

THE ORIGIN OF THE GREAT-APE-AND-HUMAN CLADE (PRIMATES: HOMINIDAE) RECONSIDERED IN THE LIGHT OF RECENT HOMINOID FINDINGS FROM THE MIDDLE MIOCENE OF THE VALLÈS-PENEDÈS BASIN (CATALONIA, SPAIN)

El origen del clado de los grandes antropomorfos y los humanos (Primates: Hominidae) reconsiderado a la luz de hallazgos recientes de hominoideos del Mioceno Medio de la cuenca del Vallès-Penedès (Cataluña, España)

David M. Alba^{1,2} & Salvador Moyà-Solà³

¹ Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona. Edifici ICP, Campus de Bellaterra s/n, 08193 Cerdanyola del Vallès, Barcelona (Spain). E-mail: david.alba@icp.cat

² Dipartimento di Scienze della Terra, Università degli Studi di Firenze. Via G. La Pira 4, 50121 Firenze (Italy).

³ ICREA at Institut Català de Paleontologia Miquel Crusafont and Unitat d'Antropologia Biològica (Dept. BABVE), Universitat Autònoma de Barcelona. Edifici ICP, Campus de Bellaterra s/n, 08193 Cerdanyola del Vallès, Barcelona (Spain).

ABSTRACT

The superfamily Hominoidea includes two extant families: hylobatids (lesser apes) and hominids (great apes and humans). As currently conceived, the Hominidae include two crown-group subfamilies (pongines and hominines), as well as several extinct members of the stem lineage. Determining the phylogenetic relationships of Miocene hominoids is absolutely essential for understanding the origins and initial radiation of the great ape and human clade from an adaptive, paleobiological and paleobiogeographic viewpoint. Kenyapithecines such as *Griphopithecus* and *Kenyapithecus* have been proposed by several researchers as likely sister-taxa of the Hominidae. However, the scarcity of available fossil remains, coupled with pervasive homoplasy in cranial and postcranial features, has thus far precluded an adequate testing of this hypothesis. In this work, we test this hypothesis on the basis of the new evidence provided by the recent discoveries of Middle Miocene hominoids from Abocador de Can Mata (ACM, Vallès-Penedès Basin, Catalonia, Spain). These findings record a previously unsuspected diversity of Middle Miocene hominoids at ca. 12 Ma, with as much as three different genera (*Pierolapithecus*, *Dryopithecus* and a new genus) being recorded. Most interesting, these putative stem hominids display a combination of kenyapithecine features with derived hominid characters. This supports the biogeographic scenario that hypothesizes a Eurasian origin of the Hominidae, coupled with a back-to-Africa dispersal of hominines. The possibility cannot be discarded, however, that the Middle Miocene Eurasian hominoids gave rise to pongines only, with putative hominid synapomorphies having independently evolved between pongines and hominines from more

primitive, afropithecoid ancestors.

Keywords. Paleoprimatology, evolution, homoplasy, Hominoidea, Dryopithecini.

RESUMEN

La superfamilia Hominoidea incluye dos familias actuales: los hilobátidos (pequeños antropomorfos) y los homínidos (grandes antropomorfos y humanos). Tal como se conciben actualmente, los Hominidae incluyen dos subfamilias del grupo corona (ponginos y homínidos), así como distintos miembros extintos del linaje basal. Determinar las relaciones filogenéticas de los hominoideos del Mioceno es absolutamente esencial para comprender los orígenes y la radiación inicial del clado de los grandes antropomorfos y los humanos desde una perspectiva adaptativa, paleobiológica y paleobiogeográfica. Kenyapitecinos como *Griphopithecus* y *Kenyapithecus* han sido propuestos por varios investigadores como probables taxones hermanos de los Hominidae. Sin embargo, la escasez de restos fósiles disponibles, junto con la gran frecuencia de la homoplasia en características craneales y postcraneales, ha impedido hasta el momento el hecho de poder testar adecuadamente esta hipótesis. En este trabajo, testamos esta hipótesis a partir de la evidencia proporcionada por los descubrimientos recientes de hominoideos del Mioceno Medio del Abocador de Can Mata (ACM, cuenca del Vallès-Penedès, Cataluña, España). Estos hallazgos testimonian una diversidad anteriormente insospechada de hominoideos del Mioceno Medio, de aproximadamente 12 Ma, con tres géneros distintos registrados (*Pierolapithecus*, *Dryopithecus* y un nuevo género). Lo que es más interesante, estos supuestos homínidos basales presentan una combinación de caracteres kenyapitecinos con caracteres derivados de los homínidos. Ello refuerza el escenario biogeográfico que hipotetiza un origen eurasiático de los Hominidae, junto con una dispersión de retorno a África de los homínidos. Sin embargo, tampoco se puede descartar la posibilidad que los hominoideos eurasiáticos del Mioceno Medio sólo hubiesen dado lugar a los ponginos, de tal forma que las supuestas sinapomorfías de los homínidos habrían evolucionado independientemente entre ponginos y homínidos a partir de ancestros afropitécidos más primitivos.

Palabras clave. Paleoprimatología, evolución, homoplasia, Hominoidea, Dryopithecini.

INTRODUCTION

Definition of Hominoidea and Hominidae

The primate superfamily Hominoidea, as currently conceived by many paleoprimatologists (e.g. Begun, 2002; Kelley, 2002), customarily includes two extant families, the Hylobatidae (gibbons and siamangs) and the Hominidae (orangutans, African apes and humans). The meaning of the Hominidae has dramatically changed during the last decades. Several years ago, the family Pongidae was still widely employed to refer to all great apes (orangutans, gorillas, chimpanzees and bonobos), while Hominidae s.s. was employed for modern humans and their closest fossil relatives (australopithecids and their kind). Following the recognition that some «pongids» (the African apes) are more closely related to humans than orangutans are, most researchers tend to classify all these taxa into a single family (Hominidae s.l.), which in its turn can be divided into two

subfamilies: Ponginae for orangutans (*Pongo*), and Homininae for African apes (*Gorilla* and *Pan*) as well as humans (*Homo*).

Systematic difficulties arise, however, when trying to classify extinct apes into this taxonomic scheme. As usual, the morphological disparity shown by fossil forms clearly surpass that displayed by extant members of the group. The concepts of crown group and stem lineage are very useful for deciphering the particular phylogenetic status of any given fossil taxon. Hominoidea are defined as the group constituted by Hylobatidae + Hominidae, as well as all extinct taxa more closely related to them than to the Cercopithecoidea (OldWorld monkeys), which are the sister-taxon of hominoids. Hylobatids, hominids and fossil forms more closely allied to one of these two families define together the crown-group of the Hominoidea, whereas fossil forms equally related to both families (i.e., preceding their evolutionary divergence) constitute the hominoid

stem lineage. Similarly, Hominidae are defined as the group containing Ponginae+Homininae, plus all extinct forms more closely related to them than to hylobatids. Fossil taxa more closely related to either pongines or hominines are part of the hominid crown-group, whereas fossil forms equally related to them both rather constitute part of the hominid stem lineage.

Fossil hominoids

Even though the broad meaning of the Hominidae is currently widely employed by many paleoprimatologists, only the phylogenetic relationships between living hominoids are well established, thanks to molecular studies and the large amount of anatomical information available. On the contrary, the phylogenetic position—and, by implication, also the systematic status—of many fossil putative hominoids is far from being definitively settled. Begun (2001, 2005), following Begun *et al.* (1997), employs the terms 'Eohominoidea' and 'Euhominoidea' to informally refer to hominoids of archaic and modern aspect, respectively. These terms, however, are in fact equivalent to stem and crown hominoids, respectively, so that the former will be no longer employed here.

The status of Late Oligocene and Early to Middle Miocene forms has been subject to different interpretations (Andrews, 1992; Harrison, 2002). Harrison (2002), in particular, has argued that most purported fossil 'apes' from the Late Oligocene and Early Miocene of Africa are indeed stem catarrhines, preceding the cercopithecoid and hominoid divergence (Harrison, 1987, 1988, 2002; Harrison & Rook, 1997). On the other hand, it has been argued in the past that some of these forms (*Proconsul* and allied genera) might be stem hominids (Walker, 1997). Although the latter view seems now definitively abandoned (e.g. Rae, 1999), most authors currently consider that proconsulids are stem hominoids, postdating the cercopithecoid-hominoid splitting (Andrews, 1992; Begun *et al.*, 1997; Kelley, 1997; Ward, 1997; Rose, 1997; Rae, 1999; Ward & Duren, 2002). Harrison (2002) distinguished three subfamilies within the Proconsulidae: Proconsulinae, Nyanzapithecinae and Afropithecinae. Several authors, however, remove *Afropithecus* from that family, and include it, together with allied forms, into

a distinct family Afropithecidae (Cameron, 2004) or even as a subfamily within the Hominidae (Ward & Duren, 2002).

Recognizing the stem lineage of hominids among the Middle Miocene hominoid record is not an easy task. Moreover, deciphering this issue is further hampered by the virtual lack of Miocene fossil evidence on the origin of hylobatids (but see Harrison *et al.*, 2008). It is currently uncertain whether hylobatids and hominids diverged in Eurasia, or rather originated from separate dispersal events from Africa. There seems to be no doubt that the cercopithecoid-hominoid split took place in Africa, and that stem hominoids experienced an evolutionary radiation during the Early Miocene in this continent (Harrison, 2002). During the Middle Miocene, however, the African hominoid fossil record becomes very meager, only to become more diverse again during the Late Miocene. On the contrary, there is plenty of fossil evidence indicating that great apes experienced a considerable evolutionary radiation in Eurasia during the late Middle and early Late Miocene (Begun, 2002, 2007). This has led to suggestions that hominids originated in Eurasia from more primitive ancestors of African origin, and radiated in that continent into pongines and hominines, with the latter subsequently dispersing again into Africa (e.g. Begun, 2001). This biogeographic scenario is strengthened by the presence in several European and Turkish localities of two afropithecoid genera (Andrews & Kelley, 2007), *Griphopithecus* and *Kenyapithecus*, which might be considered reasonable ancestors of crown hominids.

Recent discoveries of late Middle Miocene hominoids in several localities from Abocador de Can Mata in the Vallès-Penedès Basin (Moyà-Solà *et al.*, 2004, in press, in prep.; Alba *et al.*, 2006) have shown a previously unsuspected diversity in the European Mediterranean region by this time, at around 12 Ma. In this communication, we review the several possible phylogenetic hypotheses and biogeographic scenarios for the origin of the great-ape-and-human clade in the light of the above-mentioned recent findings.

NEW FINDINGS FROM THE VALLÈS-PENEDÈS BASIN

The scarcity of fossil hominoid remains implies a high reliance upon dental evidence for proposing phylogenetic hypotheses. Unfortunately, however, the dental morphology of Miocene apes is generally very conservative, so that cranial and postcranial material is further required. As such, the recent discoveries of cranial and postcranial hominoid remains at ACM has provided a renewed wealth of information that can be used to test previous hypotheses. These findings from ACM can be accurately dated on the basis of litho-, bio- and magnetostratigraphic correlation (Moyà-Solà *et al.*, in press; Casanovas-Vilar *et al.*, 2008a). Paleomagnetic analysis, in particular, has yielded a high-quality local magnetic polarity stratigraphy that can be successfully correlated with the geomagnetic polarity time scale, on the basis of the characteristic reversal pattern of the local magnetic polarity stratigraphy, and also on the basis of the location of the Aragonian/Vallesian boundary between the historical sites of Can Mata I and Can Mata III (see Moyà-Solà *et al.*, in press, for further details). The earliest record of hominoids within this area is recorded at ca. 12.3 Ma (Casanovas *et al.*, 2008a), although the most informative specimens come from three different localities with an estimated age of 11.9 Ma. The chronology of these new findings, intermediate between the Turkish Middle Miocene hominoids (ca. 13-14 Ma) and Late Miocene taxa (<11.1 Ma), gives us an excellent opportunity to test the role of the Keniapihthecini in the origin of the Hominidae.

Three different hominoid taxa are represented at ACM on the basis of cranial material:

(1) *Pierolapithecus catalaunicus* Moyà-Solà *et al.*, 2004: This taxon is recorded by a face and partial skeleton of a single individual, which were recovered from the type locality of Barranc de Can Vila I (BCVI). These remains were initially described by Moyà-Solà *et al.* (2004), and a detailed analysis of its hand phalanges has been more recently provided by Almécija *et al.* (2008, in press), whereas the taphonomic and paleoecological background is provided by Casanovas-Vilar *et al.* (2008b). Cranially, *Pierolapithecus* differs from other Middle and Late Miocene Eurasian hominoids by a prognathic facial

profile, with a low and posteriorly situated glabella, which may be interpreted as a symplesiomorphy with stem hominoids and hylobatids. This primitive profile, however, contrasts with the modern configuration of the face, including the presence of high zygomatic roots, a high nasoalveolar clivus, a deep palate, a broad nasal aperture widest at the base, and the situation of the frontal processes of the maxillae, the nasals and the orbits on the same plane. These features are synapomorphic with later hominids, and led Moyà-Solà *et al.* (2004) to propose this taxon as a stem great ape.

Postcranially, the partial skeleton of *Pierolapithecus* provides the oldest unambiguous evidence of orthogrady in the hominoid fossil record (Moyà-Solà *et al.*, 2004), including the presence of a broad and shallow thorax; this can be inferred from the marked rib curvature, the large clavicle, and the short body of the lumbar vertebrae, with the transverse processes originating from the base of the pedicle (instead of from the body). *Pierolapithecus* further resembles modern great apes by the lack of articulation between the ulna and triquetrum; this provides an increased capacity of wrist adduction, which is functionally related to vertical climbing. At the same time, *Pierolapithecus* retains several primitive, monkey-like features. The phalanges of the hand, in particular, resemble to a large extent those of other Miocene apes, displaying features related to powerful-grasping palmigrady on the basal portion, the shaft and the trochlea (Almécija *et al.*, in press). Moreover, the *Pierolapithecus* hand phalanges, unlike those of the Late Miocene *Hispanopithecus* (Almécija *et al.*, 2007), are not very elongated and lack adaptations to below-branch suspension. Orthogrady is a functional complex shared by hylobatids and hominids and, as such, can be hypothesized as a synapomorphy of crown hominoids, where it is employed for both vertical climbing and suspension. Nevertheless, the retention of palmigrade-related features in the stem hominid *Pierolapithecus* indicates that above-branch quadrupedalism still constituted a significant component of the locomotor repertoire of stem great apes and that suspensory adaptations had not yet evolved by about 12 Ma. In other words, *Pierolapithecus* indicates that the last common ancestor of crown hominoids must have been much

more primitive than it would be inferred on the basis of extant taxa alone.

(2) *Dryopithecus fontani* Lartet, 1856: This taxon is recorded by a lower face recovered from locality C3-Ae (with an estimated age of 11.8 Ma), as well as by a partial femur from locality C3-Az (with an estimated age of 11.9). These cranial remains, which have been described by Moyà-Solà *et al.* (in press), preserve the lower part of the left orbit and the zygomatic, the left maxilla with the left suture with the nasal, the premaxilla, most of the nasal aperture, a large portion of the palate, and fairly complete upper tooth rows. The attribution of these remains to *D. fontani*, mainly based on dental similarities, is very significant, because previously this taxon was mainly known only on the basis of several mandibular remains. The finding of maxillary remains has therefore enabled for the first time an adequate comparison of cranial morphology with Late Miocene species previously assigned to this genus. Contrary to previous expectations, this comparison has shown that the cranial morphology of Middle and Late Miocene species is too divergent as to be accommodated within a single genus, which has led Moyà-Solà *et al.* (in press) to reinstaurate the genus *Hispanopithecus* Villalta & Crusafont, 1944 for the late Miocene forms.

D. fontani is somewhat larger than *Pierolapithecus*, and displays several morphological differences that reaffirm that both genera are not synonymous. Moreover, anatomical and morphometric analyses of the maxilla from ACM show that this taxon displays a combination of lower facial features previously unknown in any Miocene hominoid, but closely resembling the facial morphology of gorillas (Moyà-Solà *et al.*, in press). This gorilla-like facial pattern of *D. fontani* is apparently derived relative to stem hominoids, although further evidence would be required in order to confirm whether it is homologous (indicating that this taxon might be a stem Homininae) or homoplastic (in which case *Dryopithecus* might be merely interpreted as a stem hominid).

(3) Hominidae gen. et sp. nov.: This new genus (Moyà-Solà *et al.*, in prep.) is recorded by a partial face and mandible from locality C3-Aj. The face includes the nasals, the right maxilla, some parts of the orbits and portions of both zygomatics; the

palate is almost complete, and part of the frontal is preserved, while the mandible preserved the symphysis and a large portion of the two corpora, but lacks the two rami. Both morphological and morphometric analyses indicate that this taxon displays a facial pattern previously unknown for hominids, indicating that it belongs to a new, previously undescribed genus. The most striking feature is the markedly reduced facial prognathism, which is best interpreted as autapomorphic. The new genus also displays a derived great-ape facial pattern, which indicates that, like *Pierolapithecus* and *Dryopithecus*, it can be considered a stem hominid. Most interestingly, however, the new genus further displays several cranial and dental features of kenyapithecine afropithecids, which might be indicative of a phylogenetic link between kenyapithecines and hominids (see below).

DISCUSSION AND CONCLUSIONS

The sister taxon of the Hominidae

Even though proconsulids and afropithecids lack putative crown-hominoid synapomorphies, such as those related to the orthograde bodyplan, they share with extant hominoids several facial (Rae, 1999) and postcranial (Ward *et al.*, 1991; Kelley, 1997; Rose, 1997) features confirming its hominoid status. Most notably, the lack of external tail in *Proconsul* (Ward *et al.*, 1991; Ward, 1997; Kelley, 1997) is now firmly established (Nakatsukasa *et al.*, 2004), and has been further confirmed in the afropithecid *Nacholapithecus* (Nakatsukasa *et al.*, 2003). The phylogenetic and systematic status of the several afropithecid genera, however, is far from being definitively settled. Harrison (2002) classified afropithecines (*Afropithecus*) and allied genera within the Proconsulidae as stem catarrhines, while other authors take the alternative approach of classifying afropithecines (including *Nacholapithecus* and *Equatorius*) within the Hominidae (Ward & Duren, 2002). Especially problematic is the placement of *Kenyapithecus* and *Griphopithecus*, which both Ward & Duren (2002) and Cameron (2004) classify as a distinct subfamily Kenyapithecinae within the Hominidae, while Kelley (2002) classifies *Griphopithecus* (and Griphopithecinae) within the Afropithecidae, and Begun (2002) reunites the

Kenyapithecinae and Griphopithecinae into a distinct family Griphopithecidae. In this communication, we distinguish a single subfamily Kenyapithecinae, with two distinct tribes, Equatorini (for *Nacholapithecus* and *Equatorius*, from the Middle Miocene of Africa) and Kenyapithecini (for *Kenyapithecus* and *Griphopithecus*, from the Middle Miocene of Africa and Eurasia). The preferred systematic scheme notwithstanding, the key issue here is whether afropithecines and/or kenyapithecines are more closely related to hominids than to crown hominoids as a whole (Andrews, 1992; Moyà-Solà & Köhler, 1995; Harrison & Rook, 1997), or whether these forms are rather stem hominoids predating the hylobatid-hominid divergence (Begun et al., 1997; Begun, 2001).

The kenyapithecine *Kenyapithecus* has been repeatedly considered to be closely allied with hominids due to several shared-derived features, including the moderately high zygomatic root, the high-crowned canine, the reduced molar cingula and the distal humeral morphology (Pickford, 1986; Harrison, 1992; McCrossin & Benefit, 1997; Begun, 2001, 2005, 2007; Guleç & Begun, 2003). The evidence from Middle Miocene great apes from the Vallès-Penedès Basin, here included into the tribe Dryopithecini, strengthen the view that kenyapithecines are closely related to hominids. This is supported by morphological evidence, as well as chronological and biogeographical data. Anatomically, the ACM dryopithecines combine a derived hominid morphology with kenyapithecine traits, such as the anterior position of the zygomatic root (indicating a shorter face than in the Afropithecinae), a strong mandibular inferior torus (entailing a simian shelf), and an extreme reduction of the maxillary sinus (which is situated well above the roots of the molars). Moreover, on temporal grounds, the kenyapithecines *Kenyapithecus* and *Griphopithecus* are present in Eurasia during the Middle Miocene (the former also in Africa), displaying an age range (ca. 15-13 Ma) that predates the appearance of dryopithecines (ca. 12 Ma) and Late Miocene European hominids (from 11 Ma onwards). Accordingly, it seems increasingly likely that hominids originated in Eurasia from a kenyapithecine-like ancestor.

Homoplasy in hominoid evolution

Phylogenetic analyses of hominoids have greatly relied in postcranial traits. However, when extinct taxa are incorporated into the analyses, it emerges that the last common ancestor of the group must have been much more primitive than reconstructed on the basis of extant taxa alone. Among others, the retention of primitive postcranial features in *Pierolapithecus* (Moyà-Solà et al., 2004; Almécija et al., in press) clearly illustrates that not all the traditionally recognized hominoid synapomorphies, shared between hylobatids and hominids (such as suspensory adaptations) were present in their last common ancestor and must be hence considered homoplastic. A similar blend of primitive (pronograde) and modern (orthograde) features is present in other Miocene hominoids, such as *Hispanopithecus* (Moyà-Solà & Köhler, 1996; Almécija et al., 2007) and *Sivapithecus* (Madar et al., 2002). In the past, some authors have tried to explain the lack of derived features in Miocene hominoids by arguing that they are members of an archaic clade (Pilbeam, 1996, 2002). However, given the presence of derived cranial features linking them with some extant hominoids, an alternative explanation favoring mosaic evolution (Rose, 1983; Rae, 1999; Alba, 2008; Alba & Moyà-Solà, 2008) coupled with a large degree of homoplasy (Begun & Kordos, 1997; Larson, 1998) seems more likely. A greater frequency of homoplastic evolution is conceivable in the case of the postcranial skeleton, where it can be easily explained in adaptive terms due to changes in the positional repertoire (Larson, 1998). The orthograde bodyplan of *Pierolapithecus* would be consistent with orthograde being a shared-derived functional complex inherited from the last common ancestor of crown hominoids (hylobatids and hominids). Nevertheless, an orthograde bodyplan is not present, as far as it can be ascertained, in kenyapithecines, which retain to a large extent a pronograde structure more similar to that of proconsulids and afropithecines (Begun, 1992; Begun et al., 1997; Ishida et al., 2004).

The resolution of this conundrum depends on whether hylobatids or kenyapithecines are more closely related to hominids. Hylobatids display a unique cranial morphology combining conservative and specialized characters, but given their postcranial,

orthograde-related similarities with hominids, several authors have previously hypothesized that they evolved from great ape-like ancestors, having experienced an phyletic reduction in size (Pilbeam, 1996; Young & MacLatchy, 2004; Pilbeam & Young, 2004). The fossil record is not of much aid for testing this hypothesis, since as already stated, the fossil evidence of Miocene hylobatids is virtually nonexistent. Recently, however, a new genus and species, *Yuanmoupithecus xiaoyuan*, have been recently erected by Pan (2006) on the basis of dental remains from the Late Miocene locality of Leilao (in the Yuanmou Basin, China). *Yuanmoupithecus* shows dental affinities with the Early Miocene African forms *Micropithecus* and *Limnopithecus* (Pan, 2006), but at the same time it displays several characters that, according to Harrison *et al.* (2008), permit to consider it a stem hylobatid. If correct, this would favor the alternative view that hylobatids are not a dwarfed lineage, but rather the remnants of an early hominoid offshot that originated from small-bodied, stem hominoids from Africa, which dispersed into Eurasia independently from the larger-bodied kenyanthropines that gave rise to hominids. The extensive postcranial homoplasies between hylobatids and atelines (Young, 2003), related to the acquisition of brachiation, indicate that a large degree of homoplasy is possible due to adaptation to similar types of locomotion. Accordingly, the possibility of orthograde being homoplastic between hylobatids and hominids does not seem unlikely, especially if we take into account that the evidence provided by *Pierolapithecus* indicates at least a large degree of homoplasy with regard to the acquisition of suspensory adaptations (Moyà-Solà *et al.*, 2004, 2005).

Biogeographic scenarios for hominid origins

The first dispersal of apes outside of Africa is documented ca. 14-15 Ma (MN5 or MN6) by the kenyanthropines *Griphopithecus* and *Kenyanthropus* in Turkey and eastern Europe (Begun *et al.*, 2003; Andrews & Kelley, 2007). Hominids are not recorded until later, by around 12.3 Ma in the Vallès-Penedès Basin (Casanovas-Vilar *et al.*, 2008a; Moyà-Solà *et al.*, in press), and ca. 12.5 Ma in the case of *Sivapithecus* from the Indo-Pakistan (Kappelman *et*

al., 1991). Begun and co-workers have hypothesized that crown hominoids originated in Eurasia and later dispersed into Africa from the Late Miocene onwards (Begun & Kordos, 1997; Begun *et al.*, 1997; Begun, 2001, 2002, 2003; Begun *et al.*, 2003). This hypothesis was also favored by Stewart & Disotell (1998), who coined the term «in and out of Africa» for referring to the hypothesis of a Eurasian origin for the African ape and human clade. New discoveries of African Late Miocene hominoids (Kunimatsu *et al.*, 2007; Suwa *et al.*, 2007) are beginning to fill the gap between *Kenyanthropus* and *Otaviapithecus* (ca. 12-13 Ma) and *Samburupithecus* (9.5 Ma); for the moment being, however, the evidence is still very fragmentary. Currently, a Eurasian origin and early diversification of hominids into pongines and hominines seems more likely, given the shared-derived facial and postcranial features of these taxa. However, the pervasive nature of homoplasy in hominoid evolution (as shown by the postcranial evidence) leaves open the possibility that the above-mentioned cranial features might have independently evolved to some degree in Eurasia and Africa. In other words, the possibility cannot be discarded that pongines and hominines would have evolved in parallel, in Eurasia and Africa respectively, from more primitive and different kenyanthropine ancestors. We hope that future discoveries from the Vallès-Penedès and elsewhere will help to disentangle this intricate question of great ape origins.

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