Updated chronology for the Miocene hominoid radiation in Western Eurasia

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Edited* by David Pilbeam, Harvard University, Cambridge, MA, and approved February 25, 2011 (received for review December 10, 2010)

Extant apes (Primates: Hominoidea) are the relics of a group that was much more diverse in the past. They originated in Africa around the Oligocene/Miocene boundary, but by the beginning of the Middle Miocene they expanded their range into Eurasia, where they experienced a far-reaching evolutionary radiation. A Eurasian origin of the great ape and human clade (Hominidae) has been favored by several authors, but the assessment of this hypothesis has been hampered by the lack of accurate datings for many Western Eurasian hominoids. Here we provide an updated chronology that incorporates recently discovered Iberian taxa and further reevaluates the age of many previously known sites on the basis of local biostratigraphic scales and magnetostratigraphic data. Our results show that identifiable Eurasian kenyapithecins (*Griphopithecus* and *Kenyapithecus*) are much younger than previously thought (ca. 14 Ma instead of 16 Ma), which casts serious doubts on the attribution of the hominoid tooth from Engelswies (16.3–16.5 Ma) to cf. *Griphopithecus*. This evidence is further consistent with an alternative scenario, according to which the Eurasian pongines and African hominines might have independently evolved in their respective continents from similar kenyapithecine ancestors, resulting from an early Middle Miocene intercontinental range extension followed by vicariance. This hypothesis, which would imply an independent origin of orthograde in pongines and hominines, deserves further testing by accurately inferring the phylogenetic position of European dryopithecins, which might be stem pongines rather than stem hominines.

paleoprimatology | biostratigraphy | magnetostratigraphy

Inferring the phylogeny of both living and extinct taxa is essential for understanding the evolutionary history of any particular clade. In this regard, chronostratigraphic data are of utmost significance, not only for testing paleobiogeographic scenarios but even for testing phylogenetic hypotheses (1). Current evidence indicates that hominoids originated in Africa, where they experienced an impressive early radiation during the Early Miocene (2, 3). During the Middle and Late Miocene, however, hominoids are also known from Eurasia, where they are recorded by a plethora of new forms, coinciding with a likely decline in hominoid diversity recorded in Africa. This Eurasian radiation partly reflects the acquisition of diverging adaptative strategies along several lineages in response to new habitats and changing environmental conditions through time (4–6), although geographic isolation followed by vicariance probably also played a significant role (7–9). Our understanding of the Miocene hominoid radiation in Eurasia and its implications for the origin of the great ape and human clade has been seriously hampered by the lack of a robust chronostratigraphic background and accurate datings for many sites. Here we provide an updated chronology for the Miocene hominoid sites of Western Eurasia (Europe, Turkey, and Georgia) which incorporates Iberian sites where several new hominoid taxa have recently been described. Particular emphasis is placed on those localities for which controversial and uncertain ages have been previously reported, and their implications for hominoid evolution are further discussed.

Results and Discussion

Oldest Eurasian Hominoid? A partial upper third molar from Engelswies (Bavarian Molasse Basin, Germany), previously tentatively attributed to *Griphopithecus* (a discussion of the taxonomy of Miocene Eurasian hominoids is provided in *SI Appendix, Text 1*), has been considered to be the oldest Eurasian hominoid (10) (Fig. 1). An age of ca. 17 Ma was favored for Engelswies on the basis of associated mammals and lithostratigraphic correlation with the main units of the Bavarian Molasse (10) (see *SI Appendix, Text 2* for more details on the regional chronological systems units and *Dataset S1* for additional data on the chronology of the Miocene hominoid sites of Western Eurasia). Preliminary magnetostratigraphic data (11) enabled a correlation of the short (less than 5 m) Engelswies section to longer magnetostratigraphic profiles of the Bavarian Molasse (12, 13), resulting in a correlation to geomagnetic polarity chron C5Cr (17.235–16.721 Ma) that confirmed previous age estimates. On biostratigraphic grounds, Engelswies can be correlated to the *Keramidomys–Megacricetodon bavaricus* overlap zone of the Swiss Molasse, which ranges from 16.2 to 16.7 Ma (14). The Middle Miocene biozonations for the Swiss and the Bavarian Molasse are identical but for an age discrepancy (diachrony) regarding the boundaries of the different units, so that older ages are usually proposed based on the Bavarian Molasse succession (14). Such discrepancy is attributable to the fact that the Bavarian Molasse magnetostratigraphic sections record too few geomagnetic reversals, which precludes an unambiguous correlation to the geomagnetic polarity timescale (GPTS). Therefore, correlations for the Bavarian Molasse frequently rely on second- and even third-order lithostratigraphic correlations, together with the occurrence of radiometrically dated bentonites within the successions (12, 13). If the higher-resolution record of the Swiss Molasse is considered, the reversed magnetozone of the Engelswies section best correlates either to chron C5Cn.1r (16.303–16.268 Ma) or C5Cn.2r (16.543–16.472 Ma), that is, immediately before the Langhian. Hence, if the exact stratigraphic provenance of the hominoid teeth is accurately recorded (10), hominoids would have dispersed into Eurasia by the latest Early Miocene. This earliest occurrence is, however, very surprising, because it predates the other oldest Eurasian sites by at least 1.3–1.5 Myr (see below). Even more surprising is that hominoids have not been recorded from Sandelzhausen, a temporally equivalent locality from the Bavarian Molasse that after decades of excavation has delivered more than 50,000 identifiable specimens (15).

Middle Miocene Sites. After Engelswies, the oldest hominoid sites of Western Eurasia are Paşalar and Çandır in Turkey. Both record *Griphopithecus alpani*, and recently a second hominoid, *Kenyapi-*

Author contributions: I.C.-V. and S.M.-S. designed research; I.C.-V. performed research; I.C.-V., D.M.A., M.G., and J.M.R. analyzed data; and I.C.-V. and D.M.A. wrote the paper.

The authors declare no conflict of interest.

*This Direct Submission article had a prearranged editor.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1018562108/-DCSupplemental.

Fig. 1. Early and Middle Miocene hominoid localities of Western Eurasia and their correlation to the geological timescale. Three different regional chronological systems are included (from left to right): for the Iberian Peninsula and France, for Central and Eastern Europe, and for Turkey. Preferred magnetostratigraphic correlations are indicated by solid blue lines and alternative correlations with dashed blue lines. The scale is the same for all of the magnetostratigraphic sections. Red bars indicate biostratigraphic correlations based on mammal faunas, the length of this bar referring to the uncertainty in this correlation. Correlations based on marine/freshwater stages are indicated with a green bar, and the length of this bar also refers to the uncertainty in the correlation. A question mark indicates a highly uncertain correlation because of lack of data. For additional details regarding the local/regional chronological systems used, see [SI Appendix, Text 2](#); for more data on the age of a particular site, see [Dataset S1](#).

theus kizili, was reported from Paşalar (16). On biostratigraphic grounds, Çandır can be correlated to either Mammal Neogene Zone 5(MN5) or MN6 (17, 18). Unfortunately, magnetostratigraphic results (19) do not allow an unambiguous correlation to the GPTS; three correlations are possible: C5ACn (14.095–13.734 Ma), C5ABn (13.605–13.369 Ma), or C5Cn (16.721–15.974 Ma). Although the latter correlation requires assuming large sedimentary and/or tectonic hiatuses in the Çandır section, it has been favored by some (20). Based on biostratigraphy, Çandır was initially correlated to the MN6 (18) and subsequently to the MN5 (17). The presence of *Megacricetodon collongensis* argues against the former correlation, because this taxon is last recorded in the MN4 in Central Europe and in the MN5 in Spain. However, because the disappearance of this rodent appears to be highly diachronic, an alternative correlation to the MN6 and chron C5ACn or C5ABn, as favored by Krijgsman (19), is supported by the rest of the fauna, resulting in an estimated age of *ca.* 13.4–14.1 Ma. Regarding Paşalar, the correlation must entirely rely on biostratigraphy. The rodent fauna suggests a correlation to the MN6 (21) or to the equivalent Turkish Zone F (22). Therefore, as further suggested by the macrofauna (23), Paşalar would be close in age to Çandır, although slightly older. A hominoid tooth from the Lower Sinap Member (24) in Turkey might be somewhat older, although the exact situation of this ancient find is unknown. On the basis of the associated fauna, this find has been correlated to the locality of İnönü with an estimated age of *ca.* 15 Ma (25, 26) ([Dataset S1](#)). Be that as it may, this earliest occurrence is much younger than customarily assumed by most paleoprimateologists (4, 5, 20), and postdates by at least 1.3 Myr the earliest Eurasian occurrence of hominoids as documented by Engelswies.

Regarding the hominoid sites from Slovakia (Devínská Nová Ves) and Austria (Klein Hadersdorf), they include several teeth and postcranials attributed to *Griphopithecus suessi* (= *G. darwini*; [SI Appendix, Text 1](#)). These localities occur in transitional facies that delivered a mixed assemblage of terrestrial vertebrates with both MN6 and MN7+8 elements (27). Planktonic foraminifera from the same facies allow a correlation to zones MMi9/MMi13 (28), whereas nannoplankton indicates an MNN6/MNN7 age (29), suggesting an age not older than 11.6 Ma. Similarly, the clay

pit of St. Stefan im Lavanttal (Austria), the type locality of the nominal taxon *Dryopithecus fontani carinthiacus* (here considered a junior synonym of *D. fontani*), can be correlated to the Central Paratethys stages. The mollusk fauna from this site indicates a Late Sarmatian (Upper *Ervilia* Zone) age (30), which is congruent with the results provided by the rodent fauna indicating an MN7+8 age (31).

The densest Middle Miocene hominoid record occurs at the Vallès-Penedès Basin (Catalonia, Spain) (see [SI Appendix, Text 3](#) for an updated synthesis of the biostratigraphy and magnetostratigraphy of the Vallès-Penedès record). Comprehensive fieldwork in the 250-m-thick Abocador de Can Mata (ACM) local stratigraphic series (els Hostalets de Pierola) has recently led to the description of two new genera and species, *Pierolapithecus catalaunicus* (32) and *Anoiapithecus brevirostris* (33), as well as to the recovery of new material of *D. fontani* (34) and some fragmentary hominoid remains yet to be described. High-resolution magnetostratigraphic studies at the ACM series allow an unambiguous correlation to the GPTS (34). The series spans from *ca.* 12.5 to 11.4 Ma and includes more than 150 mammal localities, enabling a detailed local biozonation. The oldest hominoid occurrence corresponds to locality ACM/C1-E*, with an estimated age of 12.2–12.3 Ma, whereas the youngest occurrence is a single tooth from Can Mata I (35), which would be close to 11.2–11.1 Ma. The remaining ACM hominoid sites cluster in a tight interval of less than 0.2 Myr (11.8–11.9 Ma). The holotype of “*Sivapithecus*” *occidentalis* (nomen dubium) has an uncertain stratigraphic provenance, so that an estimated age spanning the whole ACM series (12.5–11.4 Ma) cannot be further specified.

On biostratigraphic grounds, other hominoid sites from the Vallès-Penedès Basin can be correlated to the ACM series. Thus, Castell de Barberà and Sant Quirze correspond to the *Democricetodon crusafonti* + *Megacricetodon ibericus* Concurrent range zone and would be somewhat younger than most of the ACM hominoid sites. This local biozonation can also be recognized in France, which allows refining the age of some ancient localities, including the fissure fillings from La Grive-Saint-Alban ([Dataset S1](#) and [SI Appendix, Text 3](#)). *D. fontani* has been reported from La Grive fissures M and L3 (or L5) ([Dataset S1](#)). La Grive M is

pithecins remains to be established. On the basis of currently available evidence, it can only be confidently concluded that, after the Langhian transgression, a group of hominoids of African origin, the pronograde kenyapithecins (2, 3, 5, 58, 59), extended their geographic range into Eurasia, being first recorded in Turkey by both *Griphopithecus* (Eurasia) and *Kenyapithecus* (Eurasia and Africa). The retention of kenyapithecine features in the late Middle Miocene Iberian dryopithecins (33) at *ca.* 12 Ma suggests that the Eurasian hominoid radiation might have originated from some kenyapithecine ancestor, but it remains to be ascertained whether this radiation gave origin exclusively to extant pongines or to both pongines and hominines.

During the last decade, some authors have favored a Eurasian origin of the great ape and human clade (Hominidae) followed by a later back-into-Africa dispersal of the Homininae (4, 9, 37, 60). This biogeographic scenario is dismissed by the recent description of putative hominines from the African Late Miocene (61, 62), as well as by phylogenetic uncertainties surrounding *Hispanopithecus* and *Ouranopithecus*, interpreted either as hominines (2, 37, 60, 63) or as pongines (64–66). Deciphering the phylogenetic status of Middle Miocene European dryopithecins, previously considered stem hominids (32–34), is of much higher significance for testing this scenario, because undoubted pongines are almost simultaneously recorded in Asia *ca.* 12.5 Ma (67). This is consistent with an initial far-reaching range extension of kenyapithecins throughout Eurasia between 14 and 12.5 Ma, followed by vicariance processes giving rise to pongines in Eastern Eurasia and dryopithecins in Western Eurasia. If correct, this would indicate an independent evolution of pongines (including dryopithecins) and hominines in their respective continents from similar pronograde kenyapithecine ancestors, that is, that orthograde is homoplastic among crown hominids.

Such a high degree of homoplasy is not as unlikely as it might seem at first sight (68–70), particularly given global paleoenvironmental changes that could have prompted similar adaptive responses in both groups. In particular, the climatic deterioration initiated at 14 Ma (71) apparently acted as a trigger of the hominoid Eurasian radiation, as reflected by the wide geographic range, and increased taxonomic and ecological diversity shown by hominoids until the early Vallesian. After the late Vallesian (*ca.* 9.5 Ma), however, hominoids are no longer recorded in Western and Central Europe—with the exception of *Oreopithecus*, which survived until *ca.* 7 Ma on its insular refuge. This probably reflects a true regional extinction event (the so-called Vallesian Crisis) (72–74), resulting from the crossing of some paleoenvironmental threshold that hominoids were unable to manage. Only in the Eastern Mediterranean did hominoids survive somewhat longer (until *ca.* 8.0–7.5 Ma), probably thanks to the preexisting adap-

tations of ouranopithecins to the environmental conditions of the Greco-Iranian biome. Ultimately, however, the paleoenvironmental changes associated with increased aridification and seasonality (75, 76) completely wiped out hominoids from Western Eurasia during the Turolian, further leading to their progressive diversity decline and geographic range restriction in Asia throughout the Plio-Pleistocene (77, 78). This heavily contrasts with the evolutionary response of hominoids to climatic change in Africa where, coinciding with the extinction of European hominoids, purportedly bipedal hominins are already recorded during the Late Miocene [*ca.* 7–6 Ma by *Sahelanthropus* and *Orrorin* (79, 80)] and during the latest Miocene (5.8–5.2 Ma) and earliest Pliocene (4.4 Ma) by *Ardipithecus* (81, 82).

Materials and Methods

Chronological Framework: Regional Timescales and Correlation. For decades, the chronology of European Neogene sites has relied extensively on the use of MN zones. This biochronological system, introduced during the 1970s (83), takes into account the first and last appearances of selected taxa as well as the characteristic association of taxa within a particular unit. Furthermore, a reference fauna is attached to each unit. The system was immediately accepted and applied to all European regions, and even to Asia and Africa. Since then, MN zones have gone through successive reviews and updates and, at the same time, have witnessed the development of more refined regional biochronological and biostratigraphic scales. Recently, the system has been criticized because its accuracy and applicability across Europe is strongly affected by the provinciality of the faunas and the diachrony of first and last appearances (84, 85). Furthermore, the diachrony of important faunal events has been clearly shown (85), implying discrepancies in MN-zone boundaries sometimes exceeding 1 Myr. In the present work, we favor the use of regional chronological scales together with the correlation of magnetostratigraphic sections to the GPTS (86) (*SI Appendix, Text 2*). As such, we have only relied on the MN-zone system for rough, long-distance correlations when other relevant data are not available. In these cases, a certain error margin that can be of ± 0.5 –1.0 Myr has to be assumed.

ACKNOWLEDGMENTS. The idea of writing this paper started as a result of a conversation with R. L. Bernor in 2008 and was further inspired by a highly appreciated discussion with A. J. Van der Meulen, so we deeply thank them for encouraging us to write it. We are indebted to our colleagues H. de Bruijn, G. D. Koufos, W. Krijgsman, P. Mein, J. Prieto, and L. Rook for providing us with valuable information on several sites. We also acknowledge L. Costeur for his rather detective labor on the provenance of the hominid specimens from La Grive kept in the Museum of Basel, and E. Delson for discussion on zoological nomenclature. The suggestions and constructive comments by the editors and two anonymous reviewers are deeply appreciated. This study has been possible thanks to the support of the Spanish Ministerio de Ciencia e Innovación (CGL2010-21672/BTE, CGL2008-00325/BTE, JCI-2010-08241 contract to I.C.-V., RYC-2009-04533 contract to D.M.A.) and the Generalitat de Catalunya (Grup de Recerca Consolidat 2009 SGR 754 of the Agència de Gestió d'Ajuts Universitaris i de Recerca).

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