Hominins without fellow travellers? First appearances and inferred dispersals of Afro-Eurasian large-mammals in the Plio-Pleistocene

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ABSTRACT

Discoveries of fossil *Homo* outside Africa predating 1.0 Ma have generated much discussion about hominin dispersal routes. However, tool-using bipeds were only one element of the inter-continental mammalian dispersals that occurred during the climatic changes of the Pliocene and Pleistocene. This paper will place hominin movements in the context of those of the wider mammalian fauna, which includes carnivores, bovids and non-human primates. The distribution of these different taxa suggests that species moved individually when the environmental conditions were right for them, rather than in multi-species waves of dispersal, and allows evaluation of the contextual evidence for the newly emerging 'Out of Asia' paradigm as well as the established 'Out of Africa' model.

1. Introduction

In previous papers (O'Regan et al., 2006, Turner and O'Regan, 2007 a,b) we have discussed the biogeography of Eurasian Plio-Pleistocene mammals with particular emphasis on movements out of Africa and the timescale and direction of early hominin dispersal events. Those studies concluded that movements across the Gibraltar Straits during the Pliocene and Pleistocene can be ruled out for terrestrial mammals, with the possible exception of the hippopotamus (see O'Regan, 2008). Although a late Pliocene dispersal across the opening Bab-el-Mandeb region of the southern Red Sea may have been possible, such a route appears an unlikely choice for a Pleistocene gateway. Such evidence for human and other mammal

occupation of the Arabian Peninsula as does occur is beset by problems of chronological control but may be best explained by incursions southward from the Levant rather than by movement directly from the Horn of Africa.

Here we wish to change the emphasis from specific routes of movement and to look instead at the first appearance data for large-mammals in Afro-Eurasia in order to investigate overall patterns of dispersal between those continental areas. Various waves of Plio-Pleistocene Afro-Eurasian mammalian dispersal have previously been identified in the palaeontological literature, the best known of which are the dispersal of Proboscidea out of Africa 2.5-1.5 Ma (Tchernov and Shoshani, 1996), of bovids out of Africa ~2.7-2.5 Ma (Vrba, 1995a) and the Elephant-*Equus* and Wolf events in Europe at 2.6-2.5 Ma and ~1.7 Ma respectively (Azzaroli et al., 1988). Other dispersals of interest include the appearance of cold-tolerant faunas in Europe and of larger-bodied cervids and bovids in western parts of Eurasia during the Pleistocene (Azzaroli et al., 1988), and of course the pattern and timing of earliest hominin movements (Dennell, 2003; Roebroeks, 2001; Turner, 1992, 1999). Our results, in combination with those of several other recent studies, suggest that a number of these previous interpretations require reconsideration.

The information collated here was largely collected as part of a NERC-funded thematic programme which considered the Environmental Factors in the Chronology of Human Evolution and Dispersal (EFCHED), and thus we have concentrated on the later Pliocene and Pleistocene, from 3.0 Ma to 0.5 Ma. Since we shall examine the bearing that our results have on the questions that surround interpretations of early hominin dispersals, it will be useful to begin with a summary of the current picture of earliest hominin presence and the broad pattern of dispersals that may be inferred from it.

2. Hominin dispersals

An African origin some time during the later Pliocene/earliest Pleistocene is the most widely accepted model for the evolution of our own genus, *Homo* (Turner and O'Regan, 2007a,b). The earliest known hominin material outside Africa is from Dmanisi in Georgia (~1.7 Ma). The sample is now reasonably extensive (Gabunia et al., 2002), and in the light of relatively primitive morphology it has been assigned to either a very primitive form of *H. erectus* (Rightmire et al., 2006) or a new species *H. georgicus* based on mandible D 2600 (de Lumley et al., 2006). The most recent review of this material has placed *H. georgicus* closer to the *Homo habilis - Homo rudolfensis* lineage than to *H. ergaster/H. erectus* (de Lumley et al., 2006). This would perhaps indicate a first Late Pliocene/ Early Pleistocene dispersal of most primitive *Homo* to Dmanisi. A date of 1.8 Ma has been claimed for *Homo erectus* in Java (Swisher et al., 1994), but the earliest evidence is now considered to be from the top of the Sangiran Formation at ca 1.6 Ma (Bettis et al., 2009). Claims have been made for *Homo* sp. at 1.7 Ma in Yuanmou in southern China (Zhu et al., 2008), although Dennell (2009) has expressed strong reservations about the identity of the material. The next earliest hominin fossils, isolated teeth from 'Ubeidiya in Israel, dated to ~1.5 Ma (Belmaker et al., 2002), have been tentatively attributed to *Homo erectus* or *H. ergaster*. The Early Pleistocene hominin record has recently been extended in Europe with the publication of a hominin mandible from the Sima del Elefante at Atapuerca, dated to between 1.2-1.1 Ma (Carbonell et al., 2008).

Earliest archaeological remains have also been recovered from Dmanisi and are regarded as Oldowan (or Pre-Oldowan) by their excavators (de Lumley et al., 2005). The Oldowan is first recorded in Africa at around 2.6 Ma at Gona in Ethiopia (Semaw et al., 2005). Other Early Pleistocene sites outside Africa with Oldowan (Mode 1) technology are found in Spain (Barranco-Leon 5 and Fuente-Nueva 3 and lowest levels of Atapuerca (Martínez-Navarro et al., 1997; Gibert et al., 1998; Oms et al., 2000; Carbonell et al., 2008)), and are claimed at Pirro Nord in Italy, 1.6-1.3 Ma (Arzarello et al., 2007), the Pabbi Hills in Pakistan

~ 1.9 Ma (Dennell, 2004), Yuanmou in southern China ~1.7 Ma (Zhu et al., 2008) and Majuangou in north eastern China dated to 1.66 Ma (Zhu et al., 2004). In contrast the lithic technology at 'Ubeidiya is Acheulean, a form that first appears ~1.7 Ma at Konso Gardula in Ethiopia (Asfaw et al., 1992). Its presence at 'Ubeidiya suggests at least one hominin dispersal out of Africa occurred between 1.7 Ma and 1.5 Ma.

There are many more records of hominin fossils and archaeological sites in the Eurasian Middle Pleistocene. The earliest examples from around the Early – Middle Pleistocene transition include Gesher Benot Ya'aqov (Geraads and Tchernov, 1983), Atapuerca (Falguères et al., 1999), and Ceprano (Ascenzi et al., 2000). Archaeological material has also been reported from Flores in Indonesia at ~0.8 Ma (Morwood et al., 1998).

3. Methods

Our aim is to look for large scale patterns of dispersal. One of the problems when conducting such an analysis is the potential for variation in taxonomy over such a large area, and we have therefore examined faunal movements at the sub-family and tribal levels before going on to consider things in more detail at the generic or specific level. As we are interested in the dispersal of hominins and other medium to large terrestrial mammals, records of Chiroptera, Sirenia, Cetacea, Phocidae (earless seals) and Otaridae (walruses and sealions) are not included. Members of four other terrestrial orders are also excluded – the Lagomorpha, Rodentia, Hyracoidea and Lipotyphla (a suborder of insectivores containing amongst others hedgehogs, shrews and moles) as these contain mainly small-bodied taxa with sparse or uncertain fossil records. The remaining families are subdivided at sub-familial and tribal levels where appropriate, as shown in the supplementary data. The data used to create this table were downloaded from the Palaeobiology Database (PBD) (www.paleodb.org), a large part of the relevant section of which had been compiled by us (during the NERC funded

Palaeoinformatic context for the earliest hominin dispersals project, PACED). A total of 1335 Pliocene and Pleistocene Afro-Eurasian sites or localities with larger mammal faunas were thus examined. A few key sites were not represented in the database, so the faunal lists for these were taken from the literature (see supplementary information). In order to begin the examination of faunal differences over time in each continent the sites were binned into periods spanning 500,000 years. While other bin sizes could have been chosen it was felt that this would give us a reasonable starting point from which to consider distributions of taxa in time and space in more detail. We chose to stay with the conventional continental divisions; other divisions might have been selected, perhaps viewing Europe as a western peninsula of the Europan landmass, but again some starting point was necessary and that is how the material is generally presented in the literature. The dates were assigned using data provided in the PBD or in published records, although some sites were either too early (dated prior to 3.0 Ma) or too late (post dating 0.5 Ma), and these were removed from the dataset while others could not be assigned a date to within 1 million years and were subsequently excluded. Dates must, of course, be treated with care; resolution is variable and many are no more than estimates, so that once again the groupings that follow from assigning dates are taken as a starting point for more detailed consideration in the text.

This left a total of 904 sites or localities which have been included in the analysis. It must be noted that there is an unequal geographic spread of sites within the PBD. African sites are well represented by the ETE (Evolution of Terrestrial Ecosystems) records and much of the European and Central Asian records are covered by the PACED dataset. However, far fewer Eastern Asian sites are included, although fortunately several recent reviews of the Asian faunas have been published (Chauhan, 2008; Deng et al., 2008; Nanda, 2002, 2008; Tong, 2006, 2007; Zhu et al., 2008) and these have been incorporated where appropriate. The

breakdown of localities per continent is as follows: Asia = 63, Africa = 526, Europe = 306, and the Levant = 9. Further details can be found in the supplementary information.

4. Results

From the large-scale analysis of sites on a continental basis some broad patterns can be seen (see supplementary information table 1). The Cervidae are present in Europe and Asia, and absent from Africa, while the majority of Bovid tribes are only found in Africa. However, some finer scale detail can be identified, for example the appearance of the reindeer, a member of the Odocoilieni, in Europe and Asia after 1.0 Ma. Some bovid tribes are ubiquitous, found in all regions and all time periods, such as the Bovini and Antilopini, while others such as the Peleini have a restricted range in both time and space. Certain other groups, including the Equidae (which includes both *Equus* and *Hipparion*), the Elephantinae and the Rhinoceroti, are also found in all time periods and regions. The arrival of the Pantherinae and Hominini can be seen in Europe and Asia. Thus the broad-scale differences between continents in terms of their faunal distributions can clearly be identified, even at a high (family, subfamily or tribal) taxonomic level.

However, the details of these movements are seen at the generic or specific level, and these have been identified from the literature. Table 1 summarises all identified first appearances of taxa of African origin outside Africa. Europe, the Levant and Asia have been listed separately, although Asia includes central Asia (e.g. Georgia, Tadjikistan) as well as Eastern Asia (China, India, Indonesia). In the text we treat the patterns of movement in terms of broad continental headings and directions, since we feel this conveys the most information to the reader.

4.1 Out of Africa

For the mammalian fauna in general, relatively few taxa migrate from Africa between 3.0 – 0.5 Ma. In total, members of 13 genera dispersed from Africa during this time - *Homo, Theropithecus, Panthera, Megantereon (as M. whitei), Crocuta, Pachycrocuta, Hippopotamus, Palaeoloxodon, Hippotragus, Oryx, Damalops, Pelorovis, Kolpochoerus*. A further five genera, *Parahyaena, Giraffa, Vishnukobus, Sivacobus* and *Potamochoerus* may also have dispersed, as discussed below. Nine of these African genera are found in Europe, nine in SW Asia, six in central Asia and 10 in eastern Asia (China, India-Pakistan Siwaliks deposits). The first appearances of these taxa in Eurasia are shown in Table 1.

As summarised in the previous section, the genus *Homo* is first recorded at Dmanisi in Georgia, followed by Java and Yuanmou although these may represent a different species, and then at 'Ubeidiya but with a different tool technology. No fossils are found in Europe until 1.2-1.1 Ma, but archaeological sites may predate this occurrence (indicated by 'a' in Table 1). The only other primate to have dispersed beyond the Arabian Peninsula in the Plio-Pleistocene was *Theropithecus* cf. *T. oswaldi*, remains of which have been found in India and Spain, with more doubtful occurrences in Italy and Israel (see Hughes et al., 2008, for discussion).

The earliest find of the genus *Panthera* outside Africa may be *P. palaeosinesis* from China, although the age is not clear. Christiansen (2008) suggests that the holotype may only be of Early or Middle Pleistocene age, but claims so-far unpublished material may be from Late Pliocene horizons. The Yuanmou deposits in China contain records of *Panthera tigris* at ~1.7 Ma (Zhu et al., 2008) and there is another Eurasian member of the genus, the jaguar-sized *P. gombaszoegensis,* which is first recorded in Europe at the very end of the Pliocene (Spassov, 1998; O'Regan and Turner, 2004). Whether *P. gombaszoegensis* had an African or Asian origin, or was a European endemic species, is still unknown (Sardella and Palombo,

2007). The appearance of the modern lion (*P. leo*) and leopard (*P. pardus*) in Europe is much later; leopard is first known at Le Vallonet in France, which dates close to the Jaramillo Event, while lion is currently first seen at Pakefield in England (Parfitt et al., 2005; Turner, 2009, Lewis et al., in press). Based on the different first appearance dates of these species, it is conceivable that members of the genus *Panthera* dispersed from Africa several times during the Pleistocene. The sabretoothed cat genus *Megantereon* has recently been subject to a detailed study of cranial and dental morphometrics (Palmqvist et al., 2007), which concluded that a more primitive Eurasian species, *M. cultridens*, existed in Eurasia until the end of the Pliocene and was then replaced by the more derived African species, *Megantereon whitei,* first seen at Dmanisi.

The spotted hyaena genus *Crocuta* is first found in Asia in the upper part of the Nagrota formation (beginning at 2.5 Ma) in India, which is equivalent to the Pinjor formation of the Siwaliks (Nanda, 2002, Basu, 2004). The extant species *Crocuta crocuta* is certainly recorded by Turner (2004) at localities 68 and 73 in the Siwaliks of Pakistan, the latter dated between 1.4-1.2 Ma (Dennell et al., 2006). However the earliest known occurrence of *Crocuta crocuta* in Europe is at Atapuerca in Spain below the Brunhes-Matuyama boundary (Garcia and Arsuaga, 2001). The large, short-faced hyaena *Pachycrocuta brevirostris* is first recorded in Europe in earliest Pleistocene deposits (Turner and Antón, 1996), but it is certainly present in Asia (Turner, 2004; Dennell et al., 2008) and Africa (Turner, 1990) at around that time. The earliest date currently cited for Africa is for material from the South Turkwel site in northern Kenya (Werdelin and Lewis, 2000) in deposits dated between 3.58 and ~3.2 Ma, and although the material is scanty and less than ideal it would seem that an origin for the genus in Africa is indicated.

The extant African brown hyaena, *Parahyaena brunnea*, has recently been identified in Spain at the site of Fonelas in deposits dated to 1.8 Ma (Viseras et al., 2006). This is the first

record of this species in Europe, but it may be more plausibly explained as a late appearance of the Eurasian Pliocene species *Pliocrocuta perrieri*. This latter species disappears from European deposits at the end of the Pliocene and then reappears in the Middle Pleistocene, possibly from a refugium in Asia but also possibly from one in Portugal (Turner et al., 2008). The species are very similar morphologically, if not identical (Turner, 1990), although recent claims for an early member of the genus *Parahyaena* in Africa from around 4.0 Ma at Kanapoi (Werdelin and Lewis, 2005) could suggest an ultimate origin in Africa but before the period of concern to us here.

The other extant hyaenid that might concern us is the striped hyaena, *Hyaena hyaena*, which is found across northern Africa, the Arabian Peninsula, southern Turkey and across into India (Rieger, 1981). However, previous claims for its appearance (in the form of *Hyaena prisca*) in European Pliocene and Pleistocene deposits can now be discounted (Turner et al., 2008), and it essentially has no fossil record outside Africa (Werdelin and Solounias, 1991) so that we can offer no assessment of its dispersal pattern.

Hippos have very complex pattern of dispersal, with at least 3 different species in the Levant (Table 1) one of which appears to have been an endemic (*H. behemoth*). The first appearance of *Hippopotamus* in Europe is at Venta Micena in the Early Pleistocene (Martínez-Navarro and Palmqvist, 1995), and it is found as far East as Akhalkalaki in Georgia (Vekua, 1986; Hemmer et al., 2001) - hence its inclusion in the Asian section of Table 1. *Hippopotamus* is not found elsewhere in Asia, with the possible exception of India where both *Hexaprotodon* and *Hippopotamus* are recorded (but may in some cases be synonymous (Chauhan, 2008)). There are no reliable records of *Hippopotamus* from China (Tong, 2007).

Palaeoloxodon antiquus, the straight tusked elephant, is first found in Asia at 1.36 Ma and in Europe and the Levant after 1.0 Ma (Table 1). However, in Asia it was confined to the Palaearctic regions (Tong, 2007), and all *Palaeoloxodon* records in peninsular India now

appear to be *Elephas* (Chauhan, 2008), the genus to which the extant Indian elephant belongs. There is also a tentative identification of cf. *Elephas recki* at An Nafud in Saudi Arabia, which is dated to the Early Pleistocene (Thomas et al. 1998).

The indisputably African suid *Kolpochoerus olduvaiensis* is found at 'Ubeidiya in Israel (Geraads et al., 1986) dated to ~1.5 Ma (Belmaker et al., 2002). The second record of *Kolpochoerus* from Israel appears to be of an endemic species, *K. evronensis* (Haas, 1970) from the site of Evron Quarry, and the genus therefore seems to have dispersed from Africa but to have got no further than the Levant. However, Martinez-Navarro (2004) has mentioned that it may also occur in India. The bushpig genus *Potamochoerus* is reported in both the Siwaliks and Peninsula India by Nanda (2008), but Chauhan (2008) examines some of the same faunal localities and does not mention it. Relatively few taxa of African origin appear in India south of the Siwaliks complex, but this may in part be due to a lack of discovery or exploration of similarly aged deposits (Chauhan, 2008). A new species of *Potamochoerus* has also been identified at Fonelas in Spain by around 1.8 Ma (Viseras et al., 2006), which may indicate a dispersal from Africa or possibly Asia.

Six bovid taxa of African origin have been identified in SW Asia, central Asia and the Siwaliks deposits of southern Asia. The earliest record is of a member of the genus *Hippotragus* – *H. brevicornis* – in the Tatrot Formation of the Siwaliks in India and Pakistan (Vrba and Gatesy, 1994). The latest part of the Tatrot Formation is dated to 2.58 Ma (Nanda, 2002), indicating that the appearance of *Hippotragus* in this deposit must be the result of a middle Pliocene dispersal from Africa, prior to ~2.6 Ma at the latest. The overlying Pinjor Formation of the Siwaliks contains the best record of bovids with African origins, since *Oryx sivalensis*, *Hippotragus bohlini*, *Damalops palaeindicus*, *Vishnukobus patulicornis* and *Sivacobus palaeindicus* have all been recorded from these deposits (Vrba & Gatesy, 1994, Vrba, 1995a). Vrba (1995a: 397) suggested that this appearance might be the result of a

second wave of migration which 'involved five African emigrants very close to or soon after 2.7 Ma'. However, detailed analysis of the dating, the Siwaliks sites and the palaeoecology of the animals themselves indicates that this may not be such a clear signal. Estimates of the duration of the Pinjor Formation vary greatly throughout its geographic range, and it has generally been treated as an undifferentiated unit although Dennell et al. (2006) have attempted a subdivision of the earlier portion based on material from the Pabbi Hills of Pakistan. The upper level in contact with the overlying Lower Boulder Conglomerate has been variously estimated to be between 1.72 – 0.6 Ma depending on whereabouts in India and Pakistan the deposits are found (Nanda, 2002, 2008). As they have been found in the Pinjor Formation, these 'African' bovid specimens cannot be earlier than 2.58 Ma (the latest date of the Tatrot Formation (Nanda, 2002), but they could potentially be as young as the Middle Pleistocene. This is acknowledged by Vrba (1995a) and Vrba and Gatesy (1994) in the tabulated data, but is not made explicit in the text.

As noted above, *Hippotragus brevicornis* has previously been found in the Siwaliks, perhaps indicating that the appearance of a new species of *Hippotragus* (*H. bohlini*) in the Pinjor formation was a result of endemism and not necessarily evidence for a new dispersal out of Africa. Both *H. brevicornis* and *H. bohlini* were originally assigned to the genus *Sivatragus* by Pilgrim (1933), but were referred to *Hippotragus* by Vrba and Gatesy (1994) and Vrba (1995a). However, a cladistic analysis conducted by Vrba and Gatesy (1994) indicates that *H. bohlini* shares some features in common with later African forms, and not with the earlier *H. brevicornis,* and they suggested that *H. brevicornis* might represent a new genus and a sister taxon to *Hippotragus* sensu stricto. If *H. bohlini* were more closely related to the African hippotragines than to *H. brevicornis* that preceded it in the Siwaliks deposits then this would indicate a second, undated, out-of-Africa movement for members of this genus.

The genus *Oryx* is first recorded outside Africa as *Oryx* sp. indet. at the Pliocene site of Kvabebi in Georgia (Gabunia, 1974) and then later as *Oryx sivalensis* in the Pinjor Formation (Vrba, 1995a). Since the genus *Oryx* was already present in Eurasia it is not certain that its presence in the Siwaliks can be taken as evidence of a new dispersal out of Africa, and it may just represent movement within Asia. *Oryx* is a lineage with adaptations to arid environments, indicating that the earlier representatives could have survived in more open conditions (Estes, 1991; Vrba 1995a). By the late Early Pleistocene a desert adapted form is recorded from An Nafud in Saudi Arabia (Thomas et al. 1998). In contrast, *Sivacobus palaeindicus* from the lechwe lineage (Vrba, 1995a), and *Vishnukobus patulicornis* from the reduncine kob lineage (Vrba, 1995a) are both members of the Reduncini, a tribe which includes the extant lechwe (*Kobus leche*) and waterbuck (*Kobus ellipsiprymnus*), animals with a strong preference for flood plains and other areas close to water (Estes, 1991). The genus *Damalops* is recorded in both the Pinjor Formation (Vrba, 1995a) and at the site of Kuruksay-Navrukho in Tajikistan dated to the Late Pliocene, or MN 17 (Sotnikova et al., 1997). *Damalops* is an extinct African alcelaphine, so there are no data on the environmental preference of the genus. However, the Alcelaphini as a whole prefer an open landscape with short grass and they can also tolerate tree cover, but are not desert adapted (Estes, 1991). The sixth African bovid from the Pinjor formation is simply recorded as Alcelaphini indet., so the environmental information given for *Damalops* is also of relevance.

Indeterminate alcelaphines are also found in the palaeontological record of the SW Asia from the early Pleistocene onwards at An Nafud localities 1 and 2 and Evron Quarry (Thomas et al., 1998; Tchernov et al., 1994). Hippotragini indet. cf *Hippotragus* sp. is recorded at 'Ubeidiya by Gaudzinski (2004), but not by Belmaker (2006).

The extinct African buffalo species *Pelorovis oldowayensis* is recorded in the Levant, at 'Ubeidiya (Tchernov et al., 1994), and as *P*. cf. *P. oldowayensis* in Saudi Arabia at An Nafud

localities 1 and 3 (Thomas et al., 1998). *Pelorovis* cf. *P. bubaloides* (a north African species) was recorded at Gesher Benot Ya'acov by Martinez-Navarro (2004), although Tchernov et al. (1994) listed all large bovid remains from Gesher as *Bos* sp. As discussed in the following section, Martinez-Navarro et al. (2007) have recently suggested that all these remains should be referred to *Bos*, although there is not enough material from Gesher to permit a formal identification of the species.

The genus *Giraffa* is only found in Africa today, but probably had an Asian origin and the relationship between the African and Eurasian species have not yet been resolved (Mitchell and Skinner, 2003). However, members of the genus *Giraffa* are found in the Levant at Bethlehem and 'Ubeidiya, and the Middle Pleistocene giraffe at Latamne in Syria is suggested to be conspecific with the extant *Giraffa camelopardalis* (Guérin et al., 1993). If this is the case, then this may suggest a dispersal from Africa in the Middle Pleistocene, as *G. camelopardalis* is known in Africa from 1.0 Ma onwards (Mitchell and Skinner, 2003). However, there is a possibility that it could be a Pliocene relict, as suggested by Belmaker (2006).

Of the nine African genera found in SW Asia there are only three that may not be present elsewhere in Eurasia - *Giraffa, Kolpochoerus* and *Pelorovis* - although, as mentioned above, Martínez-Navarro (2004) suggests that *Kolpochoerus* may have dispersed into India, and the records of *Giraffa* may not indicate a dispersal. In addition to these genera some indeterminate alcelaphines have also been recorded in SW Asian sites and *Hippopotamus gorgops* is only found in the Levant. The wide range of animals dispersing from Africa suggests that there was no taxonomic or ecological bias on animals entering SW Asia, and that only a limited number of taxa became isolated and speciated there (e.g. *Kolpochoerus* and *Hippopotamus*). Belmaker (2006) provides a useful discussion of the environmental tolerances of each taxon found at 'Ubeidiya and the potential limitations to their dispersal.

There has often been an emphasis on the Levant as a key to understanding the dispersal of faunas in the Plio-Pleistocene (Tchernov, 1992; O'Regan et al., 2005, Turner, 1999), since this is considered the most likely dispersal route for macromammalian taxa (O'Regan et al., 2006; Turner and O'Regan 2007a, b). However, this approach may limit interpretations as there are only seven sites in the Levant for the time period in question, or a total of nine if the three An Nafud localities in Saudi Arabia included (Thomas et al., 1998). As we are concerned with placing the hominin fossil record in its faunal context we are interested in those animals that dispersed beyond the Arabian peninsula, as *Homo* did, so the paucity of sites in the Levant does not prevent the analysis of patterns of movement. It does however constrain our understanding of when animals may have moved, as only one site is known in the late Pliocene (Bethlehem), two in the Lower Pleistocene ('Ubeidiya, An Nafud) and four from the early-Middle Pleistocene (Gesher Benot Ya'acov, Latamne, Evron Quarry and the lowest levels of Tabun) – hence the clustering of first appearances around 2.5 Ma, 1.5 Ma and 1.0-0.8 Ma in Table 1 (and see supplementary information). In the case of taxa such as *Palaeoloxodon* it is unlikely that they could have dispersed into Eurasia without passing through the Levant, so the later Levantine appearance shown here in Table 1 is likely to be an artefact of the lack of sites. Whether the same argument can be made about *Homo* seemingly being found earlier at Dmanisi and then later at Ubeidiya is doubtful, based on the morphology of the specimens and their associated artefacts at each locality.

In summary, the latest identified dispersal from Africa is that of *Palaeoloxodon* at roughly 1.3 Ma, although it is possible that lions, leopards, *Giraffa* and *Bos* moved later (see Martínez-Navarro, 2004, Martínez-Navarro et al., 2007 and below, next section). Only seven genera of African origin are found in both Europe and Asia – *Pachycrocuta, Crocuta, Panthera, Palaeoloxodon, Homo, Theropithecus* and *Megantereon* (the latter as *M. whitei* replacing the earlier *M. cultridens*) with the possible addition of *Potamochoerus* and

Hippopotamus, although both require further investigation. Several 'African' genera that are found in Europe after 1.2 Ma, such as *Panthera, Crocuta, Palaeoloxodon* and *Homo*, are all found in Asia prior to their first appearance in Europe.

4.2 Into Africa

In comparison with the 13 genera dispersing from Africa between 3.0-0.5 Ma, only four genera definitely entered the continent over the same period: *Equus, Nyctereutes, Lycaon* and *Antilope*, although *Mammuthus meridionalis* is reported at Ain Hanech in Algeria (Sahnouni and de Heinzelin, 1998).

However, numerous members of the tribes Ovibovini (*Nitidarcus, Damalavus*, plus two indeterminate Ovibovines), Caprini (*Makapania, Bouria, Parantidorcas*, plus six indeterminate Caprines) and Alcelaphini (*Numidocapra*) are recognised within Africa. The difficulty here is to decide whether these bovids represent individual incursions into Africa, as suggested by Vrba (1995a) in the case of the Caprini, or evolution within Africa because no fossils outside that continent have been assigned to the genus, as in the case of *Numidocapra* (Vrba, 1995a). If each is regarded as a separate incursion into Africa, then there were a total of 17 movements, but if only the first appearance of each tribe is counted, and the rest assumed to be the result of in situ speciation, only six movements occurred.

Because of the uncertainty over these findings, these taxa are not included in Table 1, but their appearances and dates are summarised here as a basis for future work in this area. The data on bovid appearances are mainly from Vrba (1995a). The Eurasian genus *Antilope* has been recorded from several sites in Africa, particularly two specimens of *Antilope* aff. *A. subtorta* at Shungura C5 (2.74-2.5 Ma) (Vrba, 1995a; Bobe and Eck, 2001) and Omo L45 (2.8-2.5 Ma). In addition to *Parantidorcas latifrons* from Ain Boucherit in Algeria dating between 2.7-2.5 Ma, Vrba (1995a) recorded the appearance of 5 different types of "?Caprini

indet. A-D", and "?Caprini indet sp". All of these records are from East Africa, with

"?Caprini indet A" being found twice at Lokalalei in West Turkana between 2.52-2.35 Ma,

and again at Nariokotome in Kenya between 1.39-0.8 Ma. The next earliest in Vrba's scheme

is "Caprini indet. C", recorded from Upper Lomekwi below 2.5 Ma and at Nariokotome after

1.39 Ma. "?Caprini indet. sp." is in the Shungura formation, dated between 2.5-2.33 Ma. Both

"? Caprini indet. B" and "D" are found in the Natoo Formation, dating between 1.65-1.33 Ma.

Vrba (1995a) regards each appearance of these caprines as evidence of a separate incursion

into Africa, as the Caprines as a group originated in Eurasia. However, it is possible that some

of them could have been present in Africa in low numbers and may not represent a separate

later incursion, since "Caprini indet A" and "C" are known from both the late Pliocene and

the late Early Pleistocene. Martinez-Navarro et al. (2004) record Caprini indet from Bouri,

and Asfaw et al. (2002) have a new genus and species of caprine, *Bouria anngettyae*, recorded

from Daka (1.0-0.8 Ma). Clearly, more work needs to be done on these bovids, and at present

many questions about dispersals and distributions remain unanswered.

The only find of true *Bos* in sub-Saharan Africa is a record of *Bos* cf. *B. primigenius*

dating to 0.8-0.6 Ma at Asbole in Ethiopia (Alemseged and Geraads, 2000; Geraads et al.,

2004), indicating an early Middle Pleistocene immigration for this genus. However, a revision

of the genus *Bos* (Martínez-Navarro et al., 2007) suggests that *Pelorovis* and *Bos* may be

congeneric, forming three chronospecies, *Bos turkanensis*, *B. oldowayensis* and *B.*

primigenius, with the latter dispersing from, rather than into, Africa at around 0.6 Ma. This

study is based on a geometric morphometric analysis of a limited number of specimens, and

further work will be required to determine if this scenario is correct. Therefore we have

retained *Pelorovis* for the African and Levantine material as it highlights the arrival of

bovines with a distinctive morphology, only otherwise known in Africa, in the Arabian

Peninsula. However, we acknowledge that if Martínez-Navarro et al. (2007) are correct then

Bos would form the latest dispersal from Africa into Europe in the time period considered here, and did so at the very late date of ~ 0.6 Ma.

Only three non-bovid taxa dispersed into Africa between 3.0-0.5 Ma. Two were carnivores - the raccoon dog genus *Nyctereutes* is found in both north and South Africa from 2.5 Ma onwards (Geraads, 1997; Ficcarelli et al., 1984), whilst the African hunting dog genus, *Lycaon*, is first found in north and east Africa at ~1.8 Ma (Martínez-Navarro and Rook, 2003). Both were widespread in Eurasia before entering Africa (if *Xenocyon* and *Lycaon* are synonymous). The third genus was *Equus*, the monodactyl horse, which is found throughout Africa from 2.3 Ma onwards (Bobe and Behrensmeyer, 2004). The timings of these dispersals indicates that, with the exception of two possible caprine movements and the now doubtful first appearance of *Bos* in East Africa (Geraads et al., 2004), all arrivals of Eurasian fauna into Africa predated 1.3 Ma.

4.3 Out of Asia

Asia is a vast and diverse area, and much further work is required to fully integrate the Asian record with that from Europe and Africa. There is an absence of deposits in the Indian region south of the Siwaliks for this period, so it is difficult to determine what was happening here (Chauhan, 2008). The fauna of peninsular India appears to have followed a different evolutionary trajectory from that of other areas (Chauhan, 2008), and it is possible that it served as a dead end for dispersals. Northern China shares many species with Europe, but there was clearly a different fauna in oriental China, although there is evidence of mixture with cooler faunas from the north (Tong, 2006, 2007).

At least four of the 'African' taxa listed in Table 1, *Homo, Palaeoloxodon, Panthera* and *Crocuta,* are found earlier in Asia than they are in Europe. One explanation, suggested by recent GIS modeling of later *Homo sapiens* dispersal in the Arabian and Indian peninsulas

(Field et al. 2007), is that routes can be found up the Levantine coast, or along the coast of India. This may indicate that it was easier for some species to get into Asia than directly into Europe. Furthermore, dispersal models of *Theropithecus* (Hughes et al., 2008) found a similar pattern, and both seem to fall in line with the suggestion that an area of savannah grasslands ('Savannastan'), stretching from Africa into southwestern Asia, united areas that are traditionally placed in separate biogeographic compartments (Dennell 2003; Dennell and Roebroeks 2005).

Recent work on Pleistocene hominin dental morphology suggests complexity of movement within Eurasia during the Middle Pleistocene rather than a discontinuous series of African incursions (Martinón-Torres et al., 2007), and this picture is supported by the results of a recent computer simulation study by Hughes et al. (2007) on hominin dispersal patterns in relation to climatic changes. It may be significant for ideas about a southern route to Asia that the animals shared with peninsular India are generally omnivores or carnivores. These animals are able to move along beaches taking what they can get, while bovids, equids and proboscideans may have had more difficulty surviving en route. The impetus to continued dispersal that might come from movement close to shorelines in otherwise harsh environments was stressed by Turner and O'Regan (2007b).

In contrast to the paucity of African taxa, the source of many of the bovids and of course cervids that dispersed into Europe was Asia, at both at Pliocene-Pleistocene boundary ~1.9 Ma (Spassov, 1998) and later at around the Early-Middle Pleistocene boundary (Azzaroli et al., 1988, Martínez-Navarro and Palombo, 2004). Numerous other species appear to have been widespread in both Europe and Asia, including the woolly rhino genus *Coelodonta*, the dhole *Cuon alpinus* and *Trogontherium cuvieri*, a large extinct beaver (Tong, 2006). It appears that Asia may have provided a reservoir for taxa such as the cheetah, *Acinonyx,* or *Pliocrocuta perrieri*, or a staging post for African taxa such as *Homo, Panthera* and *Crocuta,*

as well as being the source of many of the cold-tolerant animals found in Europe in the Middle Pleistocene.

The Proboscidea have had a complicated history, since the genus *Mammuthus* originated in Africa but much of its later speciation and development appears to have occurred in Siberia and northern China in the late Pliocene and earliest Pleistocene (Lister et al., 2005). Thus they dispersed from Asia to Europe, SW Asia and perhaps north Africa from these areas (Table 1). A similar pattern is seen in the proboscidean genus *Stegodon*, which became extinct in Africa during the mid-Pliocene (Kalb, 1995), but dispersed into Asia in the Pliocene where it is found in the Tatrot formation of the Siwaliks (Nanda, 2008) and persisted until the late Pleistocene (Van den Bergh et al., 2008). In the Pleistocene it is found in the Siwaliks, peninsular India, China and Indonesia (Nanda, 2008; Chauhan, 2008; Tong, 2006; van den Bergh et al., 2001), but also reappears in SW Asia in the late early Pleistocene, having been found at Gesher Benot Ya'acov , Evron Quarry and Latamne (see O'Regan et al., 2005 and references therein), but does not return to Africa or enter Europe at this time.

5. Discussion

5.1 Previously identified dispersal events

Our investigations call into question the idea of a bovid dispersal out of Africa at 2.7-2.5 Ma based on the six 'African' bovid taxa identified in the Siwaliks deposits by Vrba (1995a). The oryx is previously known from sites elsewhere in central Asia prior to its first find in the Pinjor Formation, and its dispersal from Africa may therefore have occurred much earlier in the Pliocene. The first find of a hippotragine also predates the Pinjor Formation, although the later species *Hippotragus bohlini* may not be a descendent of the earlier animal *H. brevicornis*, and may therefore represent a second dispersal of this genus from Africa in the Pliocene. *Damalops* is a good contender for a genuine movement at ~ 2.5 Ma as it is found in two

separate areas, Tajikistan and Pakistan, at roughly the same time (although the dating problems of the Pinjor Formation must be taken into account). Both *Sivacobus* and *Vishnukobus* are from known African tribes but are new genera, suggesting that they had time to evolve after they migrated but before they appeared in the fossil record. However, this taxonomic difference may not have represented that great a difference for the animals themselves, and it appears that bovids may speciate relatively quickly (it has been estimated that the main tribes appeared within the space of a few hundred thousand years in the Late Miocene or earliest Pliocene (Vrba, 1995b)), perhaps indicating that the new genera in the Siwaliks would not have required a very long period of isolation to become differentiated. It is therefore unlikely that the presence of endemic genera in the Siwaliks can be taken as an indication of a dispersal much more than a few hundred thousand years before they are found in the deposits, and unfortunately the chronology of the deposits is unclear. Work is being undertaken to recover new specimens with accurate recording of position within the formations, but no new 'African' bovid material has yet been found (Nanda, 2002). Overall then, of the six Siwalik bovids found, it appears that only *Damalops palaeindicus* can be regarded as a genuine late Pliocene immigrant, although *Hippotragus bohlini* may also be a possibility. The other species lack independent corroboration from other sites, and are found in a formation that certainly spans one million years and possibly two in some areas. In addition, the taxa have a variety of environmental tolerances, meaning that it is unlikely that they would all have migrated together – the arid-adapted oryx with the wetland-preferring lechwe for example - but rather the evidence seems to point to them moving alone when the environment was right for each individual species, and not as a 'wave' of dispersal out of Africa at 2.7 Ma.

Mammuthus dispersal into Europe was originally thought to coincide with the arrival of the horse genus *Equus* in Eurasia at ~2.5 Ma (Lindsay et al., 1980), later referred to as the

elephant-*Equus* event by Azzaroli et al. (1988). However, the earliest mammoths and monodactyl horses have now both been found in Romania. *Equus* (= *Pleshippus*) is recorded at 3.9 Ma in the Oltet Valley (Radulesco and Samson, 1990, 2001), and *Mammuthus rumanus*, the most primitive Eurasian mammoth, is present at Tuluceşti and Cernăteşti in the Dacic Basin in deposits referred to mammalian biozone MN16a and correlated with the Gauss subchron, 3.5-3.0 Ma (Radulescu and Samson, 1990, 2001, Lister et al. 2005). This latter species is also found in the Yushe Basin in Northern China (Lister et al., 2005; Wei et al., 2006) indicating that the earliest mammoths were present in both Europe and Asia prior to 3 million years ago. This may represent a simultaneous dispersal of *Mammuthus rumanus* into both continents at the same time from an origin point in Africa (Lister et al., 2005). Tchernov and Shoshani (1996) suggested a wave of proboscidean dispersal out of Africa at 2.5-1.5 Ma, but from the information presented above it appears that the majority of proboscidean dispersals out of Africa occurred prior to 3 Ma, with the exception of *Palaeoloxodon*, which dispersed in the Early Pleistocene.

The 'wolf event' of Azzaroli et al. (1988) involving the first appearance of *Canis* is now thought to have occurred in the Pliocene rather than the earliest Pleistocene, and involved at least 4 different taxa, including the giant short-faced hyaena, *Pachycrocuta brevirostris* (Sardella and Palombo, 2007). The earliest known *Canis*, even if not demonstrably a 'wolf', is currently the material from Vialette in the Massif Central of France, dated to 3.14 Ma (Lacombat et al., 2008). Members of the African hunting dog genus *Lycaon* may be the only instance of simultaneous dispersal into Africa and Europe from Asia. The earliest find of the genus is in China at 2.4 Ma, followed by 1.9 Ma in Europe and 1.8 Ma in north Africa (Martínez-Navarro and Rook, 2003). However, acceptance of this scenario is dependent on assuming that the earliest specimens of a very rare taxon have been found, and that *Xenocyon* and *Lycaon* are congeneric.

The arrival of *Equus* in Europe was dated to 2.6 Ma and at 2.3 Ma in Africa (Lindsay et al. 1980). Despite intensive fieldwork in Africa no earlier *Equus* fossils have yet been found, but the earliest monodactyl horses in Europe now predate the dispersal into Africa by some 1.6 Ma (Radulesco and Samson, 1990, 2001).

It appears from the data we present in this paper that several of the well known faunal events in the later Pliocene and Pleistocene have been undermined. It may therefore be counterproductive to talk of the first appearance datum (FAD) of an animal or even groups of animals as an 'event', as these are constantly changing as new material is discovered and described.

5.2 Repeated dispersals

As discussed above, the record of caprine movements into Africa can either be taken as evidence of repeated incursions of taxa that have not yet been found outside Africa or as *in situ* evolution. Several other taxa also have records that suggest there may have been repeated dispersal events rather than continual occupation following their first appearances. These include carnivores, hominins and the hippos, and possibly the SW Asian alcelaphines and hippotragines. Such patterns are extremely important, as concentration simply on FADs of taxa may disguise multiple movements between continents. This may be a shortcoming of both our current perception of the evidence and also the patchy nature of the fossil record.

Arguably the sparsest, yet most examined, record of an African taxon outside Africa is that of early *Homo*. The earliest known fossil and archaeological material outside Africa from Dmanisi in Georgia (~1.7 Ma) perhaps indicating a first late Pliocene/ Early Pleistocene dispersal of most primitive *Homo*. It has also been suggested that *Homo erectus* may even have dispersed back into Africa from Asia, arriving back at roughly 1.4 Ma at Olduvai Gorge (Clarke, 2000), and our data does not exclude the possibility of an immigration at this date.

As different stone tool industries have been found sequentially in SW Asia and central Asia, it would seem logical to suggest that these are the result of separate dispersals of hominins carrying different tool types from Africa as suggested by Bar Yosef and Belfer-Cohen (2001). However, tool kits can be adapted to local needs, and therefore equating stone tool cultures with particular taxonomic or migratory groups may be too simplistic (e.g. Field et al., 2007; Turner and O'Regan, 2007b). These latter arguments are based on later dispersals of *Homo sapiens*, but may be worth considering in the context of the persistence of mode 1 (Oldowan) industries in Europe long after the Acheulean had appeared elsewhere.

Two carnivores, the European cheetah, *Acinonyx pardinensis* and the brown hyaena-like *Pliocrocuta perrieri* disappeared from Europe in the earliest Pleistocene only to reappear in the earlier stages of the Middle Pleistocene at sites such as Petralona, Mauer, Mosbach 2 and, in the case of the hyaena, at the southern French sites of L'Escale and Lunel Viel (Turner, 1995). These second, restricted dispersals did not reach Britain, but the hyaena may have reached the Iberian Peninsula, in view of the presence there of what has been identified as *Hyaena prisca* at the Portuguese Late Pleistocene locality of Furninha (Cardoso, 1992) but which is more plausibly *P. perrieri* (Turner et al., 2008). Contrary to earlier suggestions (Turner et al., 2008) it also seems to have returned to Italy where it is found at Ponte Galeria in deposits dated to 0.65-0.55 Ma (Milli and Palombo, 2005). The origins of this second dispersal into Europe may have lain in Asia, where certainly the cheetah, and perhaps also the hyaena, may have retained a presence. In the case of *P. perrieri* the return to Europe could even represent expansion from a relict population in Iberia, but we should perhaps also consider the possibility of a Middle Pleistocene dispersal from Africa in view of the similarities between *P. perrieri* and the brown hyaena discussed above in Section 2.

Dispersals by *Hippopotamus* are also of interest. The earliest find of *Hippopotamus* in Europe is in the Early Pleistocene at Venta Micena in Spain (Martínez-Navarro, 2004), and

the genus is also found at 'Ubeidiya in the Levant. However, two different species are present at 'Ubeidiya, *H. gorgops,* an African species, and *H. behemoth*, an apparent Levantine endemic (Martínez-Navarro, 2004; Belmaker 2006). *Hippopotamus* cf. *H. behemoth* has also been recorded from Latamne in Syria, dated between 0.7-0.6 Ma (Guérin et al., 1993), although Tchernov et al. (1994) believed it was earlier. The early Middle Pleistocene site of Gesher Benot Ya'aqov has *Hippopotamus ?amphibius* (Geraads & Tchernov 1983; Bar-Yosef, 1998; Tchernov et al., 1994), the extant African species. *Hippopotamus georgicus* (= *H. amphibius antiquus*) has been found in Central Asia, at the late Early Pleistocene site of Akhalkalaki in Georgia (Hemmer et al., 2001), but not so far in southern and Eastern Asia, where it is possible that its niche was filled by *Hexaprotodon*. According to Tong (2007) *Hippopotamus* is not found in China, but it is conceivable that some *Hippopotamus* sp. identifications in India are correct. An obvious question to ask is whether hippos dispersed repeatedly from Africa or survived in refugia between their various appearances in Europe, but further work is required to resolve this issue.

6. Summary and conclusion

Overall we conclude that there is now little evidence for major waves of dispersal between the Pliocene and Pleistocene mammal faunas of Africa and Eurasia. Instead the pattern seems to be highly complex, with few species moving in concert. Previously identified faunal 'events' such as the Elephant-*Equus* event and the dispersal of African bovids into Asia at 2.5 Ma have also been discounted, and it may be that talking in terms of events is too simplistic. It makes for a useful shorthand but can end up trapping things in its own logic, so that the appearance of a true *Canis* in Europe would have to be later than 1.7 Ma on the basis of earlier ideas about a 'wolf event'. We therefore need to be clear about what we can say. Can we identify a first record, and therefore *perhaps* a first appearance by a taxon in a region?

Yes. But identification of an event needs caution unless it is something like a volcanic eruption with a spread of geochemically identifiable debris, and it is worth reiterating that a First Appearance Datum is just that.

Faunal events are difficult to identify because mammals are unpredictable. We suspect that species moved alone and that *Homo* is not special; although repeated dispersal may be seen in the hominin record, it appears that other taxa such as *Panthera* may have followed a similar pattern. It is not impossible that *H. erectus* could have moved back into Africa as suggested by Clarke (2000), since it is only after 1.3 Ma that Eurasian mammals, with the possible exception of two caprines and *Bos*, seem to stop appearing in the African record. In terms of dispersal out of Africa, the majority of movements happened prior to 3 Ma or between 1.8 Ma and 1.3 Ma.

Should we expect to see other African elements in a site with hominins? No, not necessarily, if we are correct in concluding that taxa did not move together. Therefore the presence or lack of African taxa within a site cannot be used uncritically either to support or to dismiss early putative archaeological assemblages. We might also ask how long does an animal have to be out of Africa to still be considered 'African' - is the hippopotamus found in British last interglacial sites, and absent since the Cromerian, still African? Surely not; it is more likely to have re-appeared from some refugium closer to hand.

We conclude that a relatively small number of Eurasian Pleistocene taxa come from Africa and those that do have differing environmental tolerances, which alone carries the clear implication that they would not have moved together. Few taxa can be shown to have gone into Africa, and there is instead much more movement between Asia and Europe than between Africa and Europe. In other words, the predominant pattern of dispersal in the Afro-Eurasian Pliocene and Pleistocene was east-west rather than north-south. In particular, a

closer examination of the evidence for the Bovidae shows that neither dating nor palaeoenvironmental data suggest that they dispersed together in a wave from Africa.

The absence of any dispersal in concert calls into question the likelihood that *Homo* moved with other taxa, so that models of simultaneous expansion by hominins and other taxa such as that proposed by Martínez-Navarro et al. (2007) seem unlikely. Indeed the latest work on the fauna from Dmanisi states clearly that is has little overall similarity with African sites, and that it is most similar to that of Early Pleistocene Europe (Lordkipanidze et al., 2007). On face value, the known pattern of hominin fossil and archaeological evidence suggests an initial expansion through the Levant into central and eastern Asia, with expansion into Europe only in the later Early Pleistocene as evidenced by the material from sites such as Barranco Leon and Atapuerca. This would represent movement by a primitive member of *Homo* with Oldowan technology in the earliest Pleistocene at least as far eastwards as the Pabbi Hills and then later westwards into southern Europe. However, we stress that nothing said above should be taken to imply that because we see no evidence for hominin dispersal(s) occurring in concert with other species we consider hominins as having been entirely free to disperse at will in a manner unconstrained by things like climate or environments in the past. While technological developments and evolution of intelligence and physical capabilities over the past several million years obviously played a part in determining the ability of populations to cope in various situations, we see no reason to assume that they rendered early members of the genus *Homo* immune to natural factors.

Acknowledgements

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Taxon	Africa	Levant	Asia	Europe
Proboscidea				
Elephas spp. [1]	>3.0	1.0-0.8	>3.0	-
Elephas recki/Palaeoloxodon [2]	>3.0	0.8-0.7	1.36	0.9
Mammuthus spp. [3]	>3.0	1.5	>3.0	>3.0
Giraffidae				
Giraffa [4]	>3.0	2.5	>3.0	
Giraffa camelopardalis [5]	1.0	0.7-0.5	-	-
Carnivora				
Canis spp. [6]	>3.0	<2.5	<2.5	>3.0
Pachycrocuta brevirostris [7]	>3.2	-	1.66	1.5
Crocuta crocuta [8]	3.5	1.5	<2.5	0.8
Parahyaena brunnea/ Pliocrocuta perrieri [9]	>3.0	-	-	>3.0
Panthera pardus [10]	3.5	-	-	0.9
Panthera leo [11]	3.5	-	-	0.7
Panthera sp. [12]	3.5	1.5	<2.5	1.9
Megantereon whitei [13]	>3.0	1.5	1.7	1.5
Primates				
Homo spp. [14]	~2.0	1.5	1.7	1.2-1.1 (f) 1.4 (a)
Theropithecus oswaldi ssp. [15]	2.4	?1.5	0.6	1.0
Suidae				
Kolpochoerus olduvaiensis [16]	1.65	1.5	-	-
Kolpochoerus evronensis [17]	-	1.0-0.8	-	-
Potamochoerus sp. [18]	1.9	-	<2.5	1.8
Hippopotamidae				
Hippopotamus antiquus [19]		2.5	1.0	~1.3
Hippopotamus gorgops [20]	~2.0	1.5	-	-
Hippopotamus behemoth [21]	-	1.5	-	-
Hippopotamus amphibius [22] (maybe synonymous with *H. antiquus*)	<1.33	?0.8-0.7		
Bovidae *				
Hippotragus spp. [23]	>5.0	1.5	>2.5	-
Oryx sp. [24]	>2.5	1.5-1.0?	3.4-3.0	-
Damalops sp. [25]	~3.6	-	<2.5	-
Alcelaphini indet. [26]	~5.0	1.0-0.8	<2.5	-
Reduncini [27]	6.5	-	<2.5	-
Pelorovis oldowayensis [28]	>2.5	1.5	-	-

Table 1. First appearances of species, genera, or tribes of African origin outside Africa

between 3.0-0.5Ma. < = first occurrence is at this date or after, used particularly for the

Siwaliks deposits where only the terminal/earliest dates of the Formations are known in

detail. >= first occurrence is before this date. ? = possible occurrence, see individual animals for details. * all bovid movements are discussed in detail in the text. – indicates no record of the taxon in that continent. Where a locality is only attributed to a date range, the mid-point of that range has been used.

Sources of dates. **Proboscidea:** 1) Tassy (2003), Tchernov et al. (1994), Ron et al. (2003), Basu (2004). 2) Ferretti et al. (2003), Goren-Inbar et al. (1994, 2000), Agusti and Moyà-Solà (1992), Deng et al. (2008). 3) Radulescu and Samson (1990, 2001), Lister et al. (2004), Wei and Lister (2005). **Giraffidae:** 4) Mitchell and Skinner (2003), Hooijer (1958). 5) Mitchell and Skinner (2003), Guérin et al (1993). **Carnivora:** 6) Hoojier (1958), Lacombat et al. (2008), Nanda (2002). 7) Werdelin and Lewis (2000), Turner and Antón (1996), Turner (2004), Deng (2008), Dennell et al. (2008). 8) We have considered all fossil taxa to be *Crocuta crocuta* (Turner, 1990), but see Werdelin and Lewis (2005) for an alternative view, Barry (1987), Belmaker (2006), Basu, (2004), Nanda (2002), Garcia and Arsuaga (2001). 9) *Parahyaena brunnea* and *Pliocrocuta perrieri* maybe conspecific (Turner, 1990, 1995), Turner (2009), Werdelin and Lewis (2005). 10) Barry (1987), Turner (2009). 11) Barry (1987), Turner (1990), Parfitt et al. (2005). 12) Includes both *Panthera gombaszoegensis* from Europe and *Panthera* sp. from Asia - von Koenigswald (1960), O'Regan and Turner (1994), Spassov (1998), Belmaker (2006), Nanda (2002). 13) Palmqvist et al. (2007). **Primates:** 14) f = fossils, Klein (1999), de Lumley et al. (2006), Zhu et al. (2008), Carbonell et al. (2008), a = archaeology, Martínez-Navarro et al. (1997), Gibert et al. (1998), Oms et al. (2000), Ascenzi et al. (2000). 15) Hughes et al. (2008). **Suidae:** 16) Cooke (2007), Bishop et al. (2006), Geraads et al. (1986). 17) Haas (1970), Tchernov et al. (1994), Ron et al. (2003). 18) Turner et al. (1999), Bobe and Eck (2001), Nanda (2002), Viseras et al. (2006). **Hippopotamidae:** 19) Hooijer (1958), Belmaker (2006), (Hemmer et al. 2001), Martínez-Navarro (1992). 20) Turner et al. (1999), Ferretti et al. (2003), Belmaker (2006). 21) Belmaker (2006). 22) Turner

et al. (1999), Bobe and Eck (2001), Geraads and Tchernov (1983), Bar Yosef (1998).

Bovidae: 23) Gaudzinski (2004), Pilgrim (1933), Vrba (1995a), Vrba and Gatesy (1994). 24) Gabunia (1974), Vislobokova (2005), Vrba (1995a), Thomas et al. (1998). 25) Sotnikova et al. (1997), Vrba (1995a). 26) Thomas et al. (1998), Tchernov et al. (1994), Ron et al. (2003), Vrba (1995a). 27) Vrba (1995a). 28) Tchernov et al. (1994), Thomas et al. (1998), Martínez-Navarro (2004).