



General Palaeontology, Systematics and Evolution (Palaeobiogeography)

## Criteria for identifying the African origin of early Pleistocene mammalian fauna in Eurasia



### *Critères pour l'identification de l'origine africaine d'une faune mammalienne du Pléistocène inférieur en Eurasie*

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#### ARTICLE INFO

##### Article history:

Received 17 April 2017

Accepted after revision 2 August 2017

Available online 29 September 2017

Handled by Lorenzo Rook

##### Keywords:

Biogeography

Chronology

Taxonomy

Dispersal

Out of Africa

*Homo*

Early Pleistocene

#### ABSTRACT

The “Migratory Wave Hypothesis” suggests that early Pleistocene *Homo* dispersed from Africa together with a suite of other large mammals. Support for this hypothesis has been found primarily at the sites of ‘Ubeidiya, (Israel) and Venta Micena (Spain) where a high number of African taxa have been identified. This paper presents a critical evaluation of how we can identify these taxa and suggest criteria for the identification of taxa of African origin present in Eurasia during the early Pleistocene. Biogeography, taxonomy and chronology are used to develop criteria that have an effect on how we defined or identify African taxa. By critically evaluating the number of African taxa in Eurasia through the lens of these criteria, the number of African taxa may be reduced from a maximum of 30 to a minimum of six. The actual number may be either one of these two numbers, or any number in between, depending on how rigorous we are in applying the criteria. Thus, while the criteria presented in this paper have face value, they are not in any way more “correct” than other criteria, but are heuristic in presenting the difficulties in assigning an African origin to fauna found in early Pleistocene sites. This points to the need to be cautious when making inferences about the relationship between the dispersal of *Homo* with that of other African taxa.

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#### R É S U M É

Les « hypothèses de migration par vagues » suggèrent que l'*Homo* du Pléistocène inférieur s'est dispersé à partir de l'Afrique avec une série d'autres grands mammifères. Ces hypothèses trouvent leur fondement principal aux sites d'‘Ubeidiya (Israël) et de Venta Micena (Espagne), dans lesquels un grand nombre de taxons africains ont été identifiés. L'article présente une évaluation critique de la manière dont ces taxons peuvent être identifiés et suggèrent des critères pour l'identification des taxons d'origine africaine présents en Eurasie au Pléistocène inférieur. La biogéographie, la taxonomie et la chronologie sont utilisées pour développer des critères ayant un effet sur la manière dont les taxons africains sont définis ou identifiés. Par évaluation critique du nombre des taxons africains présents en Eurasie, à la lumière de ces critères, ce nombre peut être réduit d'un maximum de 30 à un minimum de six. Le nombre actuel peut être, soit l'un de ces deux nombres, soit n'importe lequel situé entre les deux extrêmes et dépendant de la rigueur avec laquelle ces critères

##### Mots clés :

Biogéographie

Chronologie

Taxonomie

Dispersion

Hors de l'Afrique

*Homo*

Pléistocène inférieur

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<https://doi.org/10.1016/j.crpv.2017.08.003>

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ont été appliqués. Ainsi, bien que les critères présentés dans cet article aient une valeur nominale, ils ne sont en aucune façon plus « corrects » que d'autres, mais sont heuristiques, dans la mesure où ils montrent les difficultés qu'il y a à assigner une origine africaine à la faune trouvée dans les sites du Pléistocène inférieur. Ceci met en évidence la nécessité d'être prudent à propos des déductions que l'on peut faire quant à la relation entre la dispersion d'*Homo* et celle d'autres taxons africains.

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## 1. Introduction

One of the main questions in paleoanthropology and human evolution is the how, what and why of early Pleistocene hominins dispersal from Africa into Eurasia (Palombo, 2013). The Southern Levant (sometimes known as Southwest Asia) has been suggested as one of the corridors through which hominins dispersed (Tchernov and Belmaker, 2004; Thomas, 1985). This unique and isolated province, with its elongated highlands and valleys, is bounded by the Mediterranean coast on the west, the Zagros and the Taurus mountains on the north, the isthmus of Suez and the Nile system on the southwest; the Arabian desert on the south and, the steppes of Syria and Trans-Jordan on the east (Bar-Yosef and Belmaker, 2011).

Several hypotheses have been developed to explain the dispersal of *Homo*. It has been hypothesized that large mammals expanded their range due to the expansion of a grassland environment stretching from northern Africa to central Asia because of a late Pliocene climate change. The term “Savannastan” (Dennell, 2003) refers to the expansion of savanna from East Africa through Asia, an expansion which would have created an ecological corridor enabling the dispersal of hominins along with other savanna-adapted taxa.

Climatic change, viewed as the ultimate driver for human evolution, has been interpreted as pulsed events in which tectonic, climatic and sea level changes altered the “permeability” of the southern Levantine land bridge. The Bab-el-Mandab Strait became a potential land bridge for the passage of fauna during cold periods, when the level of the sea decreased and more land was exposed. The Taurus–Zagros mountain chain became open to the passage of fauna during warm periods, when the mountain top climate was not too extreme. These passages functioned as a barrier or possibly a selective filter for fauna, through which only specific species could spread or pass (Tchernov, 1988).

Empirical support for the above scenario rests upon our ability to correctly identify African taxa in non-African environments. However, identification of taxa of African origin is not straightforward. This is particularly a problem as many researchers do not conduct the identification themselves, but use published reports and faunal lists (many online sites provide easy access to lists of fossil faunas across time and space) to analyze and study biogeographic patterns. Thus, the ability to critically assess what is or is not an African taxon or more accurately, what has a higher probability of being an African taxon, is the foundation for subsequent meta-analysis and reviews.

The aim of the paper is to raise awareness of inconsistencies in the literature, and to illuminate how this discord

affects the interpretation of what is an African taxon. Indeed, a reading of the current literature often obfuscates what precise definition is used by each author. I review the definition of an African taxon across the literature, and show that applying different definitions may affect the number of identified African species in Eurasia, and hence affect our interpretation of the ‘Migratory Wave Hypothesis’. While I do not side with any particular researcher on the identification of a given taxa, I draw attention to issues we need to be cognizant of when conducting literature overviews.

## 2. Identification of African taxa in Eurasia

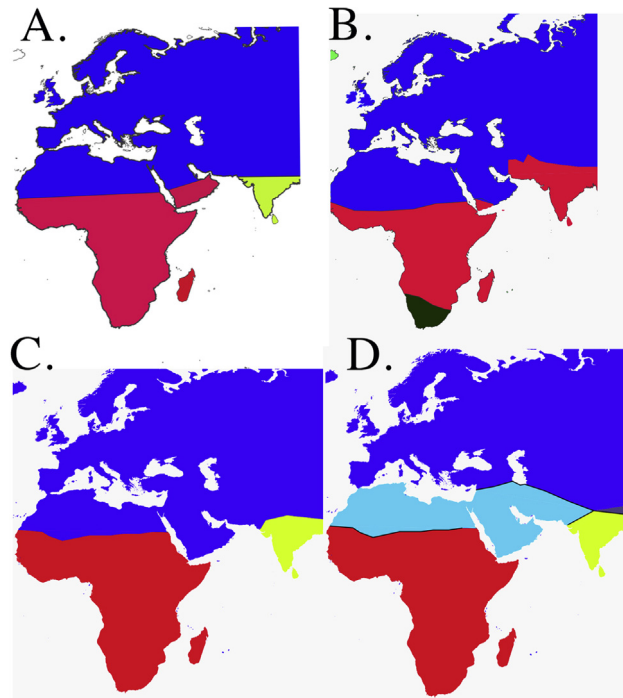
Three main issues contribute to the multiple definitions of African taxa in the literature, and are variations in the definition of biogeographic regions, taxonomy, and chronology.

### 2.1. Biogeographic regions

It is a known axiom that the current political definitions of regions do not have any meaning in paleontological studies. Thus, the identification of an “African” taxon does not refer to the current geopolitical borders of the African continent. The geographic extent of biogeographic regions varies if you consider the entire continent vs. a smaller region thereof. The definition of what constitutes an African taxon differs between species and genera, and whether we are studying plants or animals, and if the latter are mammals, birds or amphibians (Holt et al., 2013; Udvardy, 1975), and the analytical and statistical methods used to produce biogeographic regions. Indeed, a reading of the current literature often obfuscates what precise definition is used by each author.

Since the original publication of the biogeographic realms by Sclater (1858), different scholars have defined biogeographic realms differently, producing different maps (Fig. 1). Furthermore, studies by researchers of fauna and flora often do not use a common terminology (Udvardy, 1975). The different definitions used by various scientists to define the African biogeographic realm are important to the topic of this paper.

The original definition of biogeographic realms was published by Sclater (1858) based on the distribution of birds, followed by Alfred Russel Wallace in 1876 (Wallace, 1876), who expanded on the original study. Wallace identified three main regions within the old world: Ethiopian, Palearctic and Oriental. Subsequent analyses such as those developed by Takhtajan (1969) and Udvardy (1975)



**Fig. 1.** Four examples of different biogeographic division of the old world. A. Wallace (1876). B. Takhtajan (1969). C. Udvardy (1975). D. Holt et al. (2013). The following colors were used in all maps: dark blue, Palearctic; red, Ethiopian, Africotropical, Afrotropical; light green, Oriental, Indo-Malaysian; dark green, Cape Region; light blue, Saharan–Arabian; purple, Sino–Japanese.

**Fig. 1.** Quatre exemples de différentes divisions biogéographiques de l’Ancien Monde. A. Wallace (1876). B. Takhtajan (1969). C. Udvardy (1975). D. Holt et al. (2013). Les couleurs suivantes ont été utilisées dans toutes les cartes : bleu foncé, Paléarctique ; rouge, Éthiopien, Africotropical, Afrotropical ; vert clair, Oriental, Indo-Malaysien ; vert foncé, région du Cap ; bleu clair, Arabo-Saharien ; pourpre, Sino–Japonais.

suggested other biogeographic regions, each with a different geographic extent and a different name.

Wallace (1876), using the distribution of mammals, identified seven regions: Palearctic, Nearctic, Ethiopian, Oriental, Australian, Neotropical and Antarctic. The Ethiopian region included sub-Saharan Africa, along with the southern part of Arabia (see Fig. 1A). Takhtajan (1969), who based his biogeographic classification on flora, separated the southern African region (the Cape region) from the remaining parts of sub-Saharan Africa, but included the southwestern tip of Arabia along with the Indian subcontinent and Southeast Asia into a single region, which he named the Afrotropical region (see Fig. 1B). Udvardy (1975), grouping both fauna and flora, classified the region, which included sub-Saharan Africa only, without any part of Arabia, as Africotropical (see Fig. 1C). In all these classifications, North Africa, the southern Levant and southern Europe were included in the Palearctic region. Holt et al. (2013) used three orders of vertebrates (Birds, Amphibians and Mammals) to classify biogeographic regions. By incorporating phylogenetic informed statistical methods along with analysis of several vertebrate classes together, they identified five regions, which they named Palaeartic, Saharan–Arabian, Afrotropical, Oriental, and Sino–Japanese. Most of sub-Saharan Africa, with the exclusion of Madagascar and Arabia, was identified as Afrotropical. They also created a new classification for North Africa and the Near East, which

were now grouped into a region called Saharan–Arabian (see Fig. 1D).

Thus, when we study “African” taxa in Eurasia, it is necessary to clarify whether we are referring to the Palearctic region of Wallace (1876), the Ethiopian region of Takhtajan (1969), the Africotropical realm of Udvardy (1975), or the Afrotropical region of Holt et al. (2013) to name a few. To understand “dispersal” events, which involve movement of fauna from one region to the next, it is critical to be consistent in defining geographic borders of various regions. Thus, if we follow Wallace’s classification, dispersal from North Africa into the southern Levant would not constitute dispersal from “Africa” (Fig. 1A). Indeed, Tchernov (1988) suggested that the appearance of African taxa in the Levant should not be considered as an African dispersal; a sentiment echoed by Klein (1999). Similarly, if we follow Takhtajan (1969), dispersal of fauna from the Afrotropical region could refer to dispersal from the Indian subcontinent and Southeast Asia as well as dispersal from east Africa into the southern Levant (Fig. 1B). African dispersal from the Afrotropical region as defined by Holt et al. (2013) would include only dispersals from sub-Saharan Africa into both North Africa and southern Europe (Fig. 1D).

It is not the aim of this paper to discuss the merits of each classification method, but to raise the discussion of the inconsistencies that occur and the way in which they may affect our interpretation of the dispersal of early Pleistocene out-of-Africa taxa. Moreover, there have been many

more biogeographic divisions suggested in the literature (see [Udvardy, 1975](#)).

Authors need to be consistent and clear about which definitions of biogeographic regions they are using. Using the biogeographic division of [Wallace \(1876\)](#) or [Takhtajan \(1969\)](#) results in a broader definition of an African geographic region and hence inclusion of more taxa as African. Conversely, applying the classification of [Udvardy \(1975\)](#) or [Holt et al. \(2013\)](#), which both include a narrower geographic definition of African taxa, resulting in fewer Eurasian taxa identified as having an African origin.

## 2.2. Taxonomy

Specimen identification to the taxon level is often in flux. Fossils are not unearthed with tags identifying the species with 100% certainty and taxonomic identifications range between tentative to confident. The taxonomic identification of some fossils is in consensus among scholars, while others tend to be more contentious.

Since the 1960s, there has been a shift in how we approach the taxonomic identification of fossil taxa in zooarcheological assemblages. These changes have affected not only the proportion of Africa taxa identified at several paleontological and paleoanthropological sites, but also the subsequent paleoecological reconstructions derived from them. At its core, taxonomic identification of fossil elements to species (or taxa) was (and still is) based on the morphology of diagnostic elements. In mammals, common diagnostic elements are dentition and epiphyses of long bones ([Driver, 1992](#)), while the ability to identify other elements depends on their breakage pattern. Thus, assemblages subjected to a myriad of taphonomic processes ([Lyman, 1994](#)) result in a high percentage of fragmented bones, and a low proportion of diagnostic elements ([Belmaker, 2005](#)). Paleoecological analyses derived from published taxonomic lists may be affected by taphonomic processes that affected the ability to accurately identify species composition and absolute number, i.e. richness. Thus, an assemblage relatively unaffected by taphonomic processes will have many diagnostic elements, allowing for taxonomic identification to the species level. By contrast, analysis of a taphonomically altered assemblage will have fewer diagnostic elements, fewer identification to the species level, and therefore a different taxonomic list, with perhaps identification only to family or genus rather than species.

Taxonomic identification is aided by the comparison of fossils to comparative specimens in museums and those published in the literature. Identification is bolstered by access to a wide variety of large collections and literature ([Lyman, 2010](#)). However, there was a lack of interregional collaboration before the fall of the former USSR and the opening of China to the west ([Cox, 2010](#)). During the period of the Cold War, much of the travel to collections and scientific communication was confined to the Western Hemisphere and the European countries in the west, Russian and Slavic speaking countries in the East, and China in the Far East, with little to no international communication among them.

Access to comparative collections was often limited or confined to countries within each socio-political block, and access to publications was limited to those, which shared similar languages and a similar political worldview. The main result for paleoanthropology was that, within each socio-political block, specimens were identified without long-ranging biogeographical comparison to similar specimens across other regions. This resulted in an increase in scientific “endemism” and the tendency to name specimens locally, often with a new name, rather than to assign fossils to a known taxon from other regions. For example, [Lister et al. \(2005\)](#) has noted that *Mammuthus* taxonomy in China, Russia and Europe may be synonymized into fewer taxa than those originally categorized, suggesting that the original taxonomic list developed in each region might be the result of local scientific practice.

The fall of the Berlin Wall in 1989 has resulted in a gradual increase in international collaboration, which has allowed researchers to study fauna across several regions as well as to personally study and compare specimens previously unavailable to them. This resulted in a more in-depth analysis of each taxonomic group and a wider geographic and temporal comparison for each specimen. This process has progressed and has become more apparent in the 21st century, with the development of the Internet and World Wide Web (WWW) ([Lucky, 2000](#)).

This process of globalization and scientific collaboration has resulted in renaming old specimens. For example, early studies named multiple species of *Megantereon* across the old world during the Plio-Pleistocene: *M. cultridens* ([Cuvier, 1824](#)); *M. megartereon* ([Croizet and Jobert, 1828](#)); *M. nihowanensis* ([Teilhard de Chardin and Pivetau, 1930](#)); *M. falconeri* ([Pomel, 1853](#)); *M. sivalensis* ([Falconer, 1868](#)). However, more recent studies have classified all these into one species, *M. cultridens* ([Turner, 1987](#)).

In addition, recent development of paleontological methodologies such as geometric morphometrics ([Adams et al., 2013](#)), molecular techniques and multivariate statistics may be used to revise the taxonomic affinities of a fossil species. For example, geometric morphometric analysis of the shape of upper molars in Javanese cervids has suggested new affiliations for some of the specimens ([Gruwier et al., 2015](#)), and the geometric morphometric analysis of the species *Pelorovis oldowayensis* suggested a taxonomic assignment to the genus *Bos* ([Martínez-Navarro et al., 2007](#)). The advent of molecular paleontology ([Wörheide et al., 2016](#)) allows analysis of both phylogeography and taxonomy of extant ([Burger et al., 2004](#)) and fossil taxa ([Pyron, 2015](#)). Novel statistical methods that have been developed in tandem with increased computing power allow the identification of fossil specimens that previously could not be assigned to a species ([Davis and McHorse, 2013](#)).

If we only consider species that are securely assigned to taxa (i.e. with a greater consensus among researcher and across paleontological and/or molecular studies), we obtain a more conservative assessment of the number of African taxa found in Eurasia. The opposite is also true, and the inclusion of fragmentary specimens and/or from specimens with contentious species assignment results in more lenient identification of African taxa.



### 2.3. Chronology

Several chronological issues affect our interpretation of the number of African taxa in Eurasia: how do we incorporate paleontological data from sites dated back only to the informal term “Plio-Pleistocene”, only using the terminology of before/after the Plio-Pleistocene boundary? How did the revision of the Plio-Pleistocene boundary date from 1.8 Ma to 2.58 Ma affect our ability to interpret generalized dates in the literature? And what time frame do we study in relation to hominin dispersal?

The terms ‘Quaternary’, ‘Pleistocene’ and other terms in the geological timescale have been used for over 150 years (Gibbard et al., 2010), and until the expansion of radio-chronological and paleomagnetic methods, dating of the hominin specimens in Eurasia or archeological sites remained elusive, and only relative biochronological (e.g., Villafranchian) or archeological (e.g., lower Paleolithic) terminology was used. For example, the site of ‘Ubeidiya was dated in the 1960s to the Villafranchian (Stekelis et al., 1960) or the Pleistocene (Tchernov, 1968), and was associated with a glacial period between the Cromerian and the Holstein (Tchernov, 1973). In addition, the subdivisions of the Pleistocene and the Pliocene–Pleistocene border differ in the countries of the ex-Soviet Union compared to those in the West (Ljubin and Bosinski, 1995). Thus, when mining the literature, especially the older references, it may be difficult to ascertain contemporaneous sites.

Of course, there have been ongoing discussion and debates regarding the absolute date and time intervals that the terms represent (Aguirre and Rosas, 1985; Haq et al., 1977; Van Couvering, 2004). In 2010, the date of 2.58 Ma was ratified as the base of the Pleistocene from the previous 1.8 Ma (Gibbard et al., 2010). This again critically affected how we review older literature, as it is often difficult to assign a chronometric date on the basis of the more fluid terminologies that were then common. Specifically, this affected the discussion of the co-dispersal of humans with other mammals from Africa and requires us to be cognizant of the use of relative chronology terms.

The dispersal of fauna from Africa to Eurasia did not begin in the early Pleistocene. Indeed, during the Miocene (23.5–5.0 Ma), there was a land bridge connecting the African continent with Eurasia primarily through the Syrian African Rift Valley, which was considered a main crossroad between Africa and Eurasia: a gateway for northward and southward dispersal (Thomas, 1985). A period of long-distance reciprocal biotic exchange due to the dramatic lowering of the Mediterranean Sea Level occurred during the Messinian event (5.96 to 5.33 Ma) (Tchernov and Belmaker, 2004; van der Made et al., 2006). During the terminal Miocene (ca. 5 Ma), the developing Red Sea and flooding of the Mediterranean put an end to the geographic corridor through the Syrian African Rift Valley. The onset of the Pliocene (5.333–2.58 Ma) was marked by an abrupt transgression of the Mediterranean and reestablishment of the barrier between Africa and Eurasia. During this period, Sub-Saharan Africa became isolated from the rest of the world by the Saharan–Arabian arid belt (Thomas, 1985), and the southern Levant was increasingly isolated biogeographically. Towards the early Pleistocene (2–1 Ma),

another regression of the Mediterranean terminated the quasi-isolation of the region (Tchernov and Belmaker, 2004). These early biotic exchanges did not include the genus *Homo*. The Miocene dispersal included primates, but that discussion is beyond the scope of this study (Tchernov et al., 1987).

Given the long history of dispersal events between Africa and Eurasia that took place during the Miocene and the Pliocene, it is crucial to focus on those dispersals that occurred in conjunction with early hominin dispersal and not earlier for the question of the ‘Migratory Wave Hypothesis’. Determining when Afro-Eurasian biotic changes become relevant to the question of human migrations is dependent on the absolute date of earliest evidence for hominin remains in Eurasia (which may include fossils, stone tools and bone surface modification).

However, the dating of the earliest hominin dispersal from Africa has changed over time due to new finds in Eurasia as well as re-dating of old sites using radiometric dating. Going back to the site of ‘Ubeidiya that was previously mentioned, found in 1959. Originally, it was dated back to the Villafranchian biochronological stage within the Lower Pleistocene with an estimated date of approximately 500,000 years ago (Haas, 1966, 1968; Stekelis et al., 1960, 1969). By the mid-1980s, additional excavations at the site revealed fauna of African origin, leading to the dating of the site to 1.4 Ma, based on biochronology (Tchernov, 1987). Following new biochronological dating and new analysis at the site, it is currently dated back to 1.6–1.2 Ma (Belmaker, 2017). Similarly, paleontological and archeological finds in the Orce Basin in the Iberian Peninsula (Venta Micena, Baranco Leon and Fuente Neuva 3) in the 1970s were originally dated using paleomagnetism, to the Matuyama period, between the normal chrons of Jaramillo and Olduvai (Martínez-Navarro and Toro, 2003).

The discovery in 1991 (Dzaparidze et al., 1992) of hominin remains associated with lithic artefacts in lower Pleistocene deposits from Dmanisi (East Georgia, Caucasus) was originally reported to be as old as 1.6–1.8 Ma (Dzaparidze et al., 1992; Gabunia and Vekua, 1995). Subsequent dating of the site to 1.85–1.78 Ma (Ferring et al., 2011) marked this site as the oldest confirmed evidence for hominins out of Africa with extensive hominin remains, lithic and faunal material with evidence of human butchery (Lordkipanidze et al., 2007). Thus, up to 2010, many of the discussions of the co-occurrence of early *Homo* and African taxa focused on the dispersal of hominin during the Olduvai–Matuyama reversal, and the onset of early Pleistocene *grosso modo*. Taxa that appear in Eurasia after that date were considered as “African taxa” with a putative dispersal together with early *Homo*.

However, there have been continuously publications of new discoveries suggesting that early *Homo* may have dispersed earlier than that into Eurasia. In Yiron, Israel, cores and flakes have been retrieved from the gravels in a major crevice apparently below a lava flow of 2.4 Ma (Ronen, 1991; Ronen et al., 1980) and the ‘Erq el Ahmar’ Formation (Horowitz, 1979) located about 14 km south of the Sea of Galilee, in the Jordan Valley, and accumulated prior to the ‘Ubeidiya Formation. Artifacts found in the deposits (Tchernov, 1995) were suggested to predate

the early Pleistocene. Similarly, some artifacts found in Pabbi Hills, Pakistan, were suggested to be dated back to 2.0 Ma (Dennell et al., 1988). These early pre-2.0 Ma were contested on stratigraphic, archeological and chronological grounds (Bar-Yosef and Belmaker, 2011).

Recently, Olduvai Chron paleoanthropological sites such as Longgupo (China), ca. 2.2 Ma (Han et al., 2017), and Masol (India), ca. 2.5 Ma (Dambricourt Malassé et al., 2016; Moigne et al., 2016; Tudryn et al., 2016), have been found. If these dates are indeed confirmed, the anthropogenic origin of sites such as Yiron, 'Erq el Ahmar and Pabbi Hills should be reconsidered. Most importantly, if the anthropogenic origin of these sites were confirmed, the date for the earliest presence of hominins out of Africa would be pushed back to the earliest Pleistocene (2.58–1.8 Ma) or even the late Pliocene (> 2.58 Ma). This will expand the discussion of the 'Migratory Wave Hypothesis' to include dispersal events dated to 2.1 Ma (for example the wolf–*Equus* event (Azzaroli, 1983; Azzaroli et al., 1988) dated to the Middle–Late Villafranchian transition). However, at the current state of research today, studies that focus on Afro-Eurasian biotic exchanges in the middle Pliocene (such as the site of Bethlehem, Palestine (Rabinovich and Lister, 2016) or Kvabebi, Georgia (Agustí et al., 2009; Martínez-Navarro, 2004) may not be pertinent to the discussion at hand, and while very informative on biogeographic routes and ecological process, they may not be as critical for the evaluation of the co-dispersal of large mammals with humans.

The determination of the cut-off date is somewhat of a moving target; it is important to clearly delineate which dispersals are being discussed within the context of faunal biogeographical processes (with their own merit), and which dispersals are analyzed in conjunction with early *Homo* dispersals.

### 3. A short history of research finds

Throughout the history of research, the number of African taxa in Eurasia, and the species that are identified as African has changed, depending on the definition of biogeographic realms, taxonomy and chronology, and of course, new finds in the paleontological record.

The Levantine corridor has been known to include African taxa since the 1930s. The first site found to include African taxa in the Levantine corridor was discovered at Bethlehem, Palestine. It included a small faunal assemblage associated with a Giraffoid (Gardner and Bate, 1937), later identified as belonging to the African genus *Giraffa* sp. (Hooijer, 1958). At the time of excavation, the site was dated back to the middle Villafranchian, based on the fauna biochronology. At the same time, several African species were identified in central and southern Asia (Pinjor Formation and upper Siwaliks, dated back to the late Pliocene and early Pleistocene), including *Sivatragus bohlini*, *Oryx sivalensis*, *Vishnocobus patulicornis*, *Sivacobus palaeindicus*, and *Damalops palaeindicus* (Pilgrim, 1939). When these finds were originally published, the earliest dispersal of hominins from Africa was dated much later than the late Pliocene and early Pleistocene, and these events were not associated with hominin dispersal. The interest in these

faunas was reignited when evidence began to emerge that the dispersal out of Africa may be dated as early as 2.5 Ma and with confidence to 2 Ma (Han et al., 2017).

A large African fauna was discovered in 'Ubeidiya, Israel, in the 1970s and was dated back to 1.4 Ma based on long-range faunal correlations (Tchernov et al., 1987). The original faunal publication by Haas (1966, 1968), which identified fauna from the first three seasons of excavation, did not identify any African taxa in 'Ubeidiya. Additional finds between 1966 and 1985 led to the seminal publication by Tchernov (Tchernov, 1986). In this publication, the appearance of African taxa was emphasized. Taxa noted as having a Palearctic origin were *Gazella* sp., *Oryx* sp., *Paleorovis oldowayensis*, *Giraffa* sp. *Kolpochoerus olduvaiensis*, *Hippopotamus gorgops*, *Equus tabeti*, *Crocota crocuta* and *Herpestes* sp. (Tchernov, 1986). Additional finds at the site in the 1990s further increased the number of African taxa. This included Cercopithecidae cf. *Theropithecus* (Belmaker, 2010) and *Mellivora* sp. (Belmaker, 2006).

Faunal assemblages of the early middle Pleistocene sites of Latamne, Syria and of Evron, Israel, revealed the presence of the putative African species *Giraffa camelopardalis* in Latamne (Guérin et al., 1993) and the presence of the African genus cf. *Alcelaphus* in Evron (Tchernov et al., 1994). In addition, *Kolpochoerus evronensis* was found in Evron and was considered as an endemic species that evolved from the 'Ubeidiya population (Tchernov et al., 1994). The relative high frequency of the taxa identified as African in the southern Levant was put forth as evidence that the hominin dispersal evident in 'Ubeidiya was not a true "out of Africa", but rather an expansion of African ecosystems northward into the southern Levant (Tchernov, 1992a, b).

The discovery of Venta Micena, (1.6–1.5 Ma), Baranco Leon (1.4 Ma) and Fuente Nueva 3 (1.3 Ma) in the Orce Basin in the 1970s, promoted increased interest in African taxa in western Europe. The sites revealed taxa that were identified as African: *Megantereon whitei*, *Canis falconeri*, *Pachycrocuta brevirostris*, *Hippopotamus antiquus* and *Equus altidens* (Martínez-Navarro, 2004, 2010; Martínez-Navarro and Palmqvist, 1995). The finding of *Theropithecus oswaldi* in Cueva Victoria (Gilbert et al., 1995) in conjunction with a *Theropithecus delsoni* in India (Gupta and Sahni, 1981) further raised the importance of African faunal dispersal.

The site of Fonelas-1, Spain (2.1–2.0 Ma), was discovered in 2000 and has been excavated since 2001. Analysis revealed the earliest presence of the African taxon *Pachycrocuta brevirostris*, known from younger sites in Europe, as well as that of the African taxa *Parahyaena brunnea* and *Potomochoerus magnus* (Arribas et al., 2009). The dispersal into Western Europe of these African species was suggested to coincide with the arrival of *Panthera gombaszoegensis* in Europe, first found at a site in Tegelen, the Netherlands (2.2–1.7 Ma) (Martínez-Navarro and Rabinovich, 2010).

The earliest evidence for *Hippopotamus* dispersal into western Europe are specimens found in the middle Villafranchian assemblage of Coste San Giacomo, Italy, dated back to 2.1 Ma and in Greece, dated back to 2.0–1.8 Ma (Pandolfi et al., 2015). An earlier appearance may be noted in Bethlehem, dated back to 3.0–3.5 Ma (Rabinovich and Lister, 2016) identified by Gardner and Bate (1937). However, Hooijer (1958) noted in a later publication that this

was a misidentification. Indeed, the current collection of the Bethlehem fauna at the British Museum of Natural History in London does not include any hippo remains.

A dispersal of an additional *Hippopotamus* species is evident in the Levant. In western Europe, two species have been identified, *Hippopotamus amphibius* and *Hippopotamus antiquus*, while two other species were found in 'Ubeidiya, the African *H. gorgops* and the endemic *H. behemoth* (Faure, 1986). This suggests an earlier migration of *H. amphibius* to western Europe ca. 2.1 Ma and a later dispersal of *H. gorgops* into the Levant ca. 1.6 Ma.

The finding of taxa identified as African in western European archeological sites associated with human artifacts in the 1970s–1980s led to reanalyses of fossil assemblages from early Pleistocene sites in western Europe as well as in East Asia, revision of previous taxonomic identifications, and reassignment of some Eurasian taxa to African ones (and vice versa). Specifically, *Megantereon* specimens which had previously been identified as the Eurasian taxa *M. megartereon* and *M. cultridens* were re-identified as the African species *M. whitei* at sites in Dmanisi, Apollonia-1, Pirro Nord and 'Ubeidiya (Martínez-Navarro and Palmqvist, 1996).

The “Migratory Wave Hypothesis” (sensu Agustí and Lordkipanidze, 2011) suggested that hominins dispersed from Africa together with other taxa in the early Pleistocene. Since both hunting and scavenging have been proposed as main methods of carcass acquisition, two similar hypotheses were posited. One suggested that as hunters, hominins followed their prey, i.e. large ungulates, into new regions. The other hypothesis suggested that the increased reliance of hominins on meat of scavenged carcasses led to hominins following large African predators into Eurasia (Arribas and Palmqvist, 1999; Turner, 1984, 1992). Thus, our understanding of how many African taxa dispersed into Eurasia is crucial to evaluating these hypotheses.

#### 4. How many African taxa?

As we try to reconstruct the biogeography of early *Homo* dispersal events out of Africa, we can constrain the discussion based on three criteria:

- biogeographic region;
- taxonomy;
- chronology.

##### 4.1. Biogeography

In his seminal work on the fauna of 'Ubeidiya, Tchernov (1986) assigned several taxa to a paleotropical biogeographic kingdom. It is unclear which specific author he followed when assigning his divisions. The paleotropical taxa were assigned either to the Ethiopian region (a sub division of the Paleotropics): *Crocota crocuta*, *Herpestes* sp. *Kolpochoerus olduvaiensis*, *Giraffa* gen. indet., *Hippopotamus gorgops*, and *Pelorovis oldowayensis*, while *Felis* cf. *chaus*, *Bos* sp. and *Hystrix indica* were assigned to the Oriental region (another sub division of the Paleotropics). In addition, several species (*Gazella* sp., *Oryx* sp., *Equus tabeti*) were identified as coming from the North African

or Saharan–Arabian region. However, this also exemplifies how the definition of biogeographic realms can have a direct impact on how we quantify African species. If we accept a maximizing definition of Paleotropics as reflective of “African” taxa, then the number of African species in 'Ubeidiya is 12. On the other hand, if we use another definition, such as that by Holt et al. (2013), who applied a phylogenetic framework to traditional biogeographic divisions, Afrotropical taxa are sub-Saharan taxa and do not include species from North Africa or Arabia.

If we apply a more stringent definition of biogeographic realms following Holt et al. (2013), *Equus tabeti*, *Gazella* sp., and *Oryx* sp. assigned as African by Tchernov (1986), are assigned to the Saharan–Arabian region. Similarly, taxa from South and Southeast Asia (*Felis* cf. *chaus*, *Bos* sp. and *Hystrix indica*) by Tchernov (1986), maybe assigned to the oriental region by Holt et al. (2013), are excluded from the list of African taxa.

##### 4.2. Taxonomy

Of course, there is no absolute method to guarantee that taxonomic identifications are indeed correct and different views and opinions are prevalent in the taxonomic literature. We can therefore envision a continuum between taxonomic identifications in consensus across researchers and which are based on methods with a high probability of correct identification and those identifications, which are highly contested. Two issues need to be addressed:

- the taxonomic identification of a fossil specimen;
- the evolutionary and biogeographic history of the taxon.

There are fossil specimens in Eurasia that are securely assigned to species and have a clear evolutionary link to African ancestors. These include *Theropithecus oswaldi*, *Paleorovis oldowayensis*, *Kolpochoerus olduvaiensis*, cf. *Alcelaphus*, *Giraffa camelopardalis*, and *Herpestes* sp. representing only six taxa. The identification of other fossil specimens as African species is contested by some. I have detailed below the main arguments for and against the identification of specific fossils as those of species of either African origin or non-African origin. The aim of this section is not to favor one opinion over the other, but to exemplify how taxonomic issues may plague our ability to quantify the number of taxa of African origin in Eurasia.

##### 4.2.1. Carnivores

One of the main contentious species is the *Megantereon*. There has been disagreement regarding the specific identification of *Megantereon* fossils from the Eurasian early Pleistocene. There is a consensus that the Pliocene *Megantereon* population belongs to the single species *M. cultridens*. However, the agreement ends there. Some view the early Pleistocene populations of *M. cultridens* as a single species with large sexual dimorphism (Turner, 1987) that extended over Eurasia and Africa, while others suggest that the populations of *M. cultridens* differ at the species level. Thus, *M. megartereon* has been classified as an early Pliocene taxon, *M. cultridens* as a late Pliocene taxon (both

present in Eurasia) and *M. whitei* as an early Pleistocene African taxon that dispersed into Eurasia from Africa.

Some identified *M. whitei*, an African taxon, in Dmanisi, Apollonia-1 and 'Ubeidiya (Martínez-Navarro and Palmqvist, 1996; Martínez-Navarro and Rabinovich, 2010; Palmqvist et al., 2004, 2007). However, Koufos suggested that the species designations of these finds are not secure (Koufos, 2014). The presence of fossil specimens whose morphology displays similarities with *M. whitei* in Yanliang Cave, Fusui, Guangxi, South China, dated back to 2.0 Ma (Zhu et al., 2014), supports the broader lumping taxonomic scheme. Specifically, a recent analysis of *Megantereon* finds throughout Eurasia could not confirm the distinction between *M. cultridens* and *M. whitei* (Zhu et al., 2014, 2017), supporting the position that *Megantereon* is a single widely distributed species. Nonetheless, even if we accept the splitting taxonomy (i.e. *M. cultridens* and *M. whitei*), several sites have only scant remains, which while diagnostic to genus, are not diagnostic to species and therefore cannot be assigned to either *M. cultridens* or *M. whitei* with any degree of certainty. The 'Ubeidiya specimens (upper canine, lower canine and second phalanx) are too scant to be assigned to species (Lewin and Werdelin, 2010), even though they were previously assigned to *M. whitei* (Martínez-Navarro et al., 2009a).

*Canis falconeri* has been identified as an African taxon (Arribas and Palmqvist, 1999). However, Martínez-Navarro and Rook (2003) suggested that *Canis falconeri* should be assigned to the genus *Lycaon* as the forbearer of the lineage of the African hunting dog *Lycaon pictus* rather than to the *Canis* lineage. They suggested that these represent a chrono-species that evolved from *Lycaon falconeri* through *Lycaon lycaonoides*, and finally the extant *Lycaon pictus* (Martínez-Navarro, 2004). In accordance with the reclassification of Martínez-Navarro and Rook (2003), *Canis falconeri* or *Xenocyon falconeri* finds across Eurasia were re-identified as *Lycaon falconeri*. Specimens of *Xenocyon lycaonoides* recovered in Venta Micena, Barranco Leon, Fuente Neuva 3 and 'Ubeidiya among others were identified as *Lycaon lycaonoides*, an Eurasian taxon that evolved in Europe (Martínez-Navarro and Rook, 2003; Martínez-Navarro et al., 2009b).

While earlier publications suggested that these canids were an African taxon (Arribas and Palmqvist, 1999; Martínez-Navarro and Palmqvist, 1995), new finds and discussion of the origin of the species suggest a possible Eurasian origin of this taxon (Martínez-Navarro and Rook, 2003). Nonetheless, Hartstone-Rose et al. (2010) suggested that both *Xenocyon falconeri* and *Xenocyon lycaonoides* should be assigned to the genus *Canis*. The genus *Canis* has been recovered from the Pliocene deposits of Mursi Formation, Omo Group, Kenya, dated back to 4.5–4.0 Ma (Werdelin and Lewis, 2005), and clearly has an African origin. However, the first Eurasian *Canis* is from Viallette, France, dated back to ca. 3.14 Ma, after which the genus rapidly diverged and dispersed into Eurasia (Palombo, 2017). Thus, the appearance of *Canis* in the early Pleistocene of Western Europe probably represents a Eurasian dispersal and not an African one. Moreover, Hartstone-Rose et al. (2010) suggest that the origin of the hunting dog *Lycaon pictus* can be found in the species *Lycaon sekowei*

from Cooper's Cave, South Africa, dated to 1.9 Ma and not in the earlier *Canis* (= *Xenocyon*) *lycaonoides*. There is an interesting dispersal of *Lycaon pictus* into the Levant during MIS 6 (Stiner et al., 2001), but this is beyond the temporal scope of this study.

The giant, short-faced hyaena *Pachycrocuta brevirostris* was first found in Africa in strata dated back to 3.2–3.6 Ma and its appearance in Fontelas-P1 was viewed as dispersal of an African taxon (Arribas et al., 2008). However, it is also known in East Asia under the junior synonym *Pachycrocuta licenti*. Werdelin (1999) hypothesized that the species originated in Asia, dispersed to Africa at ca. 3.5 Ma and to Western Europe at ca. 1.6 Ma (Werdelin, 1999). Therefore, we cannot be sure if the appearance of this taxon in western Europe is the result of an African or Asian dispersal event.

The extant species, *Crocuta crocuta*, has been identified in 'Ubeidiya, Israel, (Ballesio, 1986) dated back to 1.6–1.2 Ma and has often been cited as a clearly African taxon. The earliest *C. crocuta* in Western Europe was found in at Casal Selce (Rome, Italy) and may be dated back to the Brunhes/Matuyama boundary (Sardella and Petrucci, 2012). The earliest fossil record of the genus is known in Africa from ca. 3.5–4.0 Ma (Werdelin and Lewis, 2008) and several species are known from the Pliocene of Asia under the name *C. honanensis* (Qiu, 1987). *Crocuta crocuta* (as a synonym of *Crocuta sivalensis*) is present in Asia (Nargota Formation, India) and has been dated back to 1.5–1.8 Ma (Dennell, 2008). However, there is a disagreement about the number of *Crocuta* species present, ranging from a single highly variable single species *C. crocuta* (Turner, 1984) (suggesting that the origin of the European species may not be African but Eurasian) to the identification of several distinct species found in different biogeographical regions and different time periods. Two genetic studies suggested alternative results for the phylogeny of *Crocuta crocuta*. Rohland et al. (2005) suggested a panmixia in Africa with dispersals into Eurasia dating back to 2.25–5.09 Ma; 1.26–1.46 Ma. In contrast, Sheng et al. (2014) suggested that the panmixia occurred in Asia, with two dispersal events into Africa.

The brown hyena, *Parahyaena brunnea*, has been found in Fonelas-1, Spain, dated back to 2.1–2.0 Ma. There is little debate that this is a typical African species. An early member of the genus *Hyaena* in Africa has been described from ca. 4.0 Ma at Kanapoi, Kenya (Werdelin and Lewis, 2005), close to the estimated date of divergence of *Hyaena hyaena* and *Hyaena brunnea* based on genetic studies (Koepfli et al., 2006). The species *Hyaena brunnea* is found in Sterkfontein 4, South Africa, 2.8–2.4 Ma, (Turner, 1990) pointing to an African origin for the species. However, the identification of the species at Fonelas-1, Spain, the only Eurasian site where this genus has been found, has been questioned (Palombo et al., 2008). The morphology of *Hyaena brunnea* is more like that of the Eurasian Pliocene species *Pliocrocuta perrieri*, which is known from European deposits from the late Pliocene (Palombo et al., 2008) and may confound the fossil record. Since Fonelas-1 is the only occurrence of this species in Eurasia, further morphological and genetic scrutiny is needed before we can securely assign this find to an African dispersal.



The European Jaguar (*Panthera gombaszoegensis*), known from Palearctic and Saharan–Arabian regions, was first identified in Eurasia ca. 2.0 Ma in Olivola, Italy and in Tegelen, the Netherlands (2.2–1.7 Ma) and recently in Fonelas-1 in the Iberian Peninsula, dated back to 2.1 Ma (Madurell-Malapeira et al., 2014). Some have proposed an African origin for the genus *Panthera*, as the oldest *Panthera* fossil is found in East Africa, dated back to ~3.46 Ma (Barry, 1987; Turner, 1990, 1997; Werdelin and Lewis, 2005), and have suggested that the taxon spread to Eurasia between 1.95 and 1.77 Myr during the time of the Olduvai polarity subchron (Argant and Argant, 2011; Martínez-Navarro and Rabinovich, 2010). However, there is also no agreement about the origin of the genus, and there has been a discussion about whether the genus *Panthera* has an African or Asian origin (Palombo and Sardella, 2007). The species identified as *Panthera onca georgicus*, which was found in Dmanisi, Georgia and dated back to 1.7–1.8 Ma, may represent another endemic subspecies (Hemmer et al., 2010). While there is no evidence that the species *Panthera onca* or *Panthera gombaszoegensis* are of African origin, the find of a stem *Panthera* cranium (IVPP V18 788.1) from the Zanda Basin of the northwestern Himalaya Range, China, with an age of 4.42 Ma has been assigned to *P. blytheae*. Genetic and paleontological analyses have suggested a geographical origin for pantherines in the central/northern Asia (Tseng et al., 2014), followed by a Miocene dispersal of the lion–leopard–jaguar clade from East Asia into Africa.

*Mellivora* sp. (Belmaker, 2006) has only been tentatively identified by an ulnar fragment. More research is needed and more finds as well so as to confirm this taxon as an African taxon.

#### 4.2.2. Suidae

*Potamochoerus magnus* has been found in Fonelas-1, Spain, dated back to 2.1–2.0 Ma, where it was classified as an African taxon (Arribas et al., 2009). However, the *Potamochoerus* genus was first found in the Tatrot Formation in the Siwaliks of India, as well as in East Asia (Kumar and Gaur, 2013), dated back to the Pliocene. In addition, genetic evidence points to a very early (ca. 7.36–14.45 Ma) divergence of the two Suinae subclades, Potamochoerini and Phacochoerini, which most probably occurred in Eurasia (Gongora et al., 2011). It has been suggested that dispersal of the genus from Eurasia into Africa occurred during the early Pleistocene (Pickford, 2012) contra (Bishop, 2011), which would point to an Asian origin of this taxon in western Europe.

#### 4.2.3. Hipopotamidae

Several species of *Hippopotamus* have been recorded in Eurasia. In the Levant (or eastern Mediterranean), two species have been identified: *H. gorgops* (found in 'Ubeidiya, Israel, at 1.6–1.2 Ma), and an endemic species, *H. behemoth* (found in 'Ubeidiya and in Latamne, Syria, at 1.0 Ma) (Faure, 1986; Guérin et al., 1993). Nonetheless, some have argued that the size range of *H. behemoth* is within the variability of *H. gorgops* (Martínez-Navarro and Rabinovich, 2010; Martínez-Navarro, 2004), suggesting the presence of a sin-

gle species in the Levant, which may have dispersed from Africa at ca. 1.6 Ma.

In parallel, western Mediterranean sites in Spain and Italy from the early Pleistocene have yielded *H. antiquus*. The dispersal of two African *Hippopotamus* species (*H. gorgops*, *H. antiquus*) at around the same time frame and the appearance of an endemic taxon displays an interesting biogeographic problem. *H. amphibius* is known from the early to late Pleistocene deposits of Olduvai Gorge (Coryndon, 1976; Coryndon and Coppens, 1973), specifically from Level G in the Shungura Formation dated back to ca. 2 Ma, and in Olduvai dated back to 1.9–1.8 Ma. While the sympatric *H. gorgops* has been identified in Olduvai strata dated back to 1.7–1.6 Ma, Petronio (1995) suggested that *H. gorgops* and *H. antiquus* be considered synonyms. If support is found for this taxonomy (Pandolfi et al., 2015), this would support a single early Pleistocene dispersal of *H. antiquus* from Africa to Eurasia, with its first appearance in western Europe at ca. 2.0 Ma and in the Levant at ca. 1.6 Ma. Younger deposits from the middle Pleistocene in both the Levant and western Europe have yielded *H. amphibius* and suggest a later dispersal of this species during the middle Pleistocene.

#### 4.2.4. Equidae

The equid at 'Ubeidiya and Latamne was identified as being *Equus* cf. *tabeti* by Eisenmann (1986) based on metapodial and tooth morphology, and has been found in 'Ain Hanech (Arambourg, 1970) and Koobi Fora (Eisenmann, 1983). However, multivariate analysis has suggested similarities between the equids from the *E. numidius*–*E. tabeti* lineage and *Equus* cf. *altidens* (Guereño-Alba and Palmqvist, 1997), which have also been found in Spain (Venta Micena, Orce, Cúllar de Baza, Cueva Victoria, Huèscar-1), Italy (Pirro Nord, Selvella), France (Sainzelles), and Germany (Süssenborn) (Arribas and Palmqvist, 1999). This lineage has been named “simplicidens” and includes *E. numidicus*, *E. tabeti*, *E. altidens*, and *Equus granatensis*. Indeed, later publications have identified the species in 'Ubeidiya as *Equus altidens* (Gaudzinski, 2004). There has been a discussion with some suggesting an African origin for the species (Gibert et al., 2016), while others suggest an Asian origin (Madurell-Malapeira et al., 2014).

### 4.3. Chronology

Identification of intercontinental dispersal events has its merit when discussing the co-dispersal of hominins and African taxa. As presented in the “Migratory Wave Hypothesis”, it is crucial to confirm that we are comparing the first appearances of African taxa in Eurasia, which appear in Eurasia together or after the dispersal of hominins, but not earlier. Today, the accepted and confirmed event for the first hominin dispersal from Africa is that at Dmanisi, Georgia, dated back to 1.78–1.82 Ma (Ferring et al., 2011). While some suggestions for early dispersals have been put forth (Han et al., 2017), they are still unverified. To evaluate the “Migratory Wave Hypothesis”, some may consider only dispersals from 1.8 Ma and younger, while others may support the analysis of sites as old as 2.58 Ma.

Several species that had been identified as part of an early Pleistocene dispersal event have been revised based on chronological considerations, to predate the early Pleistocene. The five bovids (*Sivatragus bohlini*, *Oryx sivalensis*, *Vishnocobus patulicornis*, *Sivacobus palaeindicus*, and *Damalops palaeindicus*) found in South and Central Asia were originally assigned an early Pleistocene age. A reanalysis of the taxonomic identification of the species led O'Regan et al. (2011) to suggest that these bovids either appeared earlier than the late Pliocene/early Pleistocene in Asia or represent locally evolved species from previous dispersals. Indeed, all these species are endemic to South Asia, albeit assigned to a genus or family of African (*sensu lato*) origin. This supports Vrba's suggestion that the Hippotragini dispersal occurred earlier than 2.7 Ma when sea level was lower, creating a land bridge between Africa and Asia across Arabia (Vrba, 1995).

The *Giraffa* sp. identified at Bethlehem, originally dated back to 2.5 Ma, is now viewed as a mid-Pliocene dispersal, as the site has been recently dated back to 3.5–3.0 Ma (Rabinovich and Lister, 2016). This suggests that if this were indeed an out-of-Africa event, it predates the time frame of interest. Moreover, there are taxonomic reasons to doubt if *Giraffa* sp. is indeed an African taxon. There are several Pliocene *Giraffa* ssp. dated back to 4.0 Ma (Sen et al., 1998). Therefore, the find in Bethlehem may represent an expansion of these Asian populations. Similarly, the find of *Giraffa* sp. in 'Ubeidiya may also be associated with this earlier dispersal and needs not reflect a later Pleistocene dispersal. Indeed, tooth measurements have suggested that the species in 'Ubeidiya may be assigned to *G. jumae* (Robinson and Belmaker, 2010). In contrast, the *Giraffa* species in Latamne, Syria, is indeed the extant species *G. camelopardalis* present in Africa from 1.2 Ma (Guérin et al., 1993). This would suggest an early Pleistocene dispersal of this species.

## 5. Discussion and conclusion

This study suggests that some species may have a high probability of being sub-Saharan ones that dispersed from Africa into Eurasia contemporaneously with early *Homo*, and therefore should be considered as African in the discussion of the 'Migratory Wave Hypothesis', while others only have a low probability to be considered as such. The incorporation of the latter group in the study of the 'Migratory Wave Hypothesis' depends on the critical evaluation of biogeography, taxonomy, and chronology. Thus, we can count up to a maximum number of African taxa (acceptance of all species as African regardless of low probabilities) or accept only a minimum number of taxa, which excludes all taxa not in consensus and that have a very high probability of being early Pleistocene African taxa in Eurasia. Of course, this is not an all or nothing situation. One may be critical of the biogeography, but not of the taxonomy, or any other combination thereof.

Considering that the base of the Pleistocene is dated back to 2.58 Ma and that there is increasing evidence for the presence of hominins in Eurasia during this time period, we can list the maximum number of African taxa in Eurasia. These will include taxa from the largest biogeographic

area identified, which includes Sub-Saharan Africa (i.e. the Paleotropic region of Udvardy), those found in Eurasian sites dated back to the earliest Pleistocene, and those that have been taxonomically identified as African despite being contested. A total of 30 taxa meet these criteria: the large rodent *Hystrix indica*; the primate *Theropithecus oswaldi*; the Hippopotamidae *Hippopotamus amphibius*, *Hippopotamus antiquus* and *Hippopotamus gorgops*; the Bovidae *Sivatragus bohlini*, *Oryx sivalensis*, *Vishnocobus patulicornis*, *Sivacobus palaeindicus*, *Damalops palaeindicus*, *Oryx* sp., *Pelorovis oldowayensis*, cf. *Alcelaphus*, *Gazella* sp., and *Bos* sp.; the Giraffidae *Giraffa camelopardalis* and *Giraffa* cf. *jumae*; the Equidae *Equus tabeti* and *Equus altidens*; the Suidae *Potomochoerus magnus* and *Kolpochoerus olduvaiensis*; the Carnivores *Pachycrocuta brevirostris*, *Parahyaena brunnea*, *Crocuta crocuta*, *Megantereon whitei*, *Panthera gombaszoegensis*, *Felis* cf. *chaus*, *Canis falconeri*, *Herpestes* sp., and *Melliova* sp.

However, the critical application of biogeographical, taxonomical and chronological criteria results in a more conservative approach to the identification of African taxa in Eurasia. The rodent *Hystrix indica* is a South Asia species rather than an African one; the Hippopotamidae represent one vs. three dispersal events if the species were synonymized as *Hippopotamus antiquus*. The Bovidae in consensus include only two African species: *Pelorovis oldowayensis* and cf. *Alcelaphus*, as the other species dispersed in the Miocene or Pliocene into Eurasia. The Giraffid *Giraffa camelopardalis* is an early Pleistocene dispersal from Africa, while *Giraffa* sp. (perhaps *Giraffa* cf. *jumae*) may be attributed to an Asian and/or Pliocene dispersal. The Equidae *Equus tabeti* and *Equus altidens* may be considered synonymous with gracile equids that may have dispersed from Asia. The African Suidae include *Kolpochoerus olduvaiensis*, as the origin of *Potomochoerus magnus* is debated, and finally, only one carnivore can be identified as early Pleistocene African taxon: *Herpestes* sp. from 'Ubeidiya. This conservative estimate results in only six species (exclusive of *Homo*) with a very high probability to reflect dispersal from Africa into Eurasia in the early Pleistocene. Of course, these criteria are not mutually exclusive, and only one or two criteria may be chosen, resulting in any number between 6 and 30.

However, to estimate patterns of co-occurrence between *Homo* and other species, we need to consider two additional caveats of the fossil record. Indeed, as discussed by Bar-Yosef and Belmaker (2011), we tend to forget that the discovery of archeological sites is fortuitous and should not be interpreted as a continuous chronological sequence. Thus, the dispersals of large mammals and *Homo* may have occurred long before their bones were uncovered in the excavated sites, and the First Appearance Datum (FAD) of a fossil does not reflect the date of dispersal of the taxon. Furthermore, we should not only consider the FADs observed in the fossil record, but also take into consideration sampling intensity and fossil productivity (Barry et al., 2002). One of the methods used has been the calculation of 95% confidence intervals based on the probability to find a taxon within a given temporal interval (Koch and Morgan, 1988; Koch, 1987). For this calculation, we need a long and productive paleontological sequence.

In contrast to East and South Africa or the Siwaliks in Pakistan where these methods have been employed, the Saharan–Arabian region lacks the required long sequence of sites during the late Pliocene and the early Pleistocene. While we know the observed FAD of a species in the fossil record, this species may have dispersed into Eurasia earlier and thus not allow us to estimate the co-dispersal of taxa.

While we cannot demonstrate that *Homo* first appeared in Eurasia with a suite of other African taxa, we also cannot disprove that they did not disperse together (perhaps at an earlier date), which is consistent with studies by others that noted an asynchronous appearance of African taxa throughout the Levant (Bar-Yosef and Belmaker, 2011, O'Regan et al., 2011) and throughout southern Europe (Palombo, 2014).

This points to the need to be cautious when making inferences about the relationship between the dispersal of *Homo* with other African taxa. It is important to note that, while the criteria presented in this paper have face value, they are not in any way more “correct” than other ones, but are heuristic in presenting the difficulties in assigning an African origin to fauna found in early Pleistocene sites. Moreover, it is important to note that the discussion focuses on large mammals, but future studies should indeed include small mammals and other groups such as birds, reptiles and amphibians to confirm or refute these hypotheses.

Discussion of species and taxonomy will continue to plague paleontological studies. The progression over the past 30 years in paleontological methodology, concurrent with the expansion of international collaborations, will allow us to reconsider old paradigms that have dominated the literature. As eloquently put by Hooijer, “The fragmentary nature of most of the fossils as well as the frequent lack of sufficient material for comparison must put a paleontologist on his guard against drawing too far reaching conclusions.” (Hooijer, 1952).

## Acknowledgements

I would like to thank the guest editors George Konidaris and Dimitris Kostopoulos for inviting me to submit this paper to this thematic issue. The ideas presented in this paper were developed through long conversations with Ofer Bar-Yosef, for which I am grateful.

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