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Origin of hominids: European or African origin, neither or both?

El origen de los Homínidos: ¿Europeo, Africano, ambos o ninguno de ellos?

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ABSTRACT

For the last twenty years, some scientists have suggested that the African ape and humans lineages emerged in Europe, a scenario known as the “Back to Africa Hypothesis”. Even though hominoids were widespread in Eurasia during the Middle and Upper Miocene due to the tropical conditions which prevailed in this region, we cannot dismiss the fact that they were present in Africa (contra some authors). Actually, they were highly diverse at that same time (at least 10 lineages represented) even if the fossil record is less complete than in Eurasia. Postcranial elements from African species suggest that some features of modern hominoids were already present in the Lower and Middle Miocene of Africa and were not restricted to European ones. Considering the available evidence, it is not possible at this stage to favour a European origin over an African one. Hominoids were living in the tropical areas of Northern Africa and Southern Eurasia and faunal exchanges between the two continents occurred throughout the Middle and Upper Miocene, as the Tethys did not act as an effective barrier to interchanges between Europe and Asia.

Key words: Hominids, Miocene, Tethys, Back to Africa hypothesis, Eurasia, Africa

RESUMEN

Durante los últimos veinte años, algunos científicos han sugerido que los grandes monos africanos y los linajes humanos surgieron en Europa, un escenario conocido como la “ Hipótesis de la vuelta a Africa”. A pesar de que los homínidos se extendieron en Eurasia durante el Mioceno Medio y Superior debido a las condiciones tropicales que prevalecian en esta region, no podemos descartar el hecho de que ellos estuvieron presentes en Africa (contra algunos autores). En realidad, ellos tuvieron una alta diversidad al mismo tiempo (al menos 10 líneas representadas), incluso si el registro fosil es menos completo que el de Eurasia. Elementos postcraneales de especies africanas sugieren que en algunos carácteres los homínidos modernos estaban ya presentes en el Mioceno Inferior y Medio de Africa, no sólo restringidos a las formas europeas. Teniendo en cuenta las evidencias disponibles, no es posible, en el estado actual de conocimiento, favorecer más un origen europeo que otro africano. Los homínidos vivieron en áreas tropicales del Norte de África y del Sur de Eurasia, cambios faunísticos se sucedieron entre los dos continents a lo largo del Mioceno Medio y Superior, sin que el Tetis actuase como una barrera efectiva a los intercambios entre Europa y Asia.

Palabras clave: Homínidos, Mioceno, Tetis, Hipótesis de la vuelta a Africa, Eurasia, Asia

Introduction

The quest for our origins in the Pliocene was the focus of most palaeoanthropologists until 2000 when fossil evidence of the human lineage was unearthed in Kenya which suggested that our roots must be sought in Upper and maybe Middle Miocene sediments (Senut *et al*., 2001). Since Darwin (1871) resemblances between African apes and humans have been pointed out and as a result, an

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African origin for the human lineage was largely accepted. It was clear on the basis of morphological evidence that *Gorilla*, *Pan* and *Homo* shared part of their history whereas *Pongo* was more distantly related. However, some scientists, following Haeckel (1869) still accepted an Asian origin for humans. With the development of molecular studies in the second part of the 20th Century, several classifications and/or phylogenies of the Hominoidea were published which resulted in various concepts of the family Hominidae. The main drawback to these studies resides in the fact that they are based on modern hominoids which are low in diversity, contrasting strongly with the high diversity of fossil hominoids in the Miocene. There is a tendency to identify in fossil hominoids features present in modern animals but extinct taxa were different from modern ones, not only in dental but also in locomotor adaptations. Another thing which does not clarify the situation is the fact that most recent classifications are based on molecular data. However, there is still debate about molecular and morphological evidence due to the fact that a morphological feature can result from different genes. For many years, studies of DNA and specifically mitochondrial DNA have been widely developed leading to the conclusion that the chimpanzee is the closest relative of humans. An aspect which is not always taken into account is the genetic diversity of the great apes. Human and chimpanzee genomes have been sequenced. But what do we know about their variability and that of other great apes? Interestingly, a recent study of Sumatran and Bornean orang-outans revealed a high diversity between the two and even within a single species (Locke *et al.*, 2011). Surprisingly, the pygmy chimpanzee which was for some time considered to be our closest relative seems to have been forgotten. The same applies to gorillas. So, today we remain with the widely accepted idea that the chimpanzee is our closest relative. For some researchers all the great apes are in fact hominids. But what is the palaeontological evidence for these relationships? For the past twenty years, there has been a tendency among palaeontologists to try to fit their results to the neontological framework with more or less success. However, this does not bring an independent view of our history, nor of that of the apes. This probably explains why there is a heated debate and explains the difficulty of reaching a consensus.

In 1969, the first hominoid from Hungary, *Rudapithecus* (Kretzoi, 1969) was discovered and in the1990's, new collections were made which suggested to some authors that it may belong to *Dryopithecus* (Begun, 1992). On the basis of the cranio-dental anatomy Begun (1992) concluded that the European ape exhibits similarities to great apes and humans, to the exclusion of the earlier Miocene hominoids, and that all the Miocene hominoids should be placed in the Hominidae, but he admits a trichotomy between *Dryopithecus*, *Pongo* and the group of the African apes and humans (Begun 1992, fig. 2). This revived the old idea (Goodman, 1963) which supposed that the African apes and humans belong to Hominidae a point of view accepted by others; with a difference because Groves (1989, 2001) included *Pongo* in Hominidae. Interestingly enough, this was publicized as "humans are great apes" and more recently "apes are humans". This depicts the weight that the studies have in a world of media, where some ideas are more fashionable and may become politically correct. Nowadays, there is a tendency to group common chimpanzees, pygmy chimpanzees, gorillas, orang-utans and humans in the same family, Hominidae as suggested by Groves (1989). However, in his article on "Primate Taxonomy" (Groves, 2001), he wrote: *the sinking of the "family Pongidae" into the Hominidae is now widely adopted, and is obligatory on cladistic grounds unless the Pongidae are restricted to the orangutans*. Restricting Pongidae to *Pongo* is a wise position which I adopted earlier for palaeontological and palaeobiogeographical reasons (Senut, 1998, 2009). Later in the same article: *Although the evidence now seems fairly convincing that* Gorilla *is sister to a* Pan-Homo *clade, the separation times seem to have been close, and I recognize no tribes here*. This is quite a wise position and shows the difficulty of defining very close taxa because homoplasies are probably very important. Shoshani and co-authors (1996) in a comparative article based on morphological and molecular evidence accepted the concept of Hominidae, including all the great apes and humans in the sub-families Ponginae (for *Pongo*), Homininae (for the African apes and humans), the tribe Gorillini being restricted to *Gorilla* and Hominini for *Pan* and *Homo*. In this case, two subtribes were supported Panina for *Pan* and Hominina for *Homo*. This resulted in a more unrealistic classification. The possibility of a trichotomy between the African apes and humans, as proposed by Marks (1995) has generally been rejected as being "less parsimonious". But, is nature parsimonious?

This classification seems widely accepted today despite the numerous problems: it is based only on extant evidence; it does not take into account the variability of the features; and nor does it take into account the large diversity of hominoids in the past. Moreover, there is now evidence that the ancestors of the extant large hominoid lineages occur as early as the Upper Miocene as suggested by the fossil evidence from Eurasia and Africa. Their origins must thus be sought in the Middle Miocene deposits.

Eurasian origins and the "Back to Africa" hypothesis

An Asian origin for hominids was suggested as early as 1915 by Pilgrim after the discovery of *Sivapithecus indicus*; later Lewis (1934) considered *Ramapithecus* to be the best candidate. Subsequently, the debate about human origins was overshadowed by the question of whether Middle Miocene *Ramapithecus* or *Kenyapithecus* represented the earliest representative of the human lineage (Senut, 2004), *Kenyapithecus* being thought of as the African counterpart of *Ramapithecus*. The idea of a European origin for hominids (sensu stricto) is not new: it was proposed by Hürzeler (1958) when he described a complete skeleton of *Oreopithecus bambolii* from Italy. When fossils of *Rudapithecus* were discovered in Hungary, a new hypothesis emerged: hominids arose in Europe (Begun, 1992), which gave rise to the "Back to Africa Hypothesis» which suggests that after migrating from Africa to Eurasia where they evolved and dispersed, some hominoids evolved towards a hominid, a common ancestor to African apes and humans, which migrated back to Africa to give rise to the *Gorilla*, *Pan* and *Homo* lineages. In this scenario, African apes and early hominids would descend from large hominoids which inhabited Eurasia to the exclusion of Africa. For a while, *Graecopithecus* (= *Ouranopithecus*) from Greece (de Bonis *et al*., 1991) was thought to be ancestral to *Australopithecus afarensis* from the Pliocene of Ethiopia. For more than 200 years, the debate has been focused on an African versus Eurasian origin (and more recently European) for the origin of our family. Most of the anatomical traits used to support one or the other hypothesis appear to be variable and not good for systematics (enamel thickness, flatness of the face, small canine, mandibular robusticity, etc.) and they could result either from convergence, or sexual dimorphism, or arboreal adaptations.

To support the European origin hypothesis, it was reported (erroneously) that Africa was devoid of fossil apes during the Late Miocene (Begun, 1992) despite the fact that since 1967 they have been known in the Upper Miocene of Africa (Patterson *et al*., 1970; Pickford, 1975; Ishida *et al*., 1984; Senut 1998, 2010). The Lothagam mandible was thought to be 7 to 6 million years old up to the late 1990's but was later dated to the Pliocene. For almost twenty years, some authors have supported the notion that Europe was the cradle of hominids (*sensu lato*) supporting the "Back to Africa hypothesis"; whereas others think that Africa offers a better scenario. But what if both are wrong? In this respect, it is highly pertinent to include the palaeobiogeography.

The fossil hominoid evidence from the Late Middle Miocene and Upper Miocene

The European evidence

Among the oldest European hominoids is *Dryopithecus fontani* from Saint-Gaudens in France (Lartet, 1856) from MN 8 (11 to 12 Ma). The same species has recently been recorded at Can Mata in Spain (Moyà & Solà *et al*., 2009) and according to the authors, the lower face resembles that of *Gorilla* and the teeth are close to those of *Proconsul nyanzae*. A femur from the same site has been related to *Dryopithecus* and suggests a more terrestrial locomotion than in *Hispanopithecus*. But, there are some problems with the interpretations. Comparisons with the holotype of *D. fontani* and other European dryopithecines would suggest a dental morphology closer to modern chimpanzees and to a lower molar from the Middle Miocene of Kenya (Pickford and Senut, 2005). It is difficult to accept uncritically a close resemblance between the Spanish face with that of *Gorilla*. In addition, the elongated humerus of *Dryopithecus fontani* suggests climbing and/or suspensory activities, although not as derived as in *Pongo*.

In the Middle Miocene of Cataluna (12,5 Ma), *Pierolapithecus catalaunicus* provides the oldest European evidence of a skeleton associated with cranio-dental remains (Moyà-Solà *et al*., 2004). The body plan is interesting as it combines some features indicating upright posture of the trunk combined with some more monkey-like features. It has been suggested that *Pierolapithecus* can be considered to be close to the last common ancestor of great apes and humans. It confirms the large diversity of apes in the Miocene which were adapted to various environments. The discovery of a younger hominoid, *Anoiapithecus brevirostris* (11.9 Ma) (Moyà-Solà *et al.*, 2009) provided important support for the "Back to Africa" hypothesis. Dentally, it recalls the African Miocene ape, *Kenyapithecus*, which possesses thickened enamel in its postcanine teeth. Moreover, the cranio-facial angle measured on the same specimens suggests proximity with Australopithecines and *Homo*. But, we must be cautious with this measurement which is not well defined and can be highly variable (Pickford, 2005). When compared with cercopithecids and modern apes in a geometric morphometrical analysis of the face, *Anoiapithecus* clearly clusters with Colobine monkeys and gibbons which possess a weakly salient face. However a flattened face may be a homoplastic feature which may have several origins: in particular in *Anoiapithecus* it might reflect arboreal adaptations rather than proximity to hominids. A flattened face is widespread in extant primates such as *Cebus*, *Colobus* and *Hylobates* which are highly arboreal animals. In the fossil record it is also found in *Turkanapithecus*, *Micropithecus* and *Lomurupithecus*, which were arboreal animals. It also occurs in *Oreopithecus* from the Upper Miocene of Sardinia and Italy which still possessed a large component of arboreality in its behaviour. Interestingly enough, a shortened face is observed in arboreal squirrels and even carnivores when compared with their terrestrial relatives. In *Kenyapithecus* and *Proconsul* this feature is also related to the development of the canine dimorphism (Pickford, 1986).

In the Upper Miocene, another large hominoid occurs, *Hispanopithecus laietanus* from Can Llobateres (9,5 Ma)(Moyà-Solà and Koehler, 1993; 1996), the skeleton of which recalls those of modern hominoids which are adapted to orthograde postures (shortened lumbar vertebrae, reduced mobility of the lower back, enlarged thorax). Moreover, it exhibits features related to climbing and suspension and the limb proportions are close to those seen in *Pongo*. The palm of the hand is short and differs from that of extant apes; however, the phalanges are greatly elongated and indicate a climbing behaviour. In the morphology of the upper limb, *Hispanopithecus* is closer to Asian large apes than African ones as suggested by the cranio-dental features described by Moyà-Solà and Köhler in 1993 and Pickford and co-authors (1997).

This also applies to the Middle and Upper Miocene fossils, *Dryopithecus*, *Rudapithecus*, *Ankarapithecus* and *Oreopithecus*. It has been proposed that after hominoids migrated from Africa to Eurasia in the Middle Miocene, they developed some pongine features which became widespread in the Eurasian hominoids.

The Asian evidence

The history of large Asian apes seems to be clearer than that of their African cousins. If *Sivapithecus* (known in the Middle and Upper Miocene from India and Pakistan) and/or *Lufengpithecus* (known in the middle, latest Miocene and Pliocene of China) (Kelley, 1982) appear to be related to *Pongo*, new evidence from the upper Miocene of Thailand suggests that *Khoratpithecus* is probably morphologically the closest to *Pongo* (Chaimanee *et al.*, 2004).

The African evidence

Hominoids had a Panafrican distribution as early as 18 Ma (Senut *et al.*, 1997). In contradiction to the widely accepted statement that there is a large gap in the hominoid fossil record in Africa between 14 and 6 million years and even an extinction of hominoids in Africa in the Middle Miocene, several discoveries published as early as the 1970's indicate the opposite (Ishida *et al.*, 1984; Ishida et Pickford, 1988)! There has been a tendency to dismiss the data which did not fit the pattern issuing from a general consensus.

In the Middle Miocene of Namibia (12 Ma), *Otavipithecus namibiensis* (Conroy *et al.*, 1992) represents the only hominoid known in sub-equatorial Africa. The morphology of the frontal sinuses is similar to that of African apes (Pickford *et al.*, 1997).

In the Upper beds of the Ngorora Formation (12.5 Ma) in the Tugen Hills (Kenya), an upper molar probably from *Kenyapithecus* was announced in 1970 (Bishop & Chapman, 1970; Ishida & Pickford, 1998) and more recently a complete lower third molar which is similar to that of chimpanzees and Dryopithecines has been described (Pickford &

Senut, 2005). Because of this, and considering its peculiar morphology for an African Miocene ape, it has been assigned to a chimpanziform (Pickford & Senut, 2005). From the same level an upper molar was described in 1970 by Leakey (in Bishop & Chapman, 1970), which has usually been attributed to *Kenyapithecus*.

In the Upper Miocene of East Africa, *Samburupithecus kiptalami* (9.5 Ma) from the Samburu Hills (Kenya) has been known since 1982 (Ishida *et al.*, 1984; Ishida & Pickford, 1998). Several other African hominoid genera were published since 2001: *Orrorin tugenensis* from the Lukeino Formation in Kenya (6 Ma) (Senut *et al.*, 2001), *Sahelanthropus tchadensis* from Chad (Brunet *et al.*, 2002) (7 Ma) the age of which remains to be confirmed (it could be older as suggested by Pickford in 2008 on the basis of the anthracotheres), *Ardipithecus kadabba* (Haile-Selassie, 2001) (5,5 - 5,7 Ma), a gorilliform hominoid evidenced by an upper incisor and a lower molar from Kapsomin in the Lukeino Formation (6 Ma) (Pickford & Senut, 2005), *Chororapithecus abyssinicus* (10.0 to 10.5 Ma) (Suwa *et al.*, 2007) from Ethiopia, *Nakalipithecus nakayamai* from Nakali (10 Ma) (Kunimatsu *et al.*, 2007) and a fragmentary mandible of a chimpanzee from the Upper Miocene of Niger (Pickford *et al.*, 2009). Among these Miocene fossils, some can be related to modern African Apes and early hominids, but others are still a matter of debate.

The hominoid dietary and locomotor evidence

Enamel thickness in hominoids has been considered by a lot of scholars to be a good phylogenetic feature. However it appears to vary enormously in fossil hominoids and it certainly reflects dietary adaptations and is thus not necessarily a good phylogenetic trait. The taxonomic compositions of the Miocene floras in Africa were not different from the extant ones. Following climatic changes, there were transgressions and regressions of the forests, and arboreal hominoids had access to the same food (harder or softer). In the same environments, different species of hominoids would have developed different locomotor strategies to access the food. This is why postcranial adaptations tell us a lot about phylogeny and why it is probably a better approach for reconstructing hominoid phylogeny. The major problem resides in the fact that we have only a few postcranial elements associated with cranio-dental remains and this is why the debate will continue to be active.

A group of thick-enamelled hominoids, with a propensity for arboreal life, with a skeletal design showing long upper limbs contrasting with shorter hindlimbs were widespread on both sides of the Tethys as early as the Middle Miocene. It is generally assumed that the modern looking hominoid morphologies emerged in the Middle Miocene of Europe. However, some of the postcranial features were already present, even if debated, in the African Middle Miocene and they therefore not restricted to European hominoids.

Despite the long debate about the systematics of the Middle Miocene hominoids from Moroto (Uganda) (Pickford *et al*, 1999; Pickford 2002 and see bibliography), the lumbar vertebra UMP 67-28 from the site can be attributed to *Ugandapithecus*, a great ape well known from the Lower Miocene and Middle Miocene of East Africa (Senut *et al.*, 2000; Pickford *et al.*, 2009). Its vertebral morphology suggests an upright thorax, a feature similar to modern hominoids (Gommery, 2006 and see bibliography). A scapula from a large hominoid from the Lower Miocene site of Napak (Uganda) also exhibits features seen in modern apes (Senut *et al.*, 2010). The morphology of the cervical vertebra of *Otavipithecus namibiensis* recalls that of the bonobo (Gommery, 2006) but the forelimb features are closer to those of arboreal monkeys which is also the case for most of the Miocene apes (Senut & Gommery, 1997). These African fossil apes exhibit some features retained in modern hominoids, but they do not exhibit all the features, as is usually the case in fossil taxa.

The available evidence suggests that African and Eurasian hominoids diverged in their locomotor strategies after separating from a common ancestor, probably a generalized climber. Asian great apes would have been adapted to slow and cautious climbing whereas their African cousins would have evolved towards specialized terrestrial quadrupedalism in apes and bipedalism in the human lineage, an hypothesis supported by recent biomechanical work (Thorpe *et al.*, 2007, Crompton *et al.*, 2008).

Palaeoenvironments

Climatic changes cause environmental changes which can be evidenced in mammalian tooth enam-

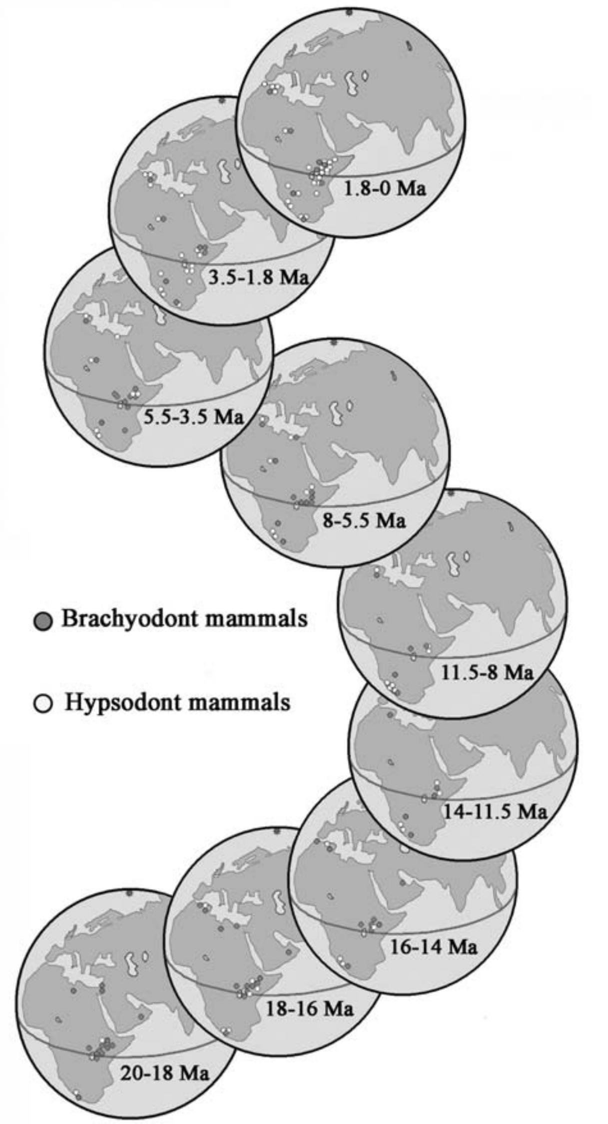

Fig. 1.—Ratios of brachyodonty/hypsodonty in Neogene mammalian faunas in Africa. Up to the Middle Miocene East Africa was inhabited predominantly by brachyodont mammals adapted to forested environments. In Southern Africa, due to global climatic changes resulting in the onset of the Namib Desert, the mammals were already adapted to more open environments as suggested by a higher diversity of hypsodont mammals. When the conditions became drier in Eastern Africa, the Southern species dispersed northwards and became established in Eastern Africa where they found suitable ecological conditions to survive.

el which reflects the dietary adaptations. Studying the diets of animals not only that of the primates, but also those of the associated fauna, helps to reconstruct the palaeoenvironments. A good demonstration is provided by the evolution of the ratio of hypsodont to brachyodont herbivores (which reflect grazing or browsing behaviours) through the Miocene (Figure 1). Whereas browsers were widespread in Africa up to the Middle Miocene, in Southern Africa, grazers were already present in the region due to the onset of the Namib Desert. When conditions became drier in Northern and Eastern Africa from the Middle Miocene, the hypsodont species from the South dispersed northwards.

Among herbivores, bovids seem to be an interesting group as grazers can be distinguished from browsers by studying the microwear and mesowear on their postcanine teeth (Fortelius & Solounias, 2000). A good example is provided in a paper on European ruminant dental wear patterns in the Upper Miocene (Merceron *et al.*, 2010). Based on analysis of microwear and mesowear of animals from Hungary, Greece and Germany, their study shows that throughout the Upper Miocene German and Hungarian ruminants changed from browsers to grazers, whereas the Eastern ones did the opposite. However, the Greek bovids appear to have lived in more opened environments than the Western European ones at the same time and the German bovids lived in a more closed habitat than the Hungarian ones. The authors conclude an environmental uniformity which would have affected primate diversity, and especially that of apes which decreased in Eurasia whereas the diversity of bovids increased. We, therefore, must be cautious with this statement as there may be a collecting bias as well. In fossil exposures, hominoids are usually rarer than other mammals. But in terms of diversity, it seems those European hominoids are less diverse than their African counterparts at the same time. Complementary evidence of the climatic events which occurred in the Neogene in Africa is provided by the study of stable isotopes of carbon and oxygen (Cerling, 1992; Ségalen *et al.*, 2006).

The biogeographic evidence – Faunal migrations

Climatic changes and faunal distribution are closely linked. As early as the beginning of the 19th century, Humboldt (1807) showed that the distribution of faunas was related to altitude and Wallace (1871) pointed out that latitude also played an important role. This led Wallace (1876) to recognise six zoogeographic realms on the globe, the limits of which vary in relation with altitude, latitude and oceanic barriers. This concept was expanded by

Fig. 2.—The Palaearctic (1), Ethiopian (2) and Oriental Biogeographic Realms (3).

Lydekker in 1896 and later applied to mammals by Sclater and Sclater (1899), which led Simpson in 1965 to define the concept of biogeography which includes the degree of humidity and of sunshine. Thus, the Old world encompasses three major realms: Palaearctic, Ethiopian and Oriental (sometimes called the Indo-Malaysian) (Figure 2). Their boundaries varied through geological time in relation with geological and climatic events which in turn controlled the faunal distribution in the Old World. This is particularly true for hominoids and to understand their distribution properly, we must take into account their evolutionary history and their palaeobiogeography and not limit ourselves to the distribution of morphological features in extant animals and cladistic phylogeny. The world experiences major tectonic, eustatic and climatic events during the Miocene which is thus a key period which witnessed the origin of modern hominoids and the split between humans and apes.

In the Middle and Upper Miocene, Eurasia and Africa experienced major faunal interchanges promoted by shifts in the climate. African Miocene mammals are relatively well known in Uganda, Egypt, Saudi Arabia, South Africa and Namibia and are well represented in the Iberian Peninsula allowing direct comparisons. A large number of mammalian species emigrated from Asia to Africa and others from Africa to Asia as a result of changes in the environments as shown by Pickford and Morales (1994) who studied the variations of the boundary between the Proto-Palaeoarctic and Proto-Ethiopian realms (Figure 3). They demonstrated that when the boundary between them is displaced northwards, the faunal similarity between Africa and Spain is greater than when the boundary is positioned in a more southerly position. This appears to be related to global scale tectonics, and astronomic events. During the Miocene, a lot of mammalian species occur (from 1 to 12) in both areas; the higher the number; the closer the areas are biogeographically. At the base of the lower Miocene, there are few taxa in common, but from 18 Ma, the quantity increases due to the tropicalisation of Southern Eurasia, as suggested by the occurrence of crocodiles and tropical flora. In the Middle Miocene, there is a general decrease in the quantity reflecting cooling in the area at a time when East Africa was more arid. At the beginning of the Upper Miocene, there is a certain amount of similarity between the Iberian Peninsula and Africa, followed by a strong decrease. Later (around 8 to 7 Ma), a strong similarity is evidenced, followed by a decrease in the Pliocene followed by an important faunal interchange at the base of the Pleistocene.

Similar major changes have been identified in other parts of the world such as Southern Africa and as such they indicate that they acted at global scales. The major climatic event which took place between 16-17 Ma in Southern Africa is well recorded in the mammalian faunas and led to the onset of the Namib Desert (Pickford and Senut., 2003; Ségalen *et al.*, 2006; Senut *et al.*, 2010) (Figure 4).

Additional evidence of the climatic changes in Eurasia is provided by palaeoichthyology (Böhme, 2004). During the Neogene, the snake-head fishes (Channidae) which are sensitive to temperature and humidity and thus live in sub-tropical and temperate areas dispersed from South-East Asia into Europe and Africa providing evidence for the installation of an Asian monsoon type of climate in Europe, which is consistent with the distribution of hominoids in Eurasia. The effect of the global climatic change is also seen in the distribution of corals throughout the Miocene. In the Northern Hemisphere, they reached high latitudes during the Middle and Upper Miocene (> 50°N) whereas they are today restricted to lower latitudes (around 30° N) (Perrin, 2002) (Fig. 5, 6, 7). Due to the tropical conditions in Southern Eurasia, many mammalian lineages including hominoids dispersed northwards from Africa to Eurasia, where they radiated. Within Africa, changes in the establishment of the deserts

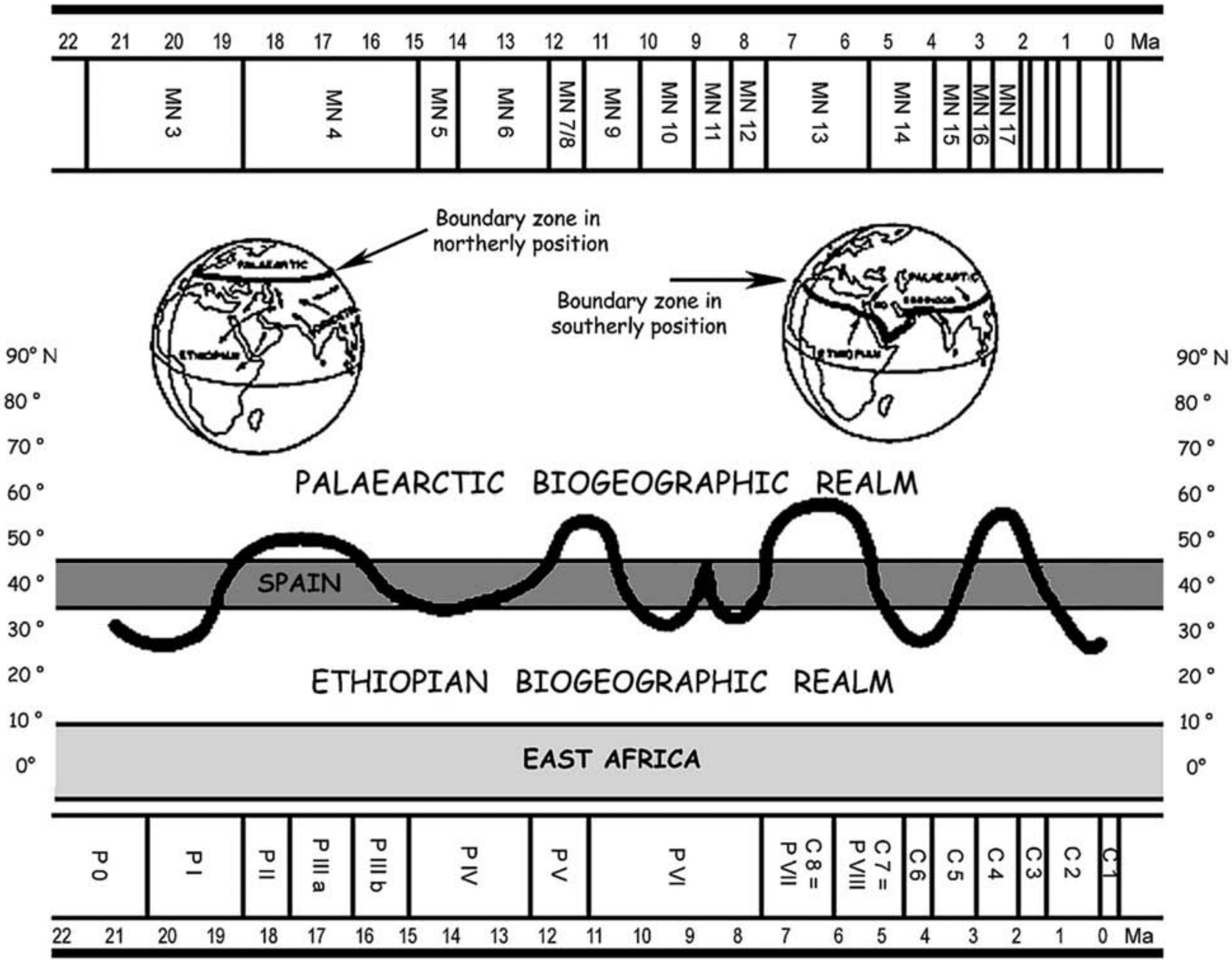

Fig. 3.—Latitudinal fluctuations of the boundary zone between the Palaearctic, Ethiopian and Oriental realms during the Neogene (after Pickford & Morales, 1996).

played an important role in the dispersal of the faunas (Figure 8) (Pickford and Senut, 2003; Senut *et al.*, 2009). In the Late Miocene, the Sahara was much more humid than today and was under influence from Eurasia where the conditions were warmer and wetter than today (Böhme et al., 2008). This is reflected in several interchanges which took place at that time (Pickford and Morales, 1996).

The "Back to Africa hypothesis"

The "Back to Africa hypothesis" is not only based on fossil hominoids, but also on the tempo of the migrations. For Heizmann and Begun (2001), the first hominoid to enter Eurasia is *Griphopithecus* around 16.5-17 Ma, recorded at Engelswies in Germany and Candir in Turkey (Begun *et al.*, 2003), but more recently *Kenyapithecus* has been recorded from Pasalar in Turkey (Kelley *et al.*, 2008). However, there is still debate about the chronological data and correlations between some hominoid-bearing sites in Europe (Pickford, 1998; Begun *et al.*, 2003; Casanovas-Vilar *et al.*, 2011 and see bibliographies included). So, African hominoids may have migrated towards Eurasia as early as the base of the Middle Miocene. The Tethys was not a permanent uncrossable barrier as is shown by the important faunal interchanges that took place between the continents. The contact between the Afro-Arabian plate and Eurasia led to the uplift of parts of the bottom of the Tethys, with the result that several islands emerged which facilitated faunal migrations. Final closure of the Tethys caused

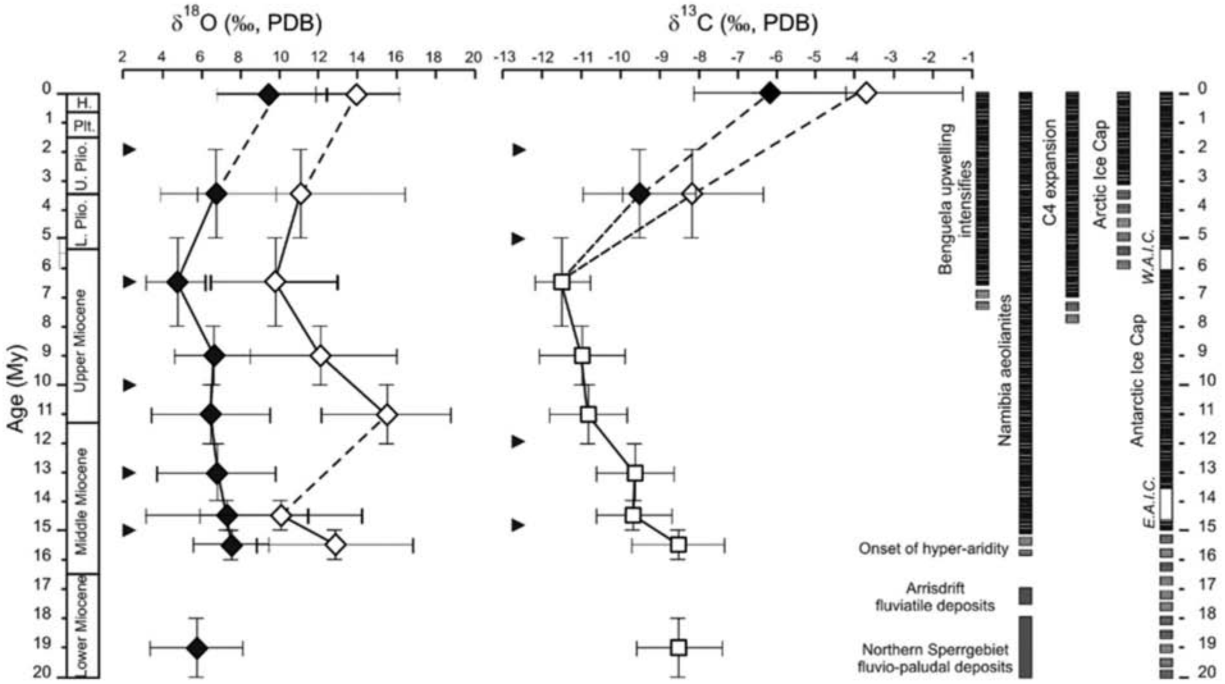

Fig. 4.—Evidence for climatic changes based on the stable isotopes of Carbon and Oxygen in ratite eggshells in Africa (from Ségalen et al., 2006; Senut et al., 2009)

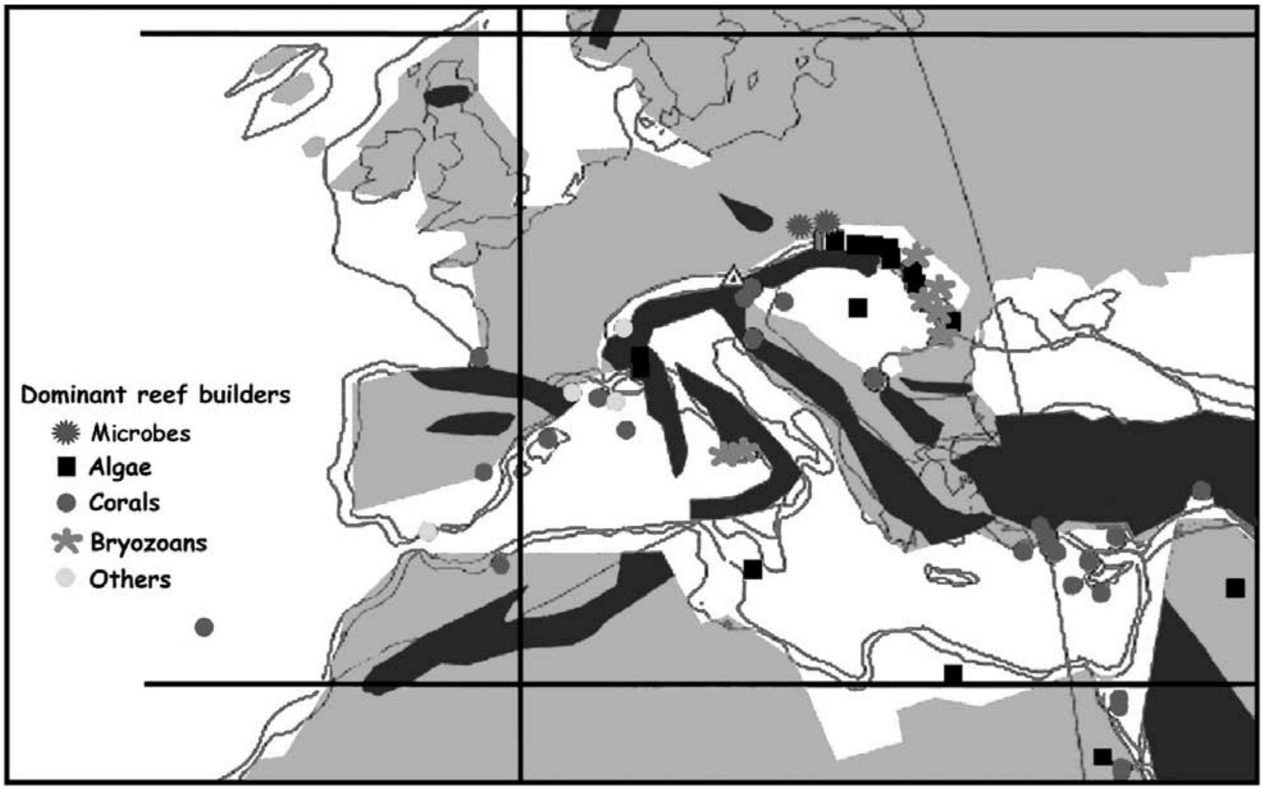

Fig. 5.—Distribution of corals in the Middle Miocene (After Perrin, 2002)

Fig. 6.—Distribution of corals in the Late Miocene and Pliocene (after Perrin, 2002)

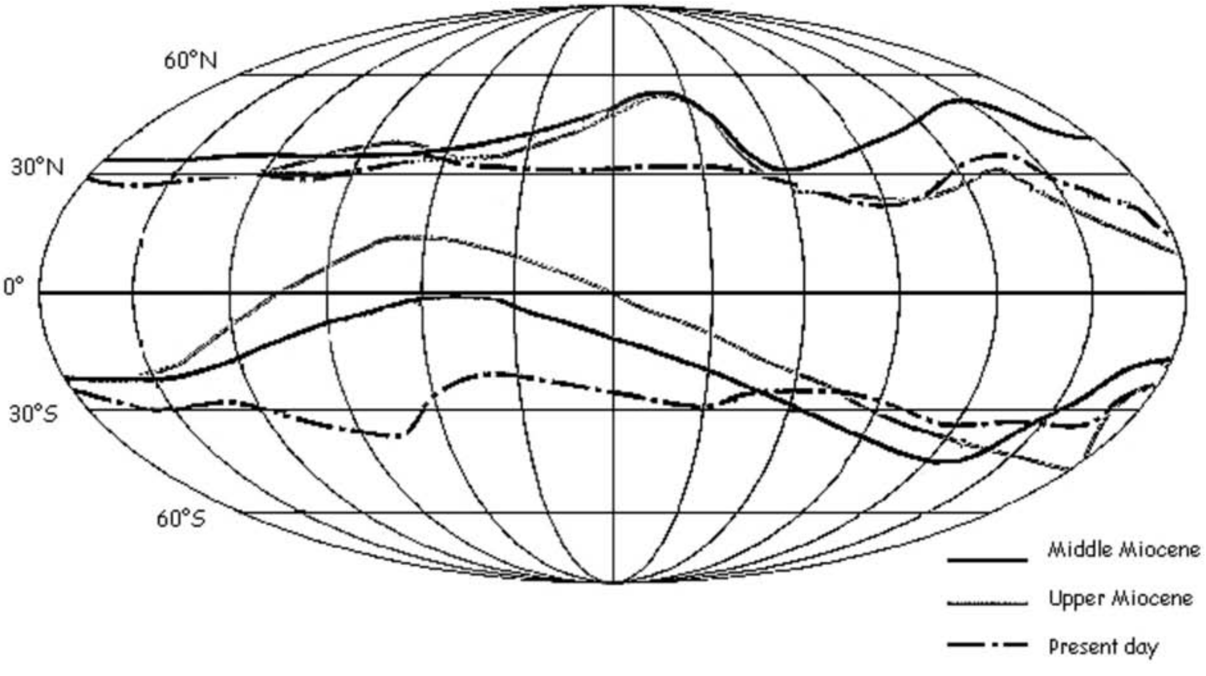

Fig. 7.—Global distribution of corals in the Neogene and today. Note that they reached high latitudes close to 50°N during the Middle and Upper Miocene, which contrasts with their modern occurrence restricted between 30°N and 30°S (after Perrin, 2002). Note that the boundary between the Proto-Palaearctic and Proto-Ethiopian Realms was situated as far as the latitude 50°N in the Lower Miocene and reached even further north in the Late Miocene.

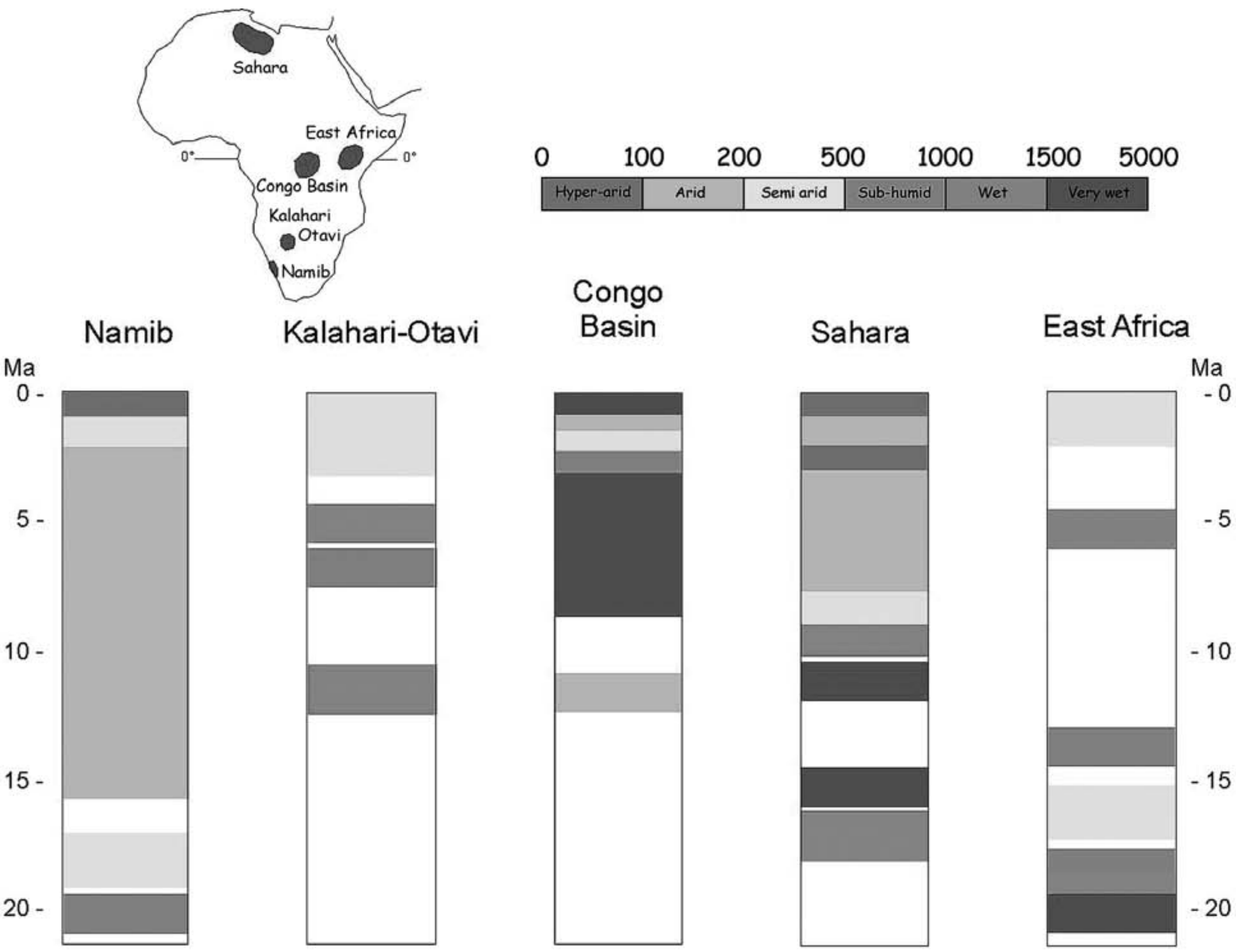

Fig. 8.—The evolution of the climates and especially desertification in Africa through the Neogene had a complex history as shown by the distribution of arid and wet zones (based on fossil evidence). Some areas became more arid or hyper-arid at the same time that others were becoming wetter (From Pickford & Senut, 2003; Senut et al., 2009).

changes in the circulation patterns of ocean currents and this affected global climates. Southern Eurasia being more tropical was suitable to tropical African faunas, including the hominoids. During the Middle Miocene, thick-enamelled semi-arboreal hominoids (such as Kenyapithecines) may have migrated from Africa towards Eurasia where they dispersed and found suitable locomotor and dietary niches. *Pierolapithecus* and *Anoiapithecus* could be descendants of these hominoids: they both retained thick enamel on their teeth and *Pierolapithecus* was an arboreal animal as was probably *Anoiapithecus*, as suggested above. Apart from *Dryopithecus*, *Anoiapithecus* and *Hispanopithecus* share thick enamel, a trait probably related to their different diets and ecological niches. We do not know the locomotor skeleton of *Anoiapithecus* yet, but it is rather well preserved in *Hispanopithecus;* it suggests a highly arboreal life. Limb proportions are close to those of *Pongo* and are not too different from *Oreopithecus* (Moyà-Solà and Koehler, 1996). This evidence indicates a pongid radiation in Eurasia. Pongids disappeared from Europe at the end of the Upper Miocene, but they survived in Asia (Chaimanee et al., 2004). Being highly diverse in Eurasia does not imply that hominoids disappeared from Africa. The idea that African hominoids went extinct (Begun *et al.*, 2003) in the Late Miocene is not supported by the African data as shown above. Due to climatic changes, hominoids probably disappeared from the tropical Southern Eurasia in the Late Miocene, but Pongidae and Hylobatidae survive today in South-East Asia which remains tropical. When Europe and a major part of Asia became more temperate, hominoids probably experienced a feeding problem. Used to inhabiting more tropical areas where

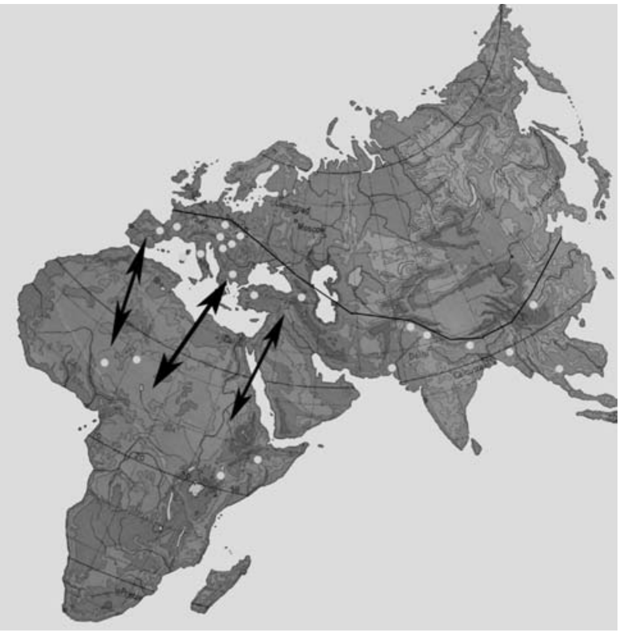

Fig. 9.—Distribution of hominoids during the Upper Miocene. The hominoids inhabited tropical areas in both Africa and Europe due to the ease of migrations between the two areas. This is probably why it will be difficult to identify a precise cradle of modern African apes and humans. There was no permanently uncrossable geographical or ecological barrier.

food is available all year long, they may have found it difficult to get access to the items or could not adapt themselves to new, more seasonally controlled food sources. It may have also been a physiological problem related to temperature and humidity which would have affected the reproductive strategies.

Conclusion

Intercontinental faunal interchanges in the Old World were important and frequent during the Neogene and included primates (in particular hominoids). With this in mind, it appears difficult to define a specific geographic cradle for hominids (*sensu lato*). Whereas, in the upper Miocene, Eurasian hominoid taxa were low in diversity but well represented by complete or sub-complete skulls and/or skeletons, the African ones were more diverse but their remains are more fragmentary. At least 10 lineages of hominoids have been identified in the African Middle and Upper Miocene and they were more widespread in the Upper Miocene than previously thought as suggested by a recent discovery in Niger (Fig. 9). Some of them are represented by taxa which already exhibited locomotor features present in extant African great apes. As the hominoids were adapted to tropical environments, and as the Tethys did not act as a permanent uncrossable barrier (as shown by the numerous faunal migrations between the Palaearctic and Ethiopian Realms, it is not possible to define a region for the origin of modern looking hominoids. Their distribution probably followed variations in the boundary of the Realms and were not restricted to a single continent (Fig. 9). In this case the “Back to Africa” hypothesis is not strongly supported on the basis of the available data.

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