

SI Appendix for

An updated chronology for the Miocene hominoid radiation in Western Eurasia

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Contents

Text 1. Systematics of Western Eurasian hominoids.....	1#
Table S1. Systematic classification of extinct Hominoidea discussed in this paper..	8#
Text 2. Regional chronological systems	9#
Text 3. The Miocene record of the Vallès-Penedès Basin: biostratigraphy and magnetostratigraphy	10#
References	14#

Text 1. Systematics of Western Eurasian hominoids

In Table S1 we provide a taxonomy of the fossil hominoids discussed in this paper. Given the scope of this paper, it is not intended to give a broad taxonomic review of the group, but rather to discuss the most contentious taxonomic and phylogenetic issues regarding the taxa treated in the paper. As such, the following discussion is restricted to extinct hominoids from Western Eurasia.

Following ref. 1 (their SI Text and Table 2), the concept of Hominoidea employed here is a broad one, i.e. including the Proconsulidae and Afropithecidae, in recognition of the likely status of these taxa as stem hominoids (2–9). This contrasts with the alternative systematic schemes of some authors, which employ a narrower definition of the Hominoidea (10–12), by distinguishing a separate superfamily Proconsuloidea. Despite lacking orthograde-related features, proconsulids already share some facial (5) and several postcranial (6–7, 13) synapomorphies with crown hominoids, such the lack of external tail—documented in both *Proconsul* and *Nacholapithecus* (6, 8, 13–15). As such, they can be considered stem hominoids. Moreover, we see no need for a new family-group name other than the superfamily Hominoidea for designating the total group that includes both crown hominoids and stem taxa more closely related to them than to cercopithecoids (contra ref. 12, where the magnafamily Hominidea was employed to include both Proconsuloidea and Hominoidea).

At the family, subfamily and tribe level, the taxonomy employed here also follows ref. 1 (their SI Text and Table S1) to a large extent, although with some significant differences, which are explained in greater detail below. We follow ref. 1 by employing a broad definition of the Hominidae that includes Ponginae, Homininae, and all extinct taxa more closely related to them than to the Hylobatidae (see also refs. 12, 16–17). Moreover, according to this scheme, afropithecids are considered a distinct family with two subfamilies, Afropithecinae and Kenyapithecinae, the latter being subdivided into the tribes Equatorini for *Equatorius* and *Nacholapithecus*, and Kenyapithecini for *Kenyapithecus* and *Griphopithecus*. Over the last decade, some authors have transferred the Kenyapithecini (as the subfamily level, Kenyapithecinae) (11, 18–19), or even all the Afropithecidae (as a subfamily, Afropithecidae) (9, 20), into the Hominidae. This is however problematic for several reasons. The presence of kenyapithecine features in the Middle Miocene dryopithecins from Spain (1), usually considered to be stem hominids preceding the divergence of pongines and hominines (1, 21–22) (but see later), might be certainly indicative of a close phylogenetic link between kenyapithecins and hominids. If so, as noted previously (1), the Afropithecidae as conceived here might be paraphyletic. This, however, depends on the relative branching order between hylobatids, afropithecids and hominids. An early divergence of hylobatids would imply that some or all afropithecids would be more closely related to hominids as conceived here, but given uncertainties regarding the phylogenetic relationships of the former, it is preferably to provisionally retain afropithecids as a separate family.

Given the fact that the nomina for both afropithecid subfamilies were erected simultaneously as two distinct tribes (Kenyapithecini and Afropithecini) in the same publication (2), some uncertainties arise regarding which of them has priority at the family level. Delson and Andrews (20) first employed the nominal taxon Kenyapithecinae for referring simultaneously to both Afropithecini and Kenyapithecini. As such, it might be argued (E. Delson, pers. comm. to SMS) that these authors established the priority of the former on the basis of the Principle of the First Reviser (ref. 23: Article 24.2.1), irrespective of whether this taxon is elevated to family rank or not. According to this reasoning, the nomen for referring simultaneously to these taxa would be Kenyapithecidae instead of Afropithecidae (contra ref. 1). Although such priority, as determined by the Principle of the First Reviser, would certainly apply if *Afropithecus* and *Kenyapithecus* were included into the same tribe, regarding the proper family-group name at higher ranks there are other articles of the Code must be taken into account. In particular, Article 35.5 (ref. 23) asserts that “If after 1999 a name in use for a family-group taxon (e.g. for a subfamily) is found to be older than a name in prevailing usage for a taxon at higher rank in the same family-group taxon (e.g. for the family within which the older name is the name of a subfamily) the older name is not to displace the younger name.” On the basis of the Principle of the First Reviser, the nomina Kenyapithecini would take priority over Afropithecini. However, given that, at the family rank, only Afropithecidae has been employed (1, 17-19, 22-24), whereas (to our knowledge) the nomen Kenyapithecidae has not been employed by any author, Kenyapithecinae is not to displace Afropithecidae at the family level. This contention is further stressed by the fact that the Principle of Priority is “to be used to promote stability and it is not intended to be used to upset a long-accepted name in its accustomed

meaning by the introduction of a name that it is its senior synonym” (ref. 23: Article 23.2).

Besides the uncertainties regarding the phylogenetic position and the systematic status of the tribe including *Kenyapithecus* and *Griphopithecus* (here included in the Kenyapithecini, following ref. 1), there are also some nomenclatural issues that deserve discussion. These two genera were classified into the subfamily Kenyapithecinae (within the family Hominidae) by some authors (9, 18). On the contrary, other authors distinguished a distinct subfamily Griphopithecinae (within the Afropithecidae) for *Griphopithecus* (17), or even a distinct family Griphopithecidae, either for *Griphopithecus* and *Afropithecus* (25), or for *Griphopithecus* and *Kenyapithecus* (16). Most recently, Begun (26) included *Griphopithecus*, *Equatorius*, *Nacholapithecus* and *Kenyapithecus* (i.e., the Kenyapithecinae as conceived here and in ref. 1) into a distinct subfamily Griphopithecinae (within the Hominidae). As previously noted (ref. 1: their SI Text), this is contrary to the principle of Priority, so that both Kenyapithecini and Kenyapithecinae must be adopted instead of Griphopithecini and Griphopithecinae. To our knowledge, Begun (25) was the first author to employ a family-group nominal taxon with *Griphopithecus* (Griphopithecidae) in 2001 (25), whereas both Afropithecini and Kenyapithecini had been previously erected by Andrews in 1992 (2). It has been previously argued that the nominal taxon Griphopithecini would be still available for a family-group taxon including *Griphopithecus*, if neither *Kenyapithecus* nor *Afropithecus* were included in it (1). This is however contrary to the Code (ref. 23: Article 16), because after 1999 it is mandatory that new nominal taxa are explicitly indicated as intentionally new (Article 16.1), and also that the type genus is cited for new family-group names (Article 16.2). These provisions were not fulfilled by Begun either in 2001 (25) or in 2002 (16). In the latter paper, it was merely specified that the nomina Griphopithecidae and Griphopithecinae were employed with “new rank” (16), but no reference was provided as to who might have previously erected a putative tribe Griphopithecini (ref. 17 also failed to specify the authorship for the Griphopithecinae). If the authorship of these family-group nominal taxa based on *Griphopithecus*, such as Griphopithecini, is to be attributed to Begun, 2001, then they all must be deemed as nomina nuda, because their erection failed to fulfill the requirements of Article 16.2 and also because new names published after 1950 with anonymous authorship are not available according to the Code (ref. 23: Article 14).

Additional nomenclatural problems arise regarding the correct binomen for the European species of *Griphopithecus*. Two nominal species were originally erected on the basis of two different holotype dental specimens from the same type locality (Devínská Nová Ves, in Slovakia) by Abel (26): *Griphopithecus suessi* and *Dryopithecus darwini*. Both taxa were subsequently considered synonymous (27–28), and after a complicated nomenclatural and taxonomic history (29–30), the genus *Griphopithecus* was finally resurrected (31) for the two Slovakian species and material from Turkey (*Griphopithecus alpani*). Remane (27) apparently acted as the First Reviser (30, contra ref. 29) in 1921, by selecting the nomen *Dryopithecus darwini*, which he considered more suitable as a type species than *Griphopithecus suessi* due to the information provided by their respective holotypes (even though

the latter binomen had page priority). This notwithstanding, the combination *Griphopithecus darwini* employed by modern authors (16, 30–31) is incorrect (29), because the two nominal species erected on the basis of the Slovakian material are not merely considered congeneric, but conspecific. Given that *Griphopithecus suessi* is the type species of the genus by original designation (ref. 23: Article 68.2.1), this binomen is to be preferred if *Griphopithecus* is considered a valid genus. In other words, since the priority of *G. darwini* over *G. suessi* was determined on the basis of the principle of the First Reviser (29–30), and given that this action is nullified when unnecessary if subsequently shown that the precedence of names can be objectively determined (ref. 23: Article 24.2.5), we concur with ref. 29 that the correct binomen is *Griphopithecus suessi* instead of *G. darwini*.

With regard to the postcranial material from Klein Hadersdorf, originally two different species were erected in 1938 (32) on the basis of two different holotype specimens: *Austriacopithecus weinfurteri* and *A. abeli*. The former nominal taxon was subsequently used for both specimens for some time (33–34). However, after the recognition of the potential affinities of this material with *Griphopithecus* (35), both nominal species were finally synonymized with *Griphopithecus darwini* (16, 31). Given the arguments provided above regarding the validity of this binomen, here the two nominal species erected on the basis of the Klein Hadersdorf material are formally considered junior subjective synonyms of *Griphopithecus suessi*, and *Austriacopithecus* is considered a junior subjective synonym of *Griphopithecus*. Finally, the partial tooth from Engelswies—variously attributed to ?*Griphopithecus* sp. (31), cf. *Griphopithecus* sp. (36) and aff. *Griphopithecus* (16)—is here attributed to Hominoidea indet. Besides the thick enamel, the information provided by this particular specimen is insufficient to warrant an attribution at the genus level. The main justification for tentatively attributing it to *Griphopithecus* was the supposed similarity in age to the Turkish and Central European localities where this genus is recognized. Given that this argument no longer applies, Engelswies predating by a substantial amount of time the remaining localities (see main text), we think it is more conservative to leave it without a formal taxonomic attribution.

The systematic position of the tribe Dryopithecini and the taxonomy of the species included in it are even more controversial. The nominal taxon Dryopithecini was employed by Begun (16) as a distinct tribe within the Homininae, including both *Dryopithecus* s.l. and *Ouranopithecus*. After the proposal that *Dryopithecus* should be restricted to Middle Miocene taxa (22), some authors (1) restricted the Dryopithecini to Middle Miocene putative stem hominids from Europe (*Dryopithecus* s.s., *Pierolapithecus* and *Anoiapithecus*), whereas Begun (37–38) continued to include Late Miocene European genera into the Dryopithecini. This issue is not only complicated by disagreements on the phylogeny of these taxa, but also by opposite taxonomic opinions among several authors regarding the validity of the several proposed genera. Here we follow ref. 1 by considering that *Pierolapithecus*, *Anoiapithecus* and *Dryopithecus* s.s. are distinct dryopithecini genera. On the contrary, Begun and co-authors (12, 39–40) suggested that *Pierolapithecus catalaunicus* might be a junior synonym of *Dryopithecus fontani* (the type species of the genus *Dryopithecus*), and more recently he formally concluded that both *Pierolapithecus* and *Anoiapithecus* are junior subjective synonyms of *Dryopithecus*,

at least at the genus level (38). However, given the striking cranial differences between the three above-mentioned genera, on the basis of the original descriptions of *Pierolapithecus* and *Anoiapithecus* (1, 21) and the newly-recovered cranial material of *D. fontani* (22), we cannot accept such synonymy (22, 24).

Furthermore, although the phylogenetic relationships of the above-mentioned genera certainly deserve further inspection, we consider unconvincing the arguments proposed to date to suggest that they are stem hominines (37–38). Instead, we consider more likely that they are stem hominids (1, 21–22). As such, instead of leaving the tribe Dryopithecini as incertae sedis at the subfamily level (1), we have elevated this taxon to subfamily rank, as previously done by other authors (18, 41). As conceived here, the Dryopithecinae include the tribes Dryopithecini, Hispanopithecini and Ouranopithecini (see later). It is currently uncertain whether dryopithecines are paraphyletic or represents a clade of stem hominids (1), and it is even conceivable that some or all of them might ultimately be more closely related to the Pongini (the tribe including extant orangutans, as well as *Ankarapithecus* and other Asian genera more closely related to *Pongo*, such as *Sivapithecus*). If this was the case, the dryopithecine tribes recognized here would be better classified into the Ponginae, but given current phylogenetic uncertainties we refrain from formally adopting this view here.

The Dryopithecinae as employed here resembles Begun's (38) concept of the Dryopithecini, which includes both Middle and Late Miocene genera, distributed into two distinct subtribes (Dryopithecina and Ouranopithecina). We, however, employ higher ranks for each of these groups, and further distinguish a third group, the Hispanopithecini. According to Begun (38), both the subtribe Dryopithecina and the genus *Dryopithecus* (according to his emended diagnosis) would be characterized by thin-enamelled teeth and large maxillary sinuses. These features, however, are not shared by either *Pierolapithecus* or *Anoiapithecus*, which display thick enamel (24) and restricted maxillary sinuses (1). Among other traits (1, 22), these features indicate that these nominal taxa should not be synonymized with *Dryopithecus*. It must be further noted that, as conceived here, the genus *Dryopithecus* is monotypic, i.e. it only includes the type species *D. fontani*. This is because *D. carinthiacus*—originally erected as a subspecies of *D. fontani* on the basis of the St. Stefan mandible (42)—is here merely considered a junior subjective synonym of the latter species, as previously recognized by other authors (16, 22, 43). More recently, this taxon was recognized as a distinct *Dryopithecus* species (38), but since no further explanation was provided, we do not follow this taxonomic opinion.

At least, some agreement has been recently reached regarding the need to restrict *Dryopithecus* to Middle Miocene taxa (1, 22, 24, 37–38, 40), after the initial resurrection of *Hispanopithecus* by ref. 22. The latter differs from previous proposals to resurrect *Hispanopithecus*, which were restricted to the Spanish material but still included the Hungarian species into *Dryopithecus* (44). However, some disagreements still persist regarding the taxonomy of *Hispanopithecus*: while some authors recently restricted this genus to the Spanish taxa (*H. laietanus* and *H. crusafonti*) and included the Hungarian species into a distinct genus *Rudapithecus* (37–38), others included all these species into *Hispanopithecus* and considered *Rudapithecus* as a junior synonym of the latter (22, 45). Here we take an

intermediate view, by considering that *Rudapithecus* and *Hispanopithecus* warrant a distinction at the subgenus level, although this taxonomic opinion should be subjected to further careful scrutiny in the future.

An agreement has also been apparently reached regarding the species nomen that must be employed for the Hungarian species (irrespective of the preferred genus nomen). Until recently, this species was attributed to *Dryopithecus brancoi*, after the nomen *Neopithecus brancoi*, erected on the basis of an isolated molar from Salmendingen and with a very restricted hypodigm. For some years, this fossil material was considered conspecific with the hominoid from Rudabánya (12, 16, 46–47). Later on, however, this nominal taxon was considered a nomen dubium (22), given the limited information provided by the material from the type locality. Most recently, Begun (38) considered that *Neopithecus brancoi* is most similar to the material from Rudabánya but that insufficient anatomy is preserved to justify the synonymy. This is precisely the reason why we ratify here our opinion that both *Neopithecus* and *N. brancoi* should be considered a nomina dubia until their taxonomic identity can be further clarified. Contrary to nomina nuda, nomina dubia are nomenclaturally valid, but of doubtful taxonomic application according to available knowledge—although they might finally prove to be valid (either as a distinct taxon, or as a senior or junior synonym of another taxon) through the study of the type specimens or new material (48). These circumstances further apply to “*Sivapithecus*” *occidentalis*, originally erected on the basis of two lower molars from Can Vila (of uncertain stratigraphic provenance) (47), and of currently uncertain generic attribution. Over the years, this nominal taxon was considered a synonym of “*Dryopithecus*” *brancoi* (46), of *Hispanopithecus laietanus* (50–51) and of “*Dryopithecus*” *laietanus* (31, 52). More recently, however, “*Sivapithecus*” *occidentalis* was considered a nomen dubium (21), although on the basis of additional material or more detailed studies it might be finally shown to be a senior subjective synonym of some other taxon in the future.

Regarding the Late Miocene European genera here provisionally attributed to the Dryopithecinae, as already mentioned above, the systematic scheme employed in this paper classifies *Hispanopithecus* and *Ouranopithecus* into two distinct tribes (Hispanopithecini and Ouranopithecini, respectively). Regarding the latter, both the nomina Graecopithecini Cameron, 1997 (18, 44) and Ouranopithecini Begun, 2009 (38) are available, and determining the correct nominal taxon to be preferred is further complicated by the taxonomic uncertainties regarding the validity of *Graecopithecus*. *Ouranopithecus macedoniensis* and *Graecopithecus freybergi* have been frequently considered synonyms (31, 44, 55), and if so, the latter should be preferred on the basis of priority. Nevertheless, this synonymy is far from clear, because *Graecopithecus* is only known from a very damaged mandible from the type locality (Pyrgos). The presence of several morphologic differences between the holotype of *Graecopithecus* and the female mandibles attributed *Ouranopithecus*, together with the age differences between Pyrgos and the known chronostratigraphic range recorded for the latter genus, have led several researchers to consider that these nominal taxa represent two different species (18) or genera (16, 38, 56). In fact, the holotype of *Graecopithecus freybergi* is so damaged as to be

inadequate for providing an accurate diagnosis, so that it is here considered here a nomen vanum (48).

This has important nomenclatural implications for the validity of family-group nomina derived from *Ouranopithecus* or *Graecopithecus*. Begun (38) erected a subtribe Ouranopithecina within the Dryopithecini for including *Ouranopithecus*, *Graecopithecus* and the hominoid from Çorakyerler (currently attributed to *Ouranopithecus turkae*, see ref. 57). Given the inclusion of *Graecopithecus*, the Ouranopithecina as originally conceived by Begun (38) must be considered a junior objective synonym of Graecopithecina Cameron, 1997, because the type genus of the latter family-group was considered to be a valid at that time (ref. 23: Article 13.2). Even if *Graecopithecus* was considered to be a junior synonym of *Ouranopithecus*, which cannot be the case—unless a reversal of priority is ruled by the International Commission on Zoological Nomenclature—, the priority of Graecopithecini over Ouranopithecini (at any family-group rank) should be maintained (ref. 23: Article 40.1). However, if *Graecopithecus* is not included into the same family-group name as *Ouranopithecus*—as in the systematic scheme employed here—then Ouranopithecini is no longer a junior synonym of Graecopithecini, and the former name must be employed for *Ouranopithecus*.

Oreopithecus, finally, is here restricted to a monotypic tribe Oreopithecini, which is left as incertae sedis at the subfamily level. It might be warranted to united *Oreopithecus* and *Hispanopithecus* into a single tribe, Oreopithecini, in recognition of the close phylogenetic link that has been hypothesized for these taxa (19, 53). Nevertheless, this supposed link strongly contrasts with the phylogenetic hypotheses favored by other authors (3). A family-group nominal taxon based on *Oreopithecus* was previously employed by several authors, either with a family (33, 54), subfamily (16, 18) and/or tribe (18–19) rank. In some instances, such nominal taxa were used to refer only to *Oreopithecus* (18–19, 46) or to *Oreopithecus* plus *Nyanzapithecus* (54), although the latter genus is currently considered a proconsulid (11). If *Oreopithecus* and *Hispanopithecus* were to be included into a single tribe, Oreopithecini Schwalbe, 1915 would take priority over Hispanopithecini Cameron, 1997 (44). Similarly, if the Oreopithecini were to be included into the same subfamily than the Dryopithecini, then Oreopithecinae Schwalbe, 1915 would also take priority over Dryopithecinae Gregory and Hellman, 1939.

Table S1. Systematic classification of extinct Hominoidea discussed in this paper.

Superfamily **Hominoidea** Gray, 1825

Family **Afropithecidae** Andrews, 1992

Subfamily **Kenyapithecinae** Andrews, 1992

Tribe **Kenyapithecini** Andrews, 1992

Genus ***Kenyapithecus*** L.S.B. Leakey, 1962

Kenyapithecus kizili Kelley, Andrews & Alpagut, 2008

Genus ***Griphopithecus*** Abel, 1902

Griphopithecus alpani (Tekkaya, 1974)

Griphopithecus suessi Abel, 1902

Family **Hominidae** Gray, 1825

Subfamily **Dryopithecinae** Gregory & Hellman, 1939

Tribe **Dryopithecini** Gregory & Hellman, 1939

Genus ***Dryopithecus*** Lartet, 1856

Dryopithecus fontani Lartet, 1856

Genus ***Pierolapithecus*** Moyà-Solà, Köhler, et al., 2004

Pierolapithecus catalaunicus Moyà-Solà, Köhler, et al., 2004

Genus ***Anoiapithecus*** Moyà-Solà, Alba, et al., 2009

Anoiapithecus brevirostris Moyà-Solà, Alba, et al., 2009

Tribe **Hispanopithecini** Cameron, 2004

Genus ***Hispanopithecus*** Villalta & Crusafont, 1944

Subgenus ***Hispanopithecus*** Villalta & Crusafont, 1944

Hispanopithecus (Hispanopithecus) laietanus Villalta & Crusafont, 1944

Hispanopithecus (Hispanopithecus) crusafonti (Begun, 1992)

Subgenus ***Rudapithecus*** Kretzoi, 1969

Hispanopithecus (Rudapithecus) hungaricus (Kretzoi, 1969)

Tribe **Ouranopithecini** Begun, 2009

Genus ***Ouranopithecus*** de Bonis & Melentis, 1977

Ouranopithecus macedoniensis (de Bonis & Melentis, 1974)

Subfamily **Ponginae** Elliot, 1913

Tribe **Pongini** Elliot, 1913

Genus ***Ankarapithecus*** Ozansoy, 1957

Ankarapithecus metei Ozansoy, 1965

Subfamily **incertae sedis**

Tribe **Oreopithecini** Schwalbe, 1915

Genus ***Oreopithecus*** Gervais, 1872

Oreopithecus bambolii Gervais, 1872

Tribe **incertae sedis**

Genus **?*Udabnopithecus*** Burtschak-Abramovich & Gabachvili, 1950

?*Udabnopithecus garedziensis* Burtschak-Abramovich & Gabachvili, 1950

Genus ***Graecopithecus*** von Koenigswald, 1982 nomen vanum

Graecopithecus freybergi von Koenigswald, 1982 nomen vanum

Genus ***Neopithecus*** Abel, 1902 nomen dubium

Neopithecus brancoi (Schlosser, 1901) nomen dubium

Genus **incertae sedis**

"*Sivapithecus*" *occidentalis* Villalta & Crusafont, 1994 nomen dubium

Text 2. Regional chronological systems

For a few areas of Western Eurasia, a high-resolution chronology resulting from the combination of a huge amount of litho-, magneto- and biostratigraphic data is available. These include some Spanish basins (Calatayud-Daroca, Teruel and the Vallès-Penedès Basin) (22, 58–61), the Swiss Molasse Basin (62) and the Turkish Sinap Formation (63–65). For these areas, magnetostratigraphic sections are long enough to allow an unambiguous direct correlation to the GPTS. In other areas, such as the Bavarian Molasse Basin in Germany (66–67) and the Axios Valley (68) in Greece, similar efforts have been conducted but the studied sections are too short to provide unique correlations to the GPTS. Magnetostratigraphic ages from these regions are strongly dependent on other, biostratigraphic or radiometric, constrains.

When no magnetostratigraphic or radiometric data are available, our correlations rely on regional biostratigraphy. Fortunately, high-resolution biozones derived from certain basins can be easily extended to nearby areas, thus enabling the refinement of the chronology of many sites. To this regard, the Vallès-Penedès biozonation for the late Aragonian and Vallesian can be recognized in nearby Spanish basins as well as in France (22, 69). Regarding the alpine region, it is worth noting that the chronostratigraphy of the Bavarian and Swiss Molasse sequences have provided a consistent biozonation, but with different magnetostratigraphy-based ages. Given that the magnetostratigraphic framework of the Bavarian molasse is relatively less robust, the Swiss Molasse chronology (62) can be extended into the Bavarian Molasse Basin by means of biostratigraphic correlation. For Turkey, a preliminary local zonation for central Anatolia has been proposed and tentatively correlated to the European MN zones (70). Unfortunately, the Anatolian local zonation does not allow a higher resolution than the MN zonation, so our correlations regarding the Turkish record emphasize magnetostratigraphic data. Finally, regarding the insular Late Miocene faunas of Tuscany, a useful local biozonation was proposed by Lorenz (71) for the faunas of the Baccinello basin, and subsequent studies have allowed the correlation of these endemic faunas to the MN zones (72–73).

Last but not least, marine-continental correlations have been taken into account for the localities from the Pannonian basin. This basin, which covers all of Hungary and Slovakia as well as part of nearby countries, connected to the Paratethys during the Middle and Late Miocene (74–75). Since many hominoid sites occur in transitional facies or interbedded with marine sediments, their age can be directly tied to marine chronostratigraphic scales, based either on planktonic foraminifera, nannoplankton or molluscs.

Text 3. The Miocene record of the Vallès-Penedès Basin: biostratigraphy and magnetostratigraphy

The Vallès-Penedès Basin (Catalonia, Spain) is a small half-graben parallel to the Catalan coastline that originated during the latest Oligocene as a result of extensional processes related to the opening of the western Mediterranean (76). The sedimentary sequences of the basin cover most of the Miocene and consist mainly of alluvial fan units. During the Middle Miocene a large part of the basin was covered by a shallow sea (76–78) as a result of the Langhian transgression (ca. 15 Ma). The continental sediments of the Vallès-Penedès Basin have been intensively surveyed for almost 70 years and have become a classical area for the study of the Miocene mammal faunas of Europe. More than 200 mammal-bearing sites have been discovered to date which make this area one of the most densely-sampled of Eurasia. Furthermore, magnetostratigraphic studies have been carried out at the most important sections further refining the correlations and age estimates (22, 58–59). Here we summarize and update the results of previous works (59, 79–83) and further refine the biozonation of the Vallès-Penedès Basin.

The Early Miocene. A dozen of localities are known from the Early Miocene sediments, some of them (els Casots, Molí de Calopa) yielding very rich assemblages. Two distinct biozones can be distinguished on the basis of the rodent fauna (79). The first biozone (*ibericus* zone of ref. 79) is characterized by the presence of the glirid *Pseudodyromys ibericus*, the muroid *Melissiodon* cf. *dominans* and the equid *Anchitherium* sp. The faunas are insufficiently known but this zone probably correlates to zone A (late Ramblian) of the Calatayud-Daroca Basin (east-central Spain) (60), thus covering the late MN3 (ca. 18–17 Ma), although somewhat younger ages (MN4) cannot be discarded. The second biozone is the *Megacricetodon minor primitivus* + *Ligerimys ellipticus* Concurrent range zone which records the first appearance of the cricetodontids *Democricetodon*, *Megacricetodon* and *Eumyarion*. This biozone is correlated to zone C (early Aragonian, later part of MN4) of the Calatayud-Daroca Basin (60), ranging from about 16.5 to 16 Ma. Primates are not recorded during the Early Miocene in the Vallès-Penedès Basin.

The Middle Miocene. During the Langhian transgression, a few mammal localities (i.e. Ca n'Almirall) are recorded in transitional facies (80) and have been correlated to the MN6. However, these faunas have yet to be studied in detail. Other localities which may correlate to the MN6 in the Vallès-Penedès Basin include Les Conilleres and a few micromammal sites from the lower part of the Abocador de Can Mata (ACM) series (22, 81–82). These localities have delivered a very poor micromammal fauna and have been correlated by the means of magnetostratigraphy to chron C5Ar.1r (12.730–12.415 Ma). Clearly more sampling is needed to adequately characterize the time interval that follows the end of the Langhian transgression until ca. 12.5 Ma in the Vallès-Penedès.

The densely sampled ACM series (81–82) has allowed the subdivision of the Late Aragonian record into two distinct biozones according to the cricetodontid species present: the *Democricetodon larteti* + *Megacricetodon ibericus* Concurrent

range zone and the *Democricetodon crusafonti* + *Megacricetodon ibericus* Concurrent range zone (69, 83). The *D. larteti* + *M. ibericus* zone is further characterized by the occurrence of a diverse rodent fauna in many sites that includes two *Hispanomys* species (*H. decedens* and *H. cf. aguirrei*) and several glirids (of the genera *Glirudinus*, *Myoglis*, *Muscardinus*, *Paraglis*, *Microdyromys* and *Paraglrulus*) although this family is not abundant. The eomyids (*Eomyops*, *Keramidomys*) and pteromyines (flying squirrels of the genera *Miopetaurista* and *Albanensia*) may occur occasionally. This biozone ranges begins at chron C5An.2n (12.415-12.207 Ma) and ends within chron C5r.3r (12.014-11.614) so we estimate an age of 11.8 Ma for the upper boundary of this biozone. Hominoids are first recorded within this biozone in the Vallès-Penedès Basin at locality C1-E* (estimated age 12.2-12.3 Ma see SI Dataset). The *D. crusafonti* + *M. ibericus* zone begins within chron C5.3r and ends at chron C5r.1n (11.154-11.118 Ma). Since many primate finds of the ACM series occur within chron C5r.3r, but these sites have not always delivered a rich rodent sample, it is not possible to this biozone or to the previous one. The *D. crusafonti* + *M. ibericus* zone is characterized by the presence of *D. crusafonti*, although its ancestor *D. larteti* still is recorded at some sites, where it is very rare. The rodent fauna does not show many changes except for the replacement of some cricetodontid species (*D. brevis brevis*, *M. minor minor*) by their putative descendants (*D. brevis nemoralis*, *M. minor debruijni*). The genus *Hispanomys* is represented by three new species (*H. lavocati*, *H. decedens*, *H. daamsi*). The beavers occur at some sites where they can be very common. To the top of this biozone the rodent fauna becomes impoverished by the temporal disappearance of many glirid species, the eomyids and the flying squirrels, which may indicate a shift towards dryer environments. This local zonation can be recognized in other Iberian basins such as Calatayud-Daroca (83) and can be further extended to France (69, 83) allowing to constrain the age of certain sites such as La Grive fissure fillings.

The Late Miocene. The Late Miocene record ends abruptly because of a pronounced marine regression by the Messinian (middle Turolian, ca. 7.2 Ma) which implied the prevalence of erosional processes over sedimentation. The beginning of the Late Miocene is particularly well represented in the basin, so a land mammal stage, the Vallesian, was erected on the basis of the Vallès-Penedès mammal successions (84). The Vallesian has been intensively sampled and the main Vallesian sites have been situated in a magnetostratigraphic framework (58–59). The lower boundary of the Vallesian is marked by the dispersal into the Old World of the hipparionine horses, of North American origin. In the Vallès-Penedès Basin, these equids are first recorded at the lower part of chron C5r.1n, which would imply an age of 11.154 Ma (58, 85). This age is congruent with the radiometric dating of key sites of Central Europe (86) but it is somewhat older than other age estimates for this event in other areas (Calatayud-Daroca Basin, Sinap Formation, Siwaliks) which range from 10.8 to 10.3 Ma (64, 87–89). The presence of *Hipparion* sensu lato characterizes the *Hipparion* s.l. + *M. ibericus* Concurrent range zone (59). Amongst the macromammals, the first occurrence of the felid *Machairodus* is also recorded (59), but the rodent fauna does not show significant differences compared to that of the latter part of the *D. crusafonti* + *M. ibericus* zone. The upper boundary of the *Hipparion* s.l. + *M. ibericus* zone is located within chron C5n.2n (11.040-9.987 Ma) with an estimated age of about 10.4 Ma (59).

Agustí and co-workers (59) defined the *Cricetulodon* zone for the rest of the early Vallesian, which is here divided into two different biozones: *Cricetulodon hartenbergeri* Local range zone and *Cricetulodon sabadellensis* Local range zone. These two biozones are distinguished on the basis of the species of the cricetid *Cricetulodon*, which is a very common component of the rodent faunas. The rodent assemblage in both zones is very diverse and many of the glirid genera that were absent since the upper half *D. crusafonti* + *M. ibericus* zone reappear in the record together with the eomyids and flying squirrels which may be recorded at certain sites. Nevertheless, all these rodent taxa are not abundant. Amongst the muroids, *M. ibericus* and *D. crusafonti* are not longer present, while the genera *Eumyarion* and *Megacricetodon* are last recorded in the *C. sabadellensis* zone. The primates are represented by the genus *Hispanopithecus* at many sites. The *C. hartenbergeri* zone covers the second half of chron C5n.2n with an estimated age of 10.4 Ma for the lower boundary and of 9.9 Ma for the upper one. This biozone comprises important sites such as Can Ponsic or Santiga and can also be recognized in the Seu d'Urgell Basin (Catalan Pyrenees). In its turn, the *C. sabadellensis* zone ranges from the base of chron C5r.1r to the top of chron C4Ar.3r, that is from 9.987 to 9.717 Ma. Since *C. sabadellensis* is endemic of the Vallès-Penedès Basin, this biozone cannot be extended to other areas. Major localities correlated to this biozone include Can Llobateres 1.

At the top of the *C. sabadellensis* zone, the first occurrence of murids (*Progonomys*) in Western Europe is recorded. This rodent family is first scarcely represented but become very abundant soon afterwards, so they characterize the first biozone of the late Vallesian, the *Cricetulodon* + *Progonomys* Interval zone. The lower boundary of this zone is not characterized by the entry of *Progonomys* but by its common occurrence. This murid first appeared in the Indian subcontinent at about 12 Ma (90) and dispersed into western Eurasia during the Vallesian, being first recorded in Turkey at about 10.135 Ma (64) and arriving into the Iberian Peninsula at about 9.7 Ma. Recently, Aguilar and co-workers (91) suggested a much older age for the *Progonomys* dispersal and the Aragonian/Vallesian boundary. According to these authors, *Progonomys* would have been already present by about 11.4 Ma, so that it would not have taken two million years to reach Western Europe from Asia. These authors reinterpret several sections where *Hipparion* s.l. and *Progonomys* co-occur, including the Can Llobateres section (see Fig. 2), and conclude that these may be nearly two million years older, since the presence of these two taxa is also congruent with this dating. Therefore, these authors ignore the composite bio-magnetostratigraphic context of the Vallès sequence and propose a new correlation of Can Llobateres to chron C5r.2n (see Fig. 2), resulting in an age estimate of 11.5 Ma for Can Llobateres 1. Such surprising results are based on the interpretation of the short (10 m-thick) Ecotet section (France), in which two mammal sites are associated with transitional marine facies that have yielded calcareous nannoplankton and planktonic foraminifera indicating a late Middle Miocene age. The very poor mammal sites have not delivered *Progonomys* or *Hipparion* s.l., but are attributed to the early Vallesian (MN9) on the basis of the presence of *D. brevis* cf. *nemoralis* and *M. minor debruijini*. These taxa, however, were already present in the late Aragonian (in our *D. crusafonti* + *M. ibericus* zone), and do not suggest an MN9 age for these sites or add any new information concerning the dispersal of *Progonomys*.

The *Cricetulodon* + *Progonomys* zone is characterized by the disappearance of many mammal taxa, an extinction event which has been termed the Vallesian Crisis (92). Amongst the rodents, many glirids and all the eomyids became very rare until finally disappearing during the next biozone. The flying squirrels and the beavers also became rarer than during the early Vallesian. Regarding the macromammals, the suids *Listriodon* and *Parachleuastochoerus*, the bovid *Miotragocerus*, and amphicyonid and nimravid carnivorans all disappear in this biozone. Finally, hominids (*Hispanopithecus laietanus*) are last recorded within this biozone at the site of La Tarumba 1. On the other hand, this biozone records a number of new occurrences, including the hypsodont cricetid *Rotundomys montisrotundi*, the suids *Microstonyx* and *Schizochoerus* and the large hyaenid *Adcrocuta*. This biozone ranges from chron C4Ar.2n to chron C4Ar.2r, that is, from 9.717 to 9.409 Ma. Important sites include Can Llobateres 2 and La Tarumba 1.

Finally, the last zone of the Vallesian is the *Rotundomys bressanus* Local range zone (59). This biozone is characterized by the presence of this hypsodont cricetid (first recorded at the base of chron C4Ar.1, that is 9.409 Ma) together with the murids of the genus *Progonomys*; unlike in other Iberian basins (such as the Teruel Basin in east-central Spain) (93), these murids are not very abundant. Amongst the macromammals, some species characteristic of Turolian faunas are first recorded, including the bovid *Tragoportax gaudryi* and the felid *Paramachairodus orientalis*. Pliopithecids are last recorded within this biozone at Torrent de Febulines, where they are represented by the crouzeline *Egarapithecus narciso* (94). The upper boundary of this zone coincides with the Vallesian/Turolian boundary and is presumably placed within chron C4An (9.098-8.769 Ma). Important sites within this biozone include Torrent de Febulines, Ceràmiques Viladecavalls, Trinxera Nord Autopista and Trinxera Sud Autopista.

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