 3.5 Ma to the Late Pleistocene (Dirks et al., 2017), with a lack of hominin fossils from the 7 to 4 Ma time range. Should this hiatus be addressed in the near future, this new record brings a potentially useful paleoecological perspective.

For the Olduvai Gorge in Tanzania, a new high-resolution paleoecological record is presented by Albert et al. (2018) on the HWK W site (Henrietta Wilfrida Korongo West), more specifically in the unexplored Tuff ID-IE stratum (1.83–1.84 Ma), characterized by Oldowan lithics and *Homo habilis* processed bones. During the last two decades, the HWK W locality has been a continuous source of paleobiological information resulting from the Olduvai Landscape Palaeoanthropology Project (OLAPP) with its abundance of fossil bones, stone artifacts and plant macrofossil remains. Olduvai as a whole is, indeed, a remarkable hominin fossil site owing to its unique sedimentary and preservational features. Alternating with erosional phases, the Olduvai Beds record two million years of accumulation of alternating lacustrine and fluvial sediments, mudflows, pyroclastic flows, surges and ashfalls.

Albert et al. (2018) carry out research on phytoliths and plant macrofossils depicting a mosaic characterized by palms, sedges, and C3 and C4 grasses. Local landscapes are physiographically diverse including vegetated fluvial channels, vegetated levées and backswamp environments. The occurrence of freshwater wetlands, although episodically dissecated, is confirmed by a fine record of diatoms and sponge spicules. The faunal record parallels the paleobotanical inference, with hippopotamus, crocodile and herbivores associated with freshwater bodies. This vegetation environment offered to hominins a survival context including potable freshwater, scavengeable carcasses, and edible plants such as a number of palm fruits, starch-rich rhizomes from sedges and *Typha* rootstock, which may have been exposed during the dry season. Climbing palms such as *Hyphaene petersiana* may have also been useful to escape from predators. The work of Albert et al. (2018) contribute substantially to former paleoecological records based on pollen analysis, fauna, and carbon isotopes (e.g. Bonnefille, 1984; Kappelman et al., 1997; Fernández-Jalvo et al., 1998). This habitat diversity is obviously determined by its geological setting, crucially topography. Bailey and King (2011) used field and remote sourced imagery from Africa and the Red Sea region to investigate the relationship of active tectonics and complex topography with archeological and fossil material. They concluded that regions that are geologically dynamic will favor the creation and maintenance of mosaic habitats through time.

Stable carbon isotopic analyses of herbivore dental tissues and carbonates from ancient soils are common proxies for reconstructing the paleovegetational context of human evolution (e.g., Sponheimer et al., 2013; Wynn et al., 2016). Using an empirical approach, Du et al. (2019) compare $\delta^{13}C$ patterns from herbivore enamel and paleosol carbonates from geological (sub)members in the Awash Valley, Ethiopia, and Turkana Basin, Kenya, from ~4.4 to 1 million years ago. Interestingly, they find that median herbivore enamel $\delta^{13}C$ is typically ~5–7 per mil (‰) higher than that from paleosol carbonates within a given (sub)member. These authors show that $\delta^{13}C$ values from herbivore enamel and paleosol carbonates offer paleovegetation data at different spatiotemporal scales, both of which are informative for hominin habitat reconstructions. It is worth emphasizing that a majority of Plio-Pleistocene fossiliferous deposits are connected with fluvial settings in which paleosol carbonates represent the surrounding floodplain woodlands and shrubs, resulting in a lower $\delta^{13}C$ (i.e. more C_3) signal. In contrast, fossil teeth of wide ranging herbivores generate an enriched (i.e. more C_4) and more variable $\delta^{13}C$ signal where some taxa fed in floodplain woodlands and others on open grasslands distal to the floodplain. It is suggested that a careful consideration of the spatial and temporal signals inherent in these and other proxies should be applied in future studies.

Experimental work in the investigation on dietary components of hominin habitats is of paramount importance. A monumental study was performed by Melamed et al. (2016) in the Acheulian site of Gesher Benot Ya'aqov, Israel. This work provided an impressive archive of food plants, some 780,000 years old, comprising 55 taxa, including nuts, fruits, seeds, vegetables, and plants producing underground storage organs. The reflected diet was extraordinarily diverse and shed light on hominin abilities to adjust to new environments and exploit different flora.

With the goal to explore how season, plant type, and plant organ affect the quality of plant foods, and bearing in mind the potential corollaries for early hominin paleoecology, Henry et al. (2019) measure the macronutrient and antifeedant properties of plant samples collected from several habitats within the Cradle of Humankind World Heritage site in South Africa. This work shows that all of these factors exert some kind of influence, both in combination and individually. Noticeably, in spite of strong temperature and rainfall variation between seasons in the region, most nutritional properties, except tannins, phenols, and protein, remained relatively constant between the wet and dry seasons. Habitats, however, displayed a most critical effect on the nutritional value, therefore suggesting that patch choice models may be appropriate for exploring hominin feeding behaviors. Surprisingly, woodland habitats were more nutritionally valuable than expected, especially due to the high protein supply of grasses which becomes essential during the dry season. Overal, wetland and river edge habitats were low in protein and calculated metabolizable energy, suggesting they were marginal for hominins in the Highveld floristic region.

The Middle Pleistocene Florisbad site is re-visited by Scott et al. (2019) providing new pollen analysis and a review of past palynological research in this thermal spring mound, renowned by have produced outstanding faunal, hominin and archeological records, and today within the grassland biome of South Africa. The site includes early Middle Stone Age (MSA) artifacts, and abundant vertebrate fauna (e.g. Grün et al., 1996; Kuman et al., 1999), and what makes the site unique is the recovery from the deepest part of the deposit of a hominin cranium with facial bones thought to be an intermediate form between *H. heidelbergensis* and *H. sapiens* (Brink, 2016). The pollen sequences are characterized by alternating pollen-rich organic peaty horizons and hiatuses or pollen-poor layers of sandy and clayey deposits. The pollen taphonomy of the site undoubtedly affects the pollen assemblages in their preservation and source areas. The lowermost beds containing the Florisbad hominin (dated to 259 ka) and its associated Middle Pleistocene fauna, experienced cool moist and grassy conditions. The overlying Middle Stone Age layers are Last Interglacial in age (MIS 5e; ca. 124–119 ka), and the pollen contents comprising upland fynbos shrubs unexpectedly suggests that cool conditions prevailed. It is concluded that the hominins occupied the Florisbad mound and surroundings under cold continental climatic conditions within a temperate grassland involving frost. Improving the paleobotanical record implies carrying out an analysis of the palynologically unstudied Test Pit 3 at the site and couple the palynological results with an ongoing phytolith study.

The Eurasian Cenozoic also offers possibilities for the paleoecological research of the patterns and processes of human evolution, largely dealing with *Homo erectus, H. heidelbergensis, H. neanderthalensis* and *H. sapiens*. The Coexistence Approach (CA) method permits the quantification of temperature and precipitation values based on pollen and macroflora assemblages. Using this protocol, Altolaguirre et al. (2019) develop a climatic quantification for the Early Pleistocene in the Iberian Peninsula through the comparison of CA patterns in several hominin-bearing sites. The time period is one of the disputes in paleoclimatic terms, because despite its obvious variability (Lisiecki and Raymo, 2005; Leroy et al., 2011), and the impacts of climatic changes on vegetation and floristic extinctions (González-Sampériz et al., 2010), it seems there were no true, eccentricity-driven glacial phases like during the later stages of the Pleistocene (Ehlers and Gibbard, 2008). The peninsula is also important for the survival of Paleotropical and Arctotertiary plant species (Postigo-Mijarra and Barrón, 2017) and for current theories on human evolution within Eurasia (Carrión et al., 2011), with special attention devoted to the southeastern sites of the Baza Basin and Atapuerca, where some of the oldest and most complete records of their presence can be found (e.g. Rodríguez et al., 2011; Bermúdez de Castro and Martinón-Torres, 2013).

In Altolaguirre et al. (2019), a picture of climatic cyclicity with latitudinal aridity gradients is postulated. The wettest conditions may have allowed for the earliest hominin communities arriving in Europe to rapidly thrive during "interglacial" periods, while they would have survived the mild glacial Early Pleistocene stages. Some particular trajectories are worth mentioning. The Gran Dolina vegetation, for example, would have developed during a climate that experienced warm summer temperatures while the site of Cal Guardiola depicts a vegetation with evidences of warmer annual and winter temperatures, as well as slightly colder summer temperatures. In general, the Iberian Peninsula shows a climate similar to the modern-day climate during the Early Pleistocene glacial stages, but somewhat wetter and warmer during the interglacials, and with a overall weaker seasonality. The shifts of coexistence intervals in the long pollen sequences of Palominas, Tres Pins, and Bòvila Ordis might show the existence of slight temperature changes during the deposition of these sections, pointing to warmer periods during "interglacials" and colder during "glacial" stages. The coexistence intervals eventually show values above the modern precipitation measurements such as in Cal Guardiola. Between-site disparities can be taken as trends in latitudinal gradients, which may account for climatic regionalizations that would have discouraged the spread of forests throughout the Iberian Peninsula, but perhaps provided habitable niches for hominins even during the less favorable episodes. The model proposed for southern Spain experienced the existence of mosaic landscapes with open environments rich in plant and animal resources. Interestingly, the climatic data obtained by the CA method for the sections of Gran Dolina, Cal Guardiola and Palominas accord with the paleoclimatic models obtained by the Mutual Climatic Range method as applied to amphibian and squamate fossil assemblages (Blain et al., 2013).

Another methodological study was carried out by Audiard et al. (2019) who explore the paleoenvironmental potential of a combined approach using a combination of taxonomical discrimination and $\delta^{13}C$ isotopic analyses on archeological charcoal from a middle Paleolithic sequence at La Combette. At different time scales, isotopic results are consistent with other paleoenvironmental data (anthracology, micromorphology, palynology) providing in some cases, better resolution information than taxonomic identification, probably due to the quicker physiological response of the plants compared to the changes in forest biodiversity under climatic pressure. This work assess the temporal relationships between the taxonomical and isotopic signals, leading to a discussion of Neanderthal fuel management and mobility patterns, as well as Neanderthal occupation in the face of climatic variability. Certainly, conventional anthracology needs to combine with other sources of paleoecological inference to make its findings robust, and this paper will contribute to it.

Phytodiversity reservoirs could have been pivotal for human survival and perhaps genetic changes conducting to speciation during the Eurasian glacial stages. Carrión et al. (2018) present pollen analyses performed on hyaena coprolites from Vanguard Cave, Gibraltar, with the aim of depicting the vegetation landscapes of the southern Iberian Neanderthals during the MIS 3 (c. 59–29 kya). This work combine with former paleobotanical research at the adjacent Gorham's Cave (Carrión et al., 2008) to provide information on the paleoenvironments during MIS 3 and MIS 2 (c. 29–14 kya). The Paleolithic vegetation of Gibraltar was diverse, with pine, oak, juniper, *Pistacia*, and mixed woodlands, savannahs, riverine forest patches, heliophytic matorrals, rocky scrub with chamaephytes and hemicryptophytes, grasslands with heaths, shrubby grasslands, steppe-like saltmarshes, and littoral vegetation. Former revisions of the paleoecological data for the Iberian and European Pleistocene (Carrión et al., 2008, 2013; González-Sampériz et al., 2010) show that the southern coasts of Iberia are unique in showing the coexistence of thermo-, meso-, and supramediterranean plant and animal species, including dry and humid, forested, and treeless biotopes. In addition, the most thermophilous plant taxa (*Maytenus, Calicotome, Withania, Periploca, Osyris, Olea, Pistacia*) only co-occur in the southernmost fossil sites in coastal areas extending from Murcia to Gibraltar. Altogether this paleovegetation picture has important implications for existing arguments about the long survival of Neanderthals in the Iberian Peninsula (Carrión, 2004; Stewart, 2005; Finlayson and Carrión, 2007; Jiménez-Espejo et al., 2007; Wood et al., 2013; Higham, 2014; Zilhão et al., 2017). The paper by Carrión et al. (2018) stresses that a major part of this scientific issue has been the inability to place paleoanthropological and archeological results in ecological context that is so critical to presenting a solid base for understanding of human behavior and evolution. This paper shows, by providing a detailed botanical perspective of the environments in which the Gibraltar Neanderthals lived, just how crucial such information is.

Surely the former study case can be extrapolated to the remaining European peninsulas in the Mediterranean Basin. The first humans of Cueva Negra (Heidelgergs) and Sima de las Palomas (Neanderthals) are also associated with environments of very high biodiversity (Carrión et al., 2003; Walker et al., 2008). A recent paleobotanical study in the Mid-Pleistocene, early Neanderthal site of Bolomor Cave, eastern Spain, strongly supports this view (Ochando et al., 2019). The conclusion on the role of phytodiversity refuges may well be extended elsewhere to worldwide strongholds of biological diversity. Carrión et al. (2011) addressed the question of whether the appearance of evolutionary novelties within hominins could be concentrated in biodiversity hotspots. Clearly, the Horn of Africa hotspot and its southern fringes in Kenya and Tanzania embrace the first occurrences for genera and most of the earliest for species of fossil hominins, including *Ardipithecus*, *Orrorin, Australopithecus, Kenyanthropus, Paranthropus,* and *Homo.* This region might also be critical for the speciation of Heidelbergs, and innovation conducting to Oldowan and Acheulean tools at 2.6 and 1.7 Ma, respectively while in other regions the southern African hotspot would have been the matrix for other australopithecines (*A. africanus, A. sediba, P. robustus*), the Caucasus for the first *Homo* occurrences in Eurasia, the Mediterranean basin for *Homo antecessor*, the Mountains of southwestern China for the Yuanmou hominins, dated to c. 1.7 Ma (Zhu et al., 2008).

A puzzling question can be why these regions should have significance for hominin speciation or morphological innovation? As mentioned above, hotspots occur in coherence with dynamic landscapes and supporting a wide array of habitats (Bailey and King, 2011), derived from a long evolutionary history as a source of phylogenetic diversity (Spathelf and Waite, 2007). Still, hotspots are regions with high levels of ecological interaction, co-evolutionary networks and biotic complexity, which altogether affect diversification by inducing speciation and reducing extinction rates (Bascompte et al., 2006; Ricklefs, 2010). Plausibly, most hominin species might have been derived from small, speciating populations developed in geographical isolation in Africa and Asia. However, allopatric speciation should not be considered exclusive. Factual information support the view that different species were able to live within the same region for long periods of time as in the case of *H. habilis* and *H. erectus* in the region of Lake Turkana (for perhaps 500 ka, Spoor et al., 2007). Similar situations have been postulated in Dmanisi (Lordkipanidze et al., 2007) and probably in other Eurasian contexts for at least three Pleistocene hominin species that would have crossed each other in their early evolutionary existence (Lalueza, 2013; Slon et al., 2018; Wolf and Akey, 2018). Sympatric speciation, probably underestimated in this field of research, can be rapid when the incipient species coexist and interbreed (Andrew et al., 2010). In fact, genes subject to strong divergent selection between incipient species, such as those relevant for habitat choice, can create differentiated regions in the genome (Kelleher and Barbash, 2010). Indeed, this model has not exclusively accounted for human evolution because, as shown by Spathelf and Waite (2007) almost all primates retain important amounts of phyletic diversity in hotspots. With these comments we wish to present a number of papers to inspire further research on paleoenvironments, especially the role of vegetation, in human evolution.

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J.S. Carrión
Department of Plant Biology, Faculty of Biology, University of Murcia, Campus de Espinardo, 30100 Murcia, Spain
Corresponding author.
E-mail address: carrion@um.es

L. Scott
Department of Plant Sciences, University of the Free State, P.O. Box 339, Bloemfontein 9300, South Africa

P. deMenocal
Lamont-Doherty Earth Observatory, Department of Earth and Environmental Sciences, Columbia University, New York, USA