First Partial Face and Upper Dentition of the Middle Miocene Hominoid *Dryopithecus fontani* from Abocador de Can Mata (Vallès-Penedès Basin, Catalonia, NE Spain): Taxonomic and Phylogenetic Implications

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ABSTRACT A well-preserved 11.8-million-years-old lower face attributed to the seminal taxon *Dryopithecus fontani* (Primates, Hominidae) from the Catalan site ACM/C3-Ae of the Hostalets de Pierola area (Vallès-Penedès Basin, Catalonia, NE Spain) is described. The new data indicate that *D. fontani* is distinct at the genus level from Late Miocene European taxa previously attributed to *Dryopithecus*, which are here reassigned to *Hispanopithecus*. The new facial specimen also suggests that *D. fontani* and the Middle Miocene *Pierolapithecus catalaunicus* are not synonymous. Anatomical and morphometric analyses further indicate that the new specimen shows a combination of lower facial features—hitherto unknown in Miocene hominoids—that resembles the facial pattern of *Gorilla*, thus providing the first nondental evidence of gorilla-like lower facial morphology in the fossil record. Considering the current evidence, the gorilla-like facial pattern of *D. fontani* is inferred to be derived relative to previously known stem hominids, and might indicate that this taxon is either an early member of the Homininae or, alternatively, a stem hominid convergent with the lower facial pattern of *Gorilla*. The biogeographic implications of both alternatives are discussed. This new finding in the Hostalets de Pierola section reinforces the importance of this area for understanding the elusive question of the Middle Miocene origin and early radiation of great apes. Am J Phys Anthropol 139:126–145, 2009. © 2009 Wiley-Liss, Inc.

FOSSIL GREAT APES FROM THE MEDITERRANEAN REGION

Great apes currently display a decimated diversity and a restricted geographical distribution. During the Miocene, they were much more diverse, ranging throughout Eurasia and Africa. The origin of the Hominidae (the great ape and human clade) is a topic vigorously discussed from a paleobiological, phylogenetic, and paleobiogeographic viewpoint, mainly because the fossil record of great apes is still far from being satisfactory. Primate fossil remains are usually scarce, and this is particularly dramatic in the case of large-bodied hominoids, so that the finding of relatively complete fossil remains is exceptional. The available fossil record suggests that hominoids[1] originated in Africa by about the Oligocene/

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[1]There are different systematic schemes available in the literature. In this article, we employ the superfamily Hominoidea in a broad sense to refer to crown apes (Hylobatidae and Hominidae) plus stem apes (Dendropithecidae, Proconsulidae and Afropithecidae). Hominoidea s.l. is thus equivalent to Begun's (2007) "magnafamily" Hominidea, which includes Proconsuloidea plus Hominoidea s.s.

Miocene transition (ca. 25 Ma), being first represented by the putative fossil ape *Kamoyapithecus* (Leakey et al., 1995). The group experienced a considerable radiation during the Early Miocene (Harrison, 2002), being represented by the families Dendropithecidae, Proconsulidae, and Afropithecidae. Some authors interpret some of these forms as primitive catarrhines (Harrison, 2002). However, several anatomical features indicate that proconsulids and afropithecids already belong to the hominoid stem lineage (Kelley, 1997; Rae, 1999; Ward and Duren, 2002; Nakatsukasa et al., 2003, 2004), with some afropithecids probably being the most derived ones. During the Middle and Late Miocene, until about 7 Ma, the African hominoid fossil record is very scarce (Ward and Duren, 2002). Until recently, it only included putative advanced afropithecids (*Nacholapithecus*, *Equatorius*, *Kenyapithecus*) and two forms of uncertain affinities (*Otavipithecus*, *Samburupithecus*). The recent description (Suwa et al., 2007; Kunimatsu et al., 2007) of the putative hominines *Chororapithecus* and *Nakalipithecus* partially fills the gap in the African record. However, the scarcity of derived forms in Africa, especially during the Middle Miocene, markedly contrasts with the great proliferation of taxa in Eurasia (Kelley, 2002; Begun, 2002, 2007).

The oldest record of hominoids outside Africa corresponds to the latest Early Miocene of Turkey and Eastern Europe, just before the Langhian transgression (Andrews and Kelley, 2007). These forms (*Griphopithecus* and *Kenyapithecus*) are still archaic as compared to other fossil Eurasian apes, although the high zygomatic root of *Kenyapithecus* suggests that this taxon may be a plausible hominid ancestor (Begun, 2007). From this time onwards, there is a great diversity of fossil hominoids in Eurasia during the late Middle Miocene and early Late Miocene. These forms are usually regarded as great apes. Some investigators have argued that great apes originated in Eurasia from more archaic forms and later dispersed into Africa (Stewart and Disotell, 1998; Begun, 2001; Begun and Nargolwalla, 2004; Begun et al., 2003, 2006), so that the virtual lack of great apes in Africa during the Middle Miocene would be a real phenomenon. On the contrary, other authors suggest that the African gap could be an artifact (Moyà-Solà et al., 1999; Cote, 2004), attributable to a forested habitat that did not favor their fossilization and/or to insufficient or geographically-inadequate sampling.

The phylogenetic relationships of the Eurasian putative fossil great apes remain controversial. The South and East Asian forms (Kelley, 2002; Begun, 2007), recorded far from the Mediterranean area, are usually considered pongines (i.e., members of the orangutan clade), particularly in the case of *Sivapithecus* (although this taxon is neither exempt from controversy). The oldest record of *Sivapithecus* dates back to 12.5 Ma (Kappelman et al., 1991), suggesting that the pongine-hominine divergence had already taken place by this time. The situation is much more confuse in the Mediterranean region (Begun, 2002), with several genera (*Pierolapithecus*, *Dryopithecus*, *Ankarapithecus*, *Oreopithecus,* and *Ouranopithecus*) distributed throughout the Aragonian and Vallesian, with *Oreopithecus* being their last representative by the Turolian (ca. 7–8 Ma). With the exception of *Ankarapithecus*, which is considered a primitive pongine by most authors (Begun and Güleç, 1998; Köhler et al., 2001a; Begun, 2007), it is very difficult to place these European fossil great apes into a coherent phylogenetic scheme. This is attributable to high degrees of homoplasy (e.g., Ward, 2007) and the current incompleteness of the record. Thus, while the discoverers of *Pierolapithecus* consider it to be a stem great ape (Moyà-Solà et al., 2004), other investigators interpret it as a hominine (Begun and Ward, 2005; Begun, 2007; Ward, 2007). Similarly, it has been suggested that other Mediterranean great apes are stem pongines (Moyà-Solà and Köhler, 1993, 1995, 1996, 1997; Köhler et al., 2001a), while other authors consider some of them (*Dryopithecus* and *Ouranopithecus*) to be stem hominines (Begun et al., 1997; Begun and Ward, 2005; Begun, 2007), and *Oreopithecus* to be a more primitive form (Harrison and Rook, 1997; Begun et al., 1997). Despite the different phylogenetic hypotheses and taxonomic opinions, there is no doubt that the Mediterranean region, from Spain to Greece and Turkey, played a very prominent role in the initial radiation of great apes during the Middle and Late Miocene. The possibility cannot be even discarded that the origin of the group and/or the splitting between pongines and hominines did occur in this area. As such, it is imperative to clarify the taxonomy and the phylogenetic relationships of these fossil forms.

HOMINOID DISCOVERIES FROM THE VALLÈS-PENEDÈS BASIN

A considerable amount of Middle and Late Miocene fossil great apes have been discovered throughout Eurasia over the last 150 years (see Begun, 2002, and Kelley, 2002, for recent reviews), beginning with the description of *Dryopithecus fontani* from St. Gaudens (France; Fig. 1) (Lartet, 1856). The first discovery from the Iberian Peninsula was made at the beginnings of the 20th Century at the clay quarry of Teuleria del Firal (Seu d'Urgell, Eastern Pyrenees) (Vidal, 1913; Woodward, 1914) (see Fig. 1). All subsequent findings have been made at the Vallès-Penedès Basin, which is placed in the NE corner of the Iberian Peninsula next to the Mediterranean coastal margin (see Fig. 1). Part of the hominoid fossil remains from this basin come from the area of Els Hostalets de Pierola (Penedès sector), whereas the other remains come from the Vallès. We report below a brief, updated summary of the chronology of hominoid discoveries in the Vallès-Penedès Basin (see also Crusafont, 1965; Crusafont and Hürzeler, 1969; Crusafont and Golpe Posse, 1973; Golpe Posse, 1982).

The fossiliferous potential of Els Hostalets de Pierola (see Fig. 1) was discovered by M. Guerín, who incidentally collected there in the 1920s an isolated M2/ of a hominoid. This specimen, however, was mistaken for a suid, not being described until much later (van der Made and Ribot, 1999). Guerín reported his findings to J. R. Bataller, who surveyed the area and discovered several sites near to the Riera de Claret (Bataller, 1938). Later on, M. Crusafont and J. F. de Villalta further surveyed the area of Hostalets, mainly comprised between Can Mata de la Garriga, Can Vila, Mas d'Ocata and Can Flaquer, further discovering some hominoid fossil remains. In 1941, Crusafont discovered a left mandibular fragment with M/2–M/3 at Can Vila, but unfortunately the stratigraphic horizon of provenance cannot be known for certain. Only 3 years later, additional hominoid remains, including a right lower tooth row and a left mandibular fragment, were discovered at La Tarumba I (near Viladecavalls; Fig. 1) at a clay quarry. The mandibular speci-
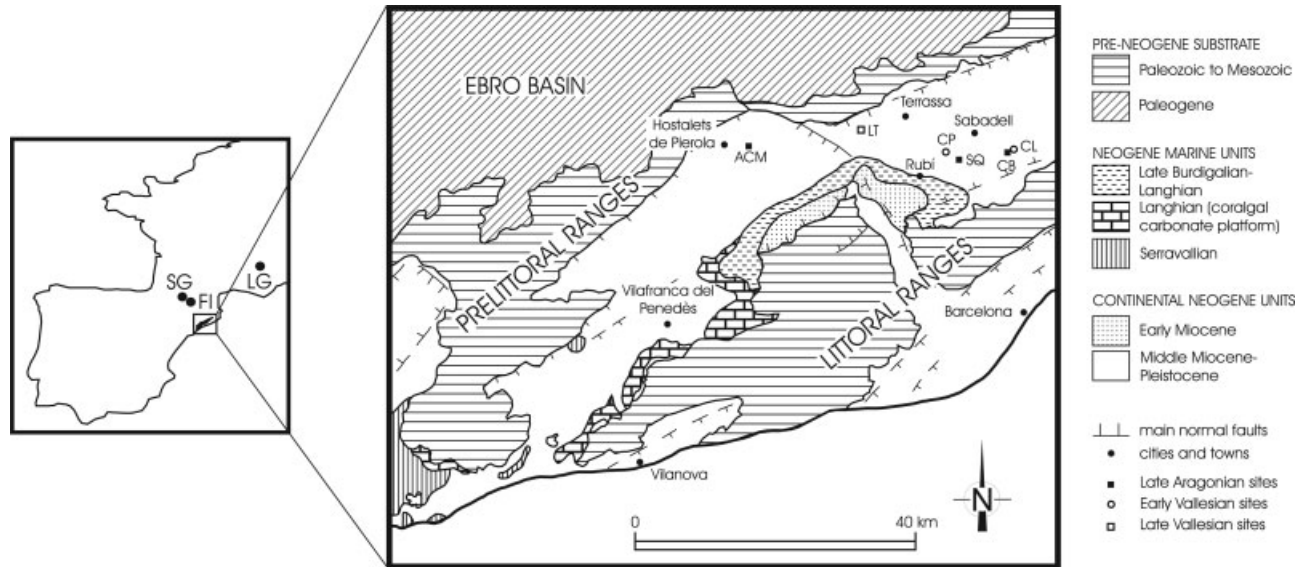
Fig. 1. Schematic geological map of the Vallès-Penedès Basin, showing the main geological units and hominoid localities mentioned in the text; modified after Agustí et al. (1985) and Garcés (1995). The situation of other hominoid localities is also indicated. Abbreviations: ACM, Abocador de Can Mata; CB, Castell de Barberà; CL, Can Llobateres; CP, Can Ponsic; FI, Teuleria del Firal; LG, La Grive; LT, La Tarumba; SG, Saint Gaudens; SQ, Sant Quirze.

men from Can Vila was initially attributed to *D. fontani* by Villalta and Crusafont (1941), but soon after the same authors (Villalta and Crusafont, 1944) erected a new species for it, *Sivapithecus occidentalis*. In the same article, the new genus and species *Hispanopithecus laietanus* was described on the basis of the remains from La Tarumba.

Further remains were subsequently discovered by Crusafont and co-workers during the 1950s to 1980s from several localities from the Vallès (see Fig. 1), including Can Ponsic, Can Llobateres, and Polinyà II (Crusafont, 1958; Crusafont and Hürzeler, 1961; Crusafont and Golpe-Posse, 1973; Golpe-Posse, 1982; Begun et al., 1990). However, only a single lower canine was discovered from Can Mata I (see Fig. 2) (Crusafont and Golpe-Posse, 1973). Besides *H. laietanus*, Crusafont and Hürzeler (1961) attributed part of the remains to *Dryopithecus piveteaui* and *Rahonapithecus sabadellensis*, two newly erected taxa that were never formally described, and which must be therefore considered nomina nuda (Simons and Pilbeam, 1965; Szalay and Delson, 1979; Moyà-Solà et al., 1989–1990; Golpe Posse, 1993). Crusafont and Hürzeler (1961) attributed the Can Vila remains to *H. laietanus*, thus synonymizing *S. occidentalis* with the former taxon. This synonymy has been accepted by subsequent authors (Moyà-Solà et al., 1989–1990; Golpe Posse, 1993; Andrews et al., 1996). Golpe Posse (1993) still maintained the nomen *Hispanopithecus laietanus* and the attribution of some specimens to *Sivapithecus indicus*, but other authors attributed all Vallès-Penedès material to *Dryopithecus* (Begun et al., 1990; Moyà-Solà et al., 1989–1990). Most of the specimens were assigned to *D. laietanus*, but a new species *D. crusafonti* was erected on the basis of material from Can Ponsic (Begun, 1992a; but see Harrison, 1991, and Ribot et al., 1996). Excavations at Can Llobateres 2 begun in 1990, leading to the discovery of a partial face and skeleton of *D. laietanus* (Moyà-Solà and Köhler, 1993, 1995, 1996; Köhler et al., 2001b). Additional

remains of this taxon have been discovered in the 2000s during excavation works at E.D.A.R. (next to Can Llobateres) (Checa and Rius, 2003). On the basis of the Principle of the First Reviser, *S. occidentalis* must be considered a junior subjective synonym of *D. laietanus* when included into the same hypodygm. Given the fragmentary nature of the Can Vila remains, and the finding of additional hominoid taxa in the Els Hostalets de Pierola (Moyà-Solà et al., 2004; this article), this is however far from clear. Following Moyà-Solà et al. (2004), it seems more advisable to provisionally consider *S. occidentalis* as a nomen dubium.

Although paleoprimatological attention in Catalonia was mainly devoted to sites from the Vallès, a rubbish dump (Abocador de Can Mata, ACM) was constructed in Els Hostalets de Pierola, near Can Mata de la Garriga (see Fig. 2), during the 1970s and 1980s. In the early 2000s, thanks to the modern legislation favoring the preservation of the paleontological heritage, a paleontological intervention was devised in order to control the removal of Miocene sediments by the diggers and bulldozers during the construction of an extension of the former dump. Excavations began in November 2002 and are still ongoing (Alba et al., 2006). Thousands of large and small mammal remains have been recovered so far, and more than a hundred fossiliferous localities placed at a continuous stratigraphic succession have been sampled. These new sites are named after the different sectors of the rubbish dump, such as the several cells that are successively excavated (e.g. C1 = Cel·la 1, and so on; see Fig. 2). On December 2002, excavations affected Barranc de Can Vila (BCV), a ravine situated close to the country house of Can Vila (see Fig. 2). A splachnocranium and several postcranial remains of a fossil great ape were unearthed, and systematic excavations during 2003 yielded as much as 83 bones or identifiable fragments of a single adult individual (IPS21350), which was attributed to a new genus and species, *Pierolapithecus catalaunicus*. After 52 months of fieldwork comprised between
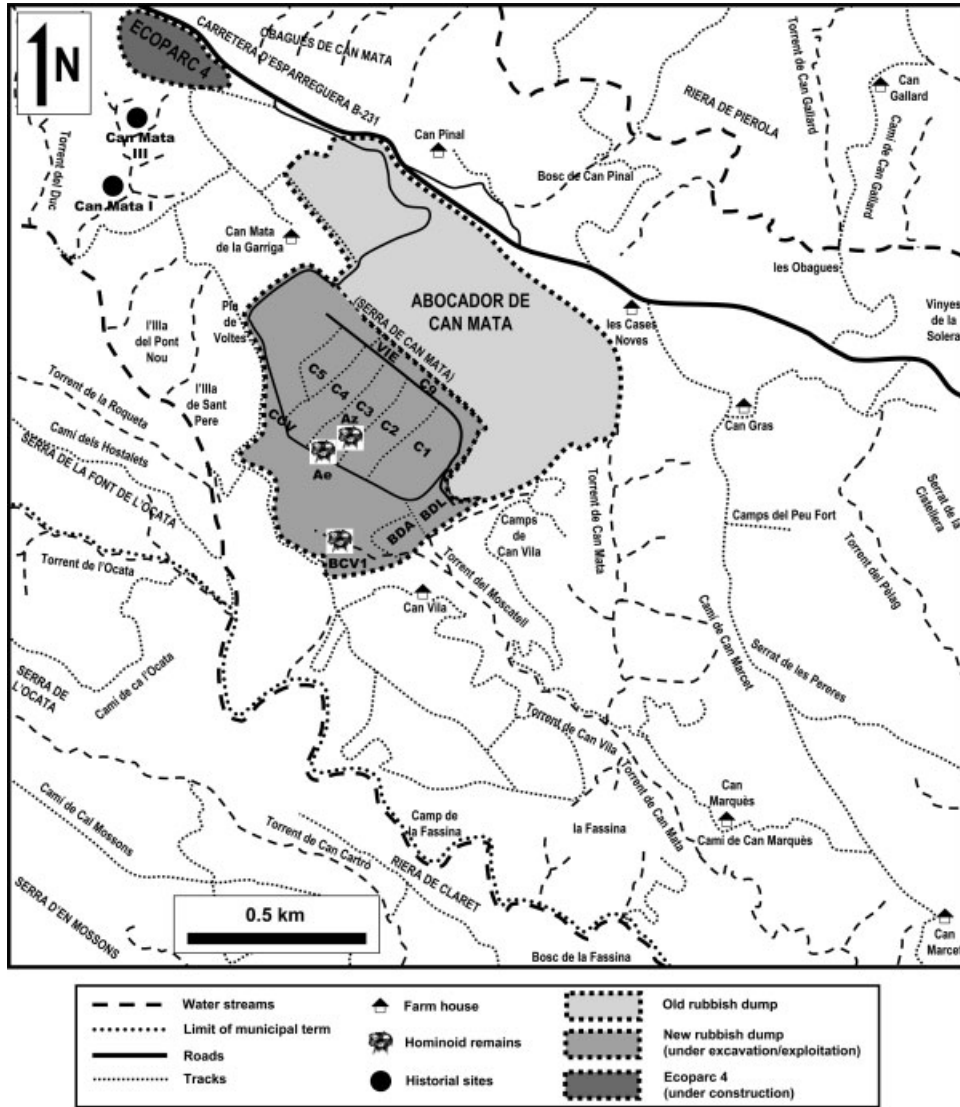
Fig. 2. Map of situation of Abocador de Can Mata. The extension of the old rubbish dump is indicated in light gray, whereas the area currently under exploitation and/or excavation is indicated in darker gray. The location of the two ACM primate sites mentioned in the text, together with two classical Can Mata localities, are indicated. Abbreviations: BCV, Barranc de Can Vila; BDA, Bassa de Decantació d'Aigües Pluvials; BDL, Bassa de Lixiviats; CCV, Camí de Can Vila; VIE, Vial Intern d'Explotació; C, Cel·la.

2002 and 2007, more than 21,000 macrovertebrate remains and thousands of small mammal teeth have been already recovered. More than 100 fossiliferous localities have been sampled from the local stratigraphic series of ACM, which spans an interval of about 2 million years (ca. 13–11 Ma). Only about 0.6% of the specimens are attributable to primates, and about 2/3 of them belong to the holotype of *P. catalaunicus*. Primate remains are recorded at 16 different localities, being represented by pliopithecids or great apes. In this article, we describe a well-preserved lower face with nearly complete upper dentition from C3-Ae, and a proximal half of a femur from C3-Az, which we attribute to *Dryopithecus fontani*. These specimens shed new light on the diversification of the great ape and human clade, confirming that *P. catalaunicus* is not a junior synonym of *D. fontani*, and further permitting us to conclude that the genus *Hispanopithecus* must be resurrected.

STRATIGRAPHY AND AGE
Geological background

The area of Els Hostalets de Pierola is located at the western margin of the Vallès-Penedès Basin, on the NE Iberian Peninsula (Catalonia, Spain) (see Fig. 1). This basin is a NNE-SSW-oriented Neogene half-graben, limited by the two (Littoral and Pre-littoral) Catalan Coastal Ranges, which originated due to the rifting of the NW Mediterranean region during the Neogene (Cabrera and Calvet, 1990, 1996; Bartrina et al., 1992; Roca and Desegaulx, 1992; Roca and Guimerà, 1992; Cabrera et al., 2004). Although Early and Middle Miocene (mainly Late Burdigalian and Langhian to Early Serravalian) marine and transitional sequences were deposited in the SW zones of the Vallès-Penedès Basin, most of the basin fill consists of proximal to distal-marginal alluvial fan sediments (Cabrera and Calvet, 1990, 1996;

Roca and Desegaulx, 1992; Cabrera et al., 2004; de Gibert and Robles, 2005).

The area of Els Hostalets de Pierola is characterized by thick Middle to Late Miocene alluvial sequences, which resulted from a high accumulation rate, most likely controlled by its proximity to the actively subsiding NW basin margin major fault. High subsidence rates determined sediment trapping at the foot of this marginal fault. The combination of high rates of both subsidence and sediment supply must have favored rapid burial in a mudstone-dominated sedimentary environment, with a positive effect on the preservation potential of vertebrate remains. The Middle Miocene sequences in the area of Els Hostalets de Pierola consist of red to brown mudstones, sandstones, breccias, and conglomerates. These sediments were deposited in the distal-to-marginal, inter-fan zones of two major coalescing alluvial fan systems: (1) the short-radius alluvial fan system of Els Hostalets de Pierola, which was sourced from the NW Pre-littoral range by very close, local catchments dominated by Paleozoic metamorphic rocks; and (2) the radially extensive Olesa alluvial fan system, sourced from the NE by more extensive catchments, where a variety of metamorphic Paleozoic and sedimentary Mesozoic and Paleogene rocks cropped out.

Biostratigraphy

More than twenty classical sites are known from the area of Els Hostalets de Pierola (Crusafont and Truyols, 1954; Golpe-Posse, 1974). Except for Can Mata I, these loosely-defined "localities" cannot be considered paleontological localities in a strict sense, because they do not correspond to a single stratigraphic level (Agustí et al., 1985). As such, these classical "localities" have been traditionally grouped into "Lower Hostalets" (Aragonian levels) and "Upper Hostalets" (Vallesian ones) (Crusafont and Truyols, 1954; Golpe-Posse, 1974; Agustí et al., 1985). The chronology of fossil localities from the European Neogene is customarily ascertained on the basis of the MN (Mammal Neogene) biozones, first proposed by Mein (1975). In the past, Upper Hostalets has been attributed to early MN 9, while Lower Hostalets would be attributable to MN 7 + 8, with some localities having been traditionally attributed to "MN 7" (e.g. Can Vila) and others to "MN 8" (e.g., Can Mata I). In fact, except for the presence of hipparionine horses from the beginning of the Vallesian onwards, the faunas from Lower and Upper Hostalets are quite similar to one another (Agustí and Gibert, 1982; Agustí et al., 1985), a situation that can be generalized for the whole Vallès-Penedès Basin (Agustí et al., 1997, 2001). The lack of detailed information on stratigraphic provenance for most of the classic localities, together with inadequate small mammal sampling, precludes assigning a precise age to the classical hominoid findings from Els Hostalets de Pierola. This situation contrasts with the ACM local stratigraphic series, which comprises more than 100 mammal sites distributed along a continuous Late Aragonian section of nearly 300 m. Thanks to the extensive outcrops generated by the digging activity, and to the continuous paleontological control, the ACM stratigraphic series is based on firm lithostratigraphic, magnetostratigraphic, and biostratigraphic grounds, which allow a precise dating of the several localities thus far discovered.

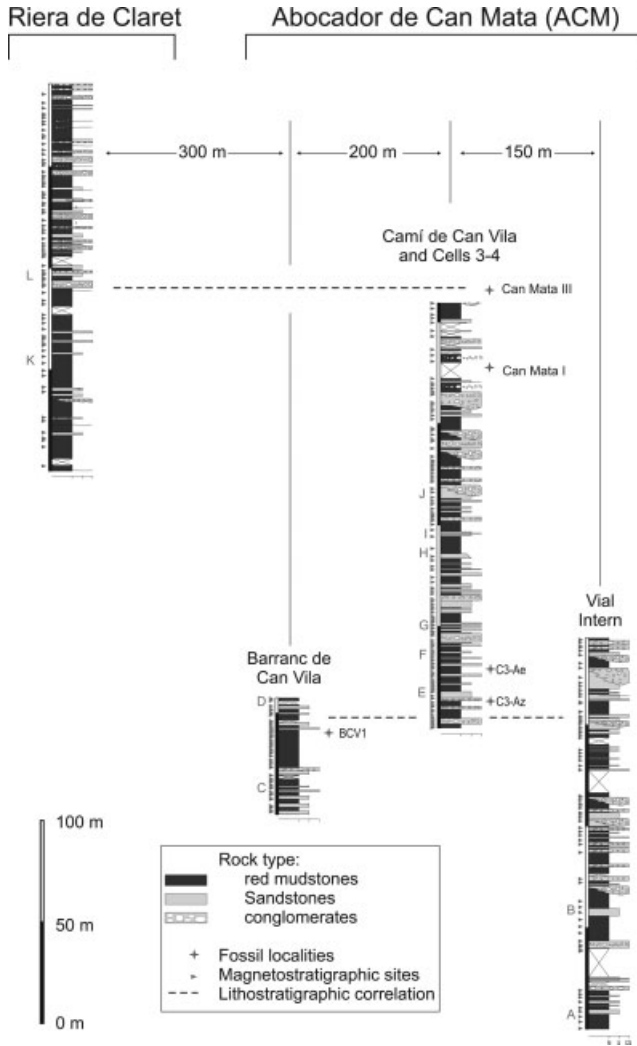The ACM stratigraphic series has been divided into three local biozones on the basis of the presence of certain cricetid genera (Alba et al., 2006). The lower 50 m of the succession are characterized by the presence of *Megacricetodon gersii* along with *M*. cf. *crusafonti*, and are correlated to MN 6 (after Agustí et al., 2001). The overlying succession is correlated to the MN 7 + 8, being characterized by the presence of *Megacricetodon ibericus*. This upper part of the sequence can be split into two biozones: a lower one, where *M. ibericus* is accompanied by *Democricetodon larteti*; and an upper one, where *M. ibericus* occurs together with *D. crusafonti*. These two biozones can be correlated, respectively, to the MN 7 and the MN 8 sensu Mein and Ginsburg (2002), which have been redefined on the basis of the fauna from La Grive fissure fillings. La Grive M is designed by these authors as the type site for MN 7 and La Grive L3 as the type site for MN 8. Interestingly, La Grive L3 has also yielded remains of *Dryopithecus fontani*. Nevertheless the geographic range of these newly erected MN 7 and MN 8 zones seems to be quite restricted, and although they can be applied to the Iberian record, it is unlikely that they would be recognized in central Europe. Since the MN zones were defined for the whole of Europe (Mein, 1975), it seems advisable to designate these regional biozones (which correspond to the early and late MN 7 + 8) with a different name. Since this is outside the scope of this article, we will retain the terms "MN 7" and "MN 8" (always with quotation marks) in the text.

Stratigraphically, the two sites from the ACM series that have yielded *D. fontani* remains, C3-Ae and C3-Az, are close to one another. C3-Ae is very close to locality C3-A2, which on the basis of micromammalian remains is thus far the lowermost ACM locality that can be securely correlated to the *M. ibericus* + *D. crusafonti* biozone. As such, C3-Ae can be attributed to "MN 8," being stratigraphically about 30 m above BCV1. The latter is thus far the uppermost locality that, on the basis of small mammals, can be securely correlated to the *M. ibericus* + *D. larteti* biozone, being attributable to "MN 7." Stratigraphically, C3-Az is situated approximately between BCV1 and C3-Ae localities, thus being either attributable to the latest "MN 7" or earliest "MN 8." Saint Gaudens (the type locality of *Dryopithecus fontani*), as well as La Grive L3, have been also correlated to "MN 8" (Mein, 1986, 1989).

Magnetostratigraphy

A magnetostratigraphic study was carried out in order to provide the mammal bearing sediments of Abocador de Can Mata with a robust absolute chronology. This paleomagnetic analysis was based on the analysis of 369 samples uniformly distributed over a 460 m thick composite section. Two sections were studied: the Abocador de Can Mata and the Riera de Claret (Fig. 2; see Supporting Information Fig. 1 for a further detailed localition).

In the area surrounding the ACM, a high-resolution sampling (samples taken at 1 m intervals) was carried out on three stratigraphically overlapping sections (see Fig. 3). Samples were taken using a portable electrical drill and oriented in situ with magnetic compass. The sampled sections within the ACM represent a composite stratigraphic interval of ∼360 m. Bed-to-bed correlation between sections was feasible thanks to the excellent outcrop conditions during excavations of the successive cells of the rubbish dump.

Fig. 3. Correlation panel of the sections sampled for magnetostratigraphy. Letters on the left of each column refer to paleomagnetic samples shown in Supplementary Figure 2.

TABLE 1. *Mean paleomagnetic directions and fisherian statistics of the Abocador de Can Mata sections. Mean paleomagnetic declination and inclination in geographic (g) and bedding corrected (s) coordinates*

Polarity	N	Dec g	Inc g	Dec s	Inc s	k	α_{95}
Reverse	251	196.0	−42.3	182.4	−45.5	9.0	3.1
Normal	105	019.2	54.8	355.8	55.5	10.5	4.5
All samples	356	016.8	46.0	000.7	48.5	9.1	2.6

unblocking temperatures in the range of 600–670°C, indicating the presence of magnetite and hematite. This high temperature characteristic magnetization yielded both normal and reverse polarities (see Fig. 4) and its direction was determined for each sample by means of principal component analysis (Supporting Information Table 1). The gentle monoclinal dip of the strata does not allow application of fold test. However, bedding correction of the gentle 15° westwards tilt allows an assessment of the age of magnetization relative to tectonic tilt. The mean normal and reverse paleomagnetic directions in geographic coordinates show a significant drift from the expected northerly directed Miocene paleomagnetic direction (Garcés et al., 1996), while bedding corrected mean directions show much better agreement (Table 1). This observation fully supports a pre-tilt age of the magnetization, while a divergence of 10° in the inclination of the reversed polarity mean direction could be likely attributed to the partial overlap with the present day field viscous component. The virtual geomagnetic pole latitude was calculated for each paleomagnetic direction in order to determine the magnetic polarity at the site (Supporting Information Table 1 and Supporting Information Fig. 3). The litho-magnetostratigraphic correlation between all the sections (Supporting Information Fig. 4) allowed the assembly of a composite magnetic polarity stratigraphy consisting of 10 magnetozones (see Fig. 5).

Correlation of the ACM magnetostratigraphy with the geomagnetic polarity time scale is straightforward on the basis of, first, the characteristic reversal pattern of the LMPS and, second, the biostratigraphic constraints on the location of the Aragonian/Vallesian boundary between the historical sites of Can Mata I and Can Mata III (Figs. 3 and 5). The Aragonian/Vallesian stage boundary, defined by the dispersal in Eurasia of the late Miocene hipparionine horses, is magnetostratigraphically well dated in the Vallès-Penedès Basin (Garcés et al., 1996, 2003; Agustí et al., 2001) as well as in other Spanish basins (Agustí et al., 2001; Garcés et al., 1997, 2003). This datum allows establishing an unambiguous correlation of the topmost 100 m thick normal magnetozone with the characteristic long normal chron C5n. On the basis of this correlation, the match of the LMPS with the GPTS is excellent, providing evidence for stratigraphic completeness and steady sedimentation over the studied interval. In this work, the absolute ages of geomagnetic reversals are taken from the astronomically tuned time scale ATNTS2004 (Lourens et al., 2004). This yields an estimated duration of the Can Mata composite section of 2 myr, spanning from 12.6 to 10.6 Ma. A mean sedimentation rate of 24 cm/kyr is in line with previous studies on late Miocene sequences further east, in the western Vallès area (Garcés et al., 1996).

The two ACM localities that have yielded fossil remains of *Dryopithecus fontani* are correlated to subchron C5r.3r, and have an estimated age of 11.8 Ma (C3-

Along the western slopes of the Riera de Claret (Supporting Information Fig. 1), a 200 m thick sedimentary sequence was sampled at 2 m intervals. This section is laterally equivalent to the top sediments of the ACM and extends upwards to include the Aragonian/Vallesian transition as reported in this area by the historical sites of Can Mata I and Can Mata III (see Fig. 2).

Paleomagnetic samples were processed at the Paleomagnetic Laboratory of the University of Barcelona–CSIC. The Natural Remanent Magnetization (NRM) was measured on a superconducting rock magnetometer (2G Enterprises). Paleomagnetic components were isolated by means of standard stepwise thermal demagnetization using a Schonstedt thermal demagnetizer TSD-1. A number of 10 to 15 demagnetization steps were applied from 100°C up to the complete demagnetization of the samples. The Zijderveld plots (Supporting Information Fig. 2) revealed the presence of a low temperature component parallel to the present geomagnetic field, which was usually removed at temperatures below 200°C. Above this temperature, samples showed a single paleomagnetic component which typically reached maximum
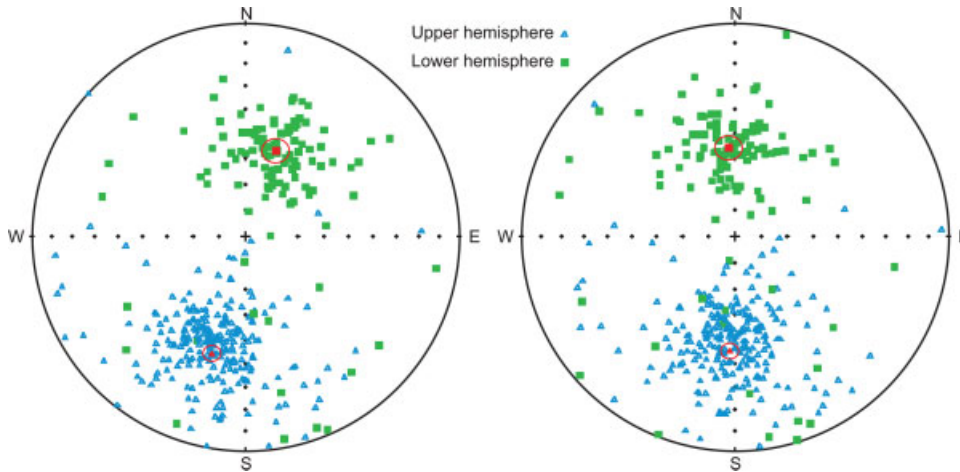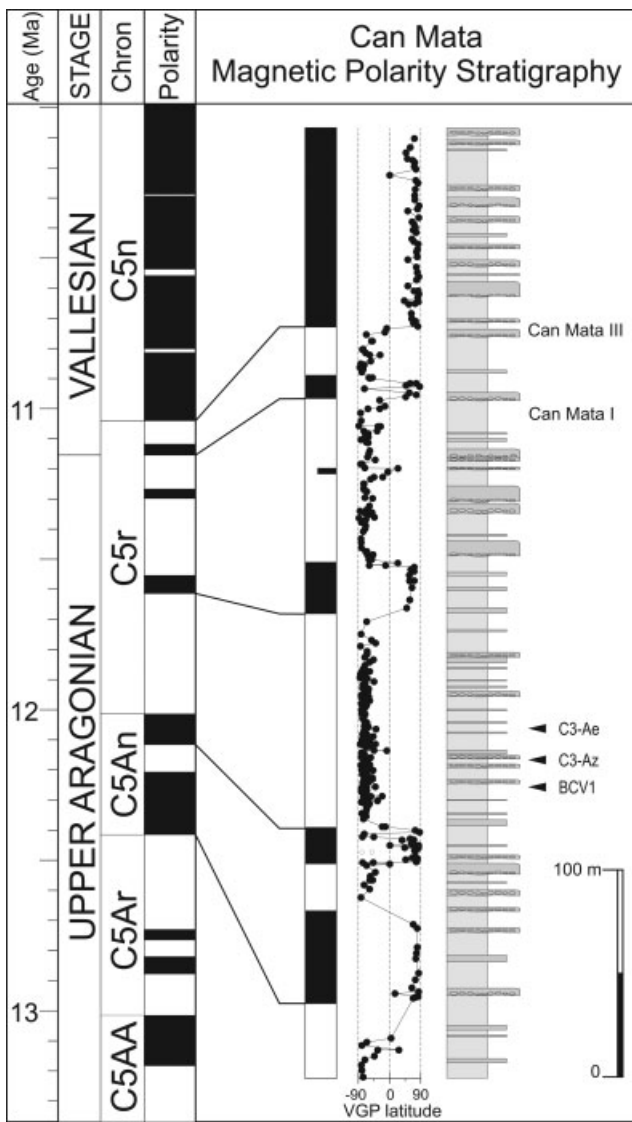
Fig. 4. Stereonet projection of the characteristic magnetization in geographic and tilt corrected coordinates. In red, mean normal and reverse directions with their α_{95} angular confidence.

Fig. 5. Composite magnetic polarity stratigraphy of Can Mata and correlation with the astronomically tuned geomagnetic polarity time scale ATNTS2004.
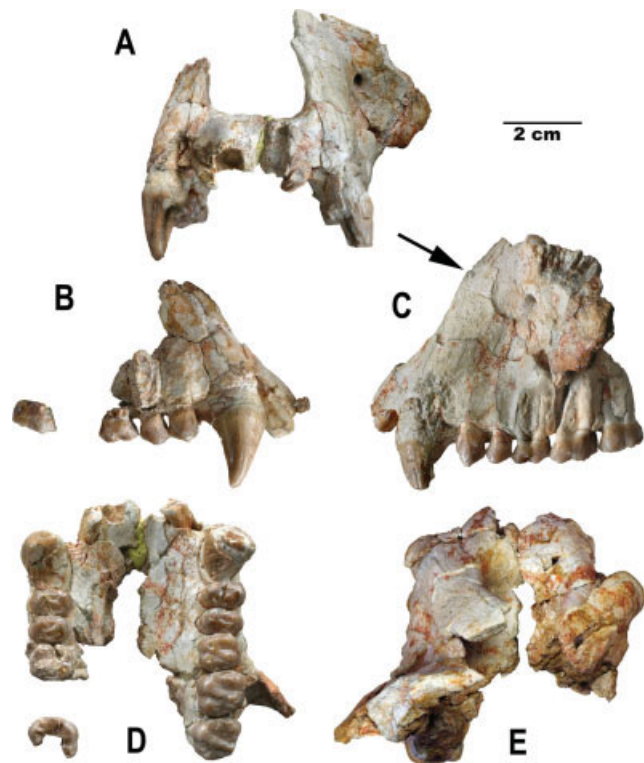
Fig. 6. Lower face IPS35026 of *Dryopithecus fontani* from ACM/C3-Ae. (**A**): frontal view; (**B**): view from the left side; (**C**): view from the right; (**D**): palatal view; (**E**): superior view; the arrow indicates the position of the most anterior nasomaxillary contact.

Ae) and 11.9 Ma (C3-Az). In a previous article (Moyà-Solà et al., 2004), BCV1 was attributed to the lowermost part of MN 7 + 8, with an estimated age of 12.5–13.0 Ma according to Agustí et al. (2001), on the basis of the presence of *Democricetodon larteti* and its similarities to populations from the Calatayud-Teruel Basin dated to ca. 12.5 Ma. The magnetostratigraphic data presented in this article, however, indicate that BCV1 (the type locality of *Pierolapithecus catalaunicus*), albeit slightly older than C3-Az (Alba et al., 2006), belongs to the same sub-

TABLE 2. *Measurements of the dentition of* Dryopithecus fontani *(IPS35026) from ACM/C3-Ae*

	Left maxilla		Right maxilla	
	Mesiodistal length (mm)	Buccolingual breadth (mm)	Mesiodistal length (mm)	Buccolingual breadth (mm)
C1	16.8	13.0	17.5	13.0
P3	7.6	12.1	8.0	12.4
P4	7.3	12.3	7.7	11.4
M1	10.5	12.5	10.1	12.2
M2	12.1	13.8		
M3	12.1	13.8		

chron (C5r.3r), with a revised estimated age of 11.9 Ma (see Fig. 5).

DESCRIPTION AND MORPHOLOGICAL COMPARISONS
Preservation of IPS35026

The lower face with upper dentition (IPS35026) from ACM/C3-Ae (see Fig. 6) is the best-preserved lower face of a hominoid from the European Miocene, comprising 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 with the lateral incisors, the alveoli of the central incisors, and fairly complete upper tooth rows (see Table 2 for measurements). The right portion of IPS35026 is a premaxillary-maxillary fragment with a partial tooth series (from I2/ to M1/, with the unattached partial crown of M3/), further preserving the I1/ alveolus, a portion of the hard palate and nasal floor (until the level of P4/-M1/), and the rim of the nasal aperture until surpassing the apex of the canine root. The left portion of IPS35026 is more completely preserved than the right one, including an almost complete tooth row (from I2/ to M3/), a larger portion of the hard palate and nasal floor, the rim of the nasal aperture until the nasomaxillary suture, the lower portion of the zygomatic process of the maxilla (the zygomatic root), the infraorbital foramen, and part of the inferior orbital rim. The anterior portion of the left I2/ alveolus, unlike the right one, is broken away, while the crown of the I2/ is similarly worn. The apex of the left canine is broken away, and the postcanine teeth are all completely preserved except for the anterior buccal root of the M2/ and the crown of the P3/ that is slightly damaged, albeit both crown proportions and occlusal morphology can be adequately evaluated.

Description of the dentition

The I1/ alveolus is subquadrangular and considerably larger than that of the I2/, indicating marked incisor heteromorphy. There is a quite large diastema between I2/ and C1/, with the former tooth being obliquely implanted and extremely worn until the crown base, with the pulp cavity exposed. The right canine is considerably worn distally but not apically, with a large honing facet from the apex to the base of the crown and also a small wear facet (against the lower canine) on the mesial side of the canine close to the base. The left canine, as far as it can be ascertained, displays more mesial and apical wear, while the distal wear is apparently more restricted. The premolars are moderately worn, with den-

tine exposure on the two main cusps. The first molars are also moderately worn, with dentine exposure on the four main cusps (although slightly more pronounced on the lingual ones). The second and the third molars display only a slight degree of wear without dentine exposure.

Both canine size and shape indicate that the specimen corresponds to a male individual, with a relatively high crown, although the canine root is relatively short. The latter is somewhat inclined backwards with respect to the crown, although without reaching the level of the P3/. The canines display a moderately-compressed oval section, with the major axis oriented sagittally. On the buccal side, the crown displays abundant secondary enamel wrinkling, whereas on the mesial aspect there are two (mesiobuccal and mesiolingual) well-developed, broad crests that run apically from the base until merging before reaching the apex, and which delimit a deep groove in between. The large wear facet on the distal aspect of the crown defines a distolingual, sharp cutting edge more than 4 mm long, indicating the presence of a well-developed honing complex. No remains of either lingual or buccal cingula can be appreciated.

The cheek teeth, in particular the molars, of IPS35026 are characterized by relatively wide and high crowns with inflated bases, large and slightly peripheralized cusps (including a large hypocone in the molars), relatively restricted basins, and presence of remains of cingula. The premolars are much wider than long (breadth/length index 148–168%) and display an elliptical (P4/) to suboval (in the P3/, where the buccal moiety of the crown is slightly longer than the lingual one) occlusal profile. The protocone is somewhat larger and more protruding than the paracone. These cusps are connected by two short and curved crests, which run from the apex of the protocone to the apex (in the P3/) or base (in the P4/) of the paracone. These transverse crests delimit a relatively restricted and shallow central fovea, which is wider than long. There is also a restricted, groove-like, straight mesial fovea, and a narrow, badly-defined, U-shaped distal fovea. The base of the crown is considerably inflated on both the buccal and lingual walls, although there are only restricted remnants of cingulum on the mesiobuccal corner of the crown in both premolars, and on the lingual aspect of the P4/.

The molars display a subquadrangular occlusal outline, being shorter than wider in all instances (breadth/length index 114–120%). The first molar is much smaller than the remaining ones, being about equally long on the buccal than on the lingual moieties of the crown, and approximately equally wide on the mesial than on the distal lobes. On the contrary, on the second and third molars, the lingual moiety of the crown is distally placed with respect to the buccal one, and the mesial lobe is clearly wider than the distal one. The buccal cusps are more protruding and somewhat more mesially placed than the corresponding lingual ones, which are nevertheless more extensive and less peripheral (especially the protocone) than the lingual cusps. A short preprotocrista runs in mesiobuccal direction until reaching a distinct paraconule (at least in M1/ and M2/), which is situated on the mesial marginal ridge, close to (M1/ and M2/) or just on (M3/) the midline of the crown. A short but distinct preparacrista merges with the mesial marginal ridge; the latter, together with the longer hypoparacrista that runs transversely until the paraconule, delimit a mesiodistally short, shallow and slit-like mesial

fovea, which is much wider than longer, and which is almost completely restricted to the buccal moiety of the crown. The trigon basin (central fovea) is much more extensively developed, and approximately equally wider than longer, being distally delimited by a well-developed crista obliqua, which is particularly thick on the M3/. On the first and second molars, the hypocone is well-developed and mesially placed with respect to the distolingual corner of the crown, whereas on the third molar, the hypocone is splitted into two tubercules, which are less protruding and more distally placed than on the preceding molars. The crown bases are inflated, and although there are no continuous cingula, there are remnants or styles on the buccal side (between the paracone and metacone), on the mesiobuccal aspect of the paracone, on the mesiolingual aspect of the protocone, and on the lingual side (between the protocone and hypocone), which become progressively less conspicuous from the first to the third molar.

Description of the face

The facial morphology of IPS35026 is highly distinctive. It displays a large and pyriform nasal aperture widest at the base, with the edges of the aperture formed by the maxillae; the palate is wide; the muzzle is long, as indicated by the long nasomaxillary suture (NMS) preserved on the left maxilla, which ends over the third premolar (see Fig. 6); the surface of the maxilla is thus long from the nasal aperture to the lower orbital rim and faces laterally; this suture is steep. The lower orbital rim is situated high above the tooth row and it is placed anteriorly to the zygomatic root (situated over M2/) at the level of the M1/; the nasal aperture and the zygomatic are highly verticalized with respect to the plane of the tooth row. In this pattern, when the alveolar plane is oriented horizontally, the upper limit of the nasal aperture, situated at the level of P3/, closely approaches the posterior pole of the nasoalveolar clivus (NAC). The zygomatic root is moderately high above the alveolar margin. It is a solid strut of bone without pneumatization that curves posteriorly. In the preserved maxillary bone, from the orbit to the zygomatic root, there is no trace of sinus. This can be ascertained due to the presence of different fractures on the specimen. The maxillary sinus is only visible as a small cell, just over the highest part of the preserved maxilla, over the M1/. The canine fossa is notably deep. Left and right parts of the NAC are completely fused in IPS35026. The area of the suture is preserved throughout its complete length but there is neither a septal groove nor any other trace of attachment of a nasal septal cartilage. The NAC is elongated posteriorly, displays an ovoid section, and the posterior limit is situated very close to the anterior pole of the palate. The NAC does not overlap the palate at the midline, but only at the most lateral rims of the palatine fenestra.

Morphological comparisons and taxonomic allocation

Considering that IPS35026 has been found in the same area that the recently described (Moyà-Solà et al., 2004) Middle Miocene fossil hominoid *Pierolapithecus catalaunicus*, a comparison between both specimens is necessary. IPS35026 differs from the holotype of *P. catalaunicus* (IPS21350) in facial and dental morphology. Both share some typical modern great-ape (hominid) fea-
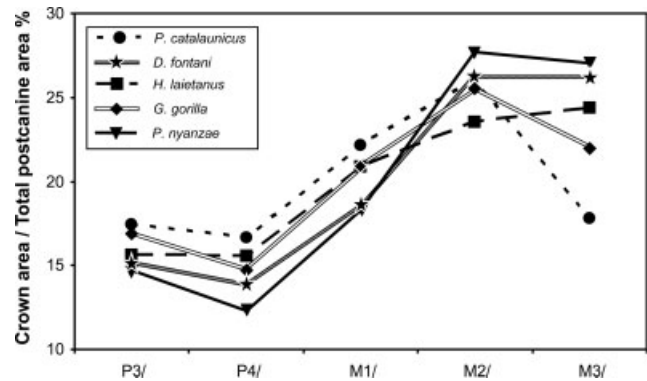
Fig. 7. Relative crown area of upper postcanine teeth of *D. fontani* (IPS35026) as compared with selected fossil and extant hominoids. Relative crown area was computed as mesiodistal length × buccolingual width/total check teeth surface × 100. Note the similar proportions between IPS35026 and *P. nyanzae*. Data for gorillas were computed from mean male data taken from Swindler (2002), since most of the fossil specimens included correspond to male individuals.

tures, such as the large and pyriform nasal aperture widest at the base, with the edges of the aperture formed by the maxillae, and the wide palate. Both specimens also share a relatively strong midfacial prognathism, shaping a long muzzle; the latter is however clearly longer in IPS35026, as shown by the nasomaxillary anterior contact point situated over the P3/, instead that over the P4/ as in *Pierolapithecus*. In spite of the aforementioned similarities, both taxa show very important differences. Thus, the frontal processes of the maxilla, collateral to the nasal bones, face laterally from the nasal suture conforming a domed muzzle in IPS35026. In *Pierolapithecus*, on the contrary, this area is a completely flat and uniform surface on which the nasals are situated on the same plane that the frontal processes of the maxilla; the latter pattern strongly resembles the morphology observed in *Ouranopithecus macedoniensis*. The nasal aperture and the zygomatic are highly verticalized (with respect to the tooth row) in IPS35026, contrasting with the strong posterior inclination observed in *Pierolapithecus*. The orbit is situated high on the face in IPS35026, while it is much lower in *Pierolapithecus*. The combination of these features determines that the superior limit of the nasal aperture, in IPS35026, is much more anteriorly situated than in *Pierolapithecus*. IPS35026 also differs from *Pierolapithecus* by the remarkably primitive size proportions between the cheek-teeth (Fig. 7; see Table 2 for measurements)—in particular the small M1/ and the large posterior molars—, and by the short and wide molars—in particular the M1/. IPS35026 further differs from *Pierolapithecus* by the moderately compressed C1/ with the major axis oriented sagittally, the short, vertical and unrotated root, which apically does not surpass the C1/-P3/ limit, and by the higher crowns of the check teeth. These differences permit to exclude IPS35026 from the hypodigm of *Pierolapithecus*.

Considering this information, only two systematic alternatives are possible for IPS35026: either it represents the unknown upper dentition of the seminal taxon *D. fontani* Lartet 1856 from Saint Gaudens (France), or it must be attributed to a new taxon. The only European upper dental specimen that is similar to IPS35026 is an upper M2/ from La Grive (France) (Depéret, 1887;

Begun, 2002). It is high-crowned, short and wide, with a large base and cusps that are less peripheral than in Late Miocene "*Dryopithecus*," showing a similar pattern to the Can Mata specimen. There is a general consensus on the attribution of this specimen to *D. fontani* (Andrews et al., 1996; Begun, 2002), although it cannot be unambiguously attributed to it, in spite of having a similar age to Saint Gaudens. In any case, the dental sample from La Grive cannot be attributed to the recently described *P. catalaunicus* (Moyà-Solà et al., 2004), with the former displaying higher-crowned and relatively much broader molars, as well as a hypsodont and narrow I1/ (instead of brachyodont and spatulate as in *Pierolapithecus*). Besides the similarities with the La Grive specimens, the attribution of IPS35026 to *D. fontani* can be further inferred from the similarities between the more complete upper dentition of IPS35026 and the lower dentition from Saint Gaudens. The specimens from both localities share some features to the exclusion of all other European species currently included in *Dryopithecus*. Dentally, they are the largest male specimens known from Western Europe. Both of them share molars and premolars with inflated bases, short and wide crowns, wide and non-peripheralized cusps, and more restricted basins than the Late Miocene taxa (Ribot et al., 1996). The hypoconulids of the lower molars from Saint Gaudens are substantially larger than in Late Miocene forms (Begun et al., 2006) and the hypocones of the upper molars are similarly larger in IPS35026. The upper first molars of IPS35026 and the lower first molars of *D. fontani* are substantially smaller than their respective second molars. Moreover, the first upper molars of IPS35026 and the lower molars from Saint Gaudens have remnants of cingula. In our opinion, these similarities support the attribution of IPS35026 to *D. fontani*. This hypothesis receives indirect support from the fact that both sites have a similar age and are situated geographically close to one another. Under the light of this evidence, the alternative solution of erecting of a new taxon for this specimen is unwarranted with the current evidence. Therefore, we consider the attribution of IPS35026 to *D. fontani* as the most reasonable and parsimonious alternative.

The facial morphology of IPS35026 confirms the distinctiveness of this specimen. In contrast to Late Miocene European hominoids, this taxon displays a long muzzle, while the zygomatic root is lower than in the Late Miocene *Dryopithecus*. Moreover, the restricted development of the maxillary sinus in this specimen is just the opposite pattern to that shown by the highly pneumatized maxillae from Can Llobateres and Rudabánya (Moyà-Solà and Köhler, 1995). On the basis of the degree of dental wear, including dentine exposure on the tips of the main cusps of the M1/, IPS35026 is a fully adult individual, and hence the maxillary sinus is unlikely to have been more extensively developed later in life. Accordingly, the differences in maxillary sinus extension with respect to Late Miocene specimens must be significant, especially when it is taken into account that the Can Llobateres individual (IPS18000), on the basis of the dental wear criterion, was only slightly older than IPS35026. The canine fossa is also notably deeper in the ACM (IPS35026) than in the Can Llobateres (IPS18000) specimen (Moyà-Solà and Köhler, 1995). Moreover, the differences in dental morphology further confirm the uniqueness of *D. fontani*, as represented by IPS35026. Apart from the aforementioned features (see Fig. 7), and

in contrast to Late Miocene "*Dryopithecus*" (Begun et al., 2006), *D. fontani* displays a greater incisor heteromorphy (i.e. size discrepancy between I2/ and I1/); a larger, vertically-implanted and nonrotated C1/, with the anterior groove more lingually placed and with a shorter and straighter root; a squared P3/ with a large protocone; a strongly developed anterior transverse crista on the upper premolars; and a large hypocone on the upper molars (and a large hypoconulid on the lower ones). On the other side, "*Dryopithecus*" from Rudabánya resembles "*D*". *laietanus* more closely than does *D. fontani*. The two former taxa share a similar pattern in the facial, dental, and postcranial material hitherto available, including a strongly developed maxillary sinus; reduced midfacial prognathism; higher zygomatic roots; reduced frontal sinus; smaller C1/ with long and rotated roots; clearly peripheralized cusps; narrower cheek teeth with noninflated bases; and larger first molars and smaller posterior molars (both upper and lower), with small protocones and hypocones. This leads us to the conclusion that the Late Miocene specimens from the Vallès-Penedès and Rudabánya are best classified into a separate genus *Hispanopithecus* (see later).

Among extant great apes, the facial pattern displayed by *D. fontani* most closely resembles the *Gorilla* condition. Stem hominoids from the Early Miocene of Africa show, to different degrees, long muzzles, but their lower facial pattern does not fit the *Gorilla* (nor *Dryopithecus*) pattern. First, they are not associated with high and steep (vertically inclined) faces and, second, the most anterior nasomaxillary contact is posteriorly placed, over the P4/. This posterior position of the nasomaxillary anterior contact obeys to the fact that these forms have the nasal aperture, as well as the zygomatic and orbits, strongly posteriorly inclined, a set of features retained in the stem hominid *Pierolapithecus* (Moyà-Solà et al., 2004). The posterior inclination of the nasal aperture is also retained in the members of the *Pongo*-clade, as shown by the low facial angles computed in *Ankarapithecus, Sivapithecus*, and *Pongo* (see Fig. 8). On the contrary, *D. fontani* shows a highly verticalized nasal aperture (high lower facial angle) and a nearly vertical zygomatic (high zygomatic angle) (see Fig. 8), although the latter figure should be taken with care do to incomplete preservation in this specimen. In this pattern, the upper nasal aperture closely approaches the posterior pole of the nasoalveolar clivus (NAC), a feature that is present only in gorillas within hominoids. On the contrary, in the stem hominid *Pierolapithecus* the upper nasal aperture is clearly posteriorly placed with respect to the posterior pole of the NAC, as occurs in proconsulids, *Afropithecus* and *Morotopithecus*, in spite of their long muzzles. Unfortunately, the available material of *Ouranopithecus* does not permit its inclusion in the quantitative analysis because the mid-facial morphology is not well preserved and accurate measurements cannot be taken. However, the preserved morphology suggests that the nasal aperture retains the primitive posterior inclination, and the most anterior nasomaxillary contact appears to be situated over the M1/, thus departing from the *D. fontani* and *Gorilla* pattern. Similarly, the lower facial morphology of *Hispanopithecus* is not well known, but the reconstructed face of *Hispanopithecus* (Köhler et al., 2001) suggests a more chimp-like reduced midfacial prognathism.

Finally, the nasal cavity and premaxilla morphology of IPS35026 is also unusual for Miocene hominoids. Left

TABLE 3. Discriminant statistics for the four indices employed in the discriminant analysis

Taxon	N	Mean	SD	95% CI	Range
NML					
Hylobates spp.	22	28.26	6.03	(25.58, 30.93)	(15.97, 41.67)
Pongo pygmaeus	21	16.91	6.85	(13.79, 20.02)	(6.50, 30.48)
Pan spp.	41	20.82	4.32	(19.46, 22.18)	(11.44, 28.66)
Gorilla gorilla	26	37.63	7.49	(34.60, 40.65)	(27.52, 54.04)
Aegyptopithecus zeuxis	1	74.29			
Afropithecus turkanensis	1	68.27			
Proconsul heseloni	1	40.92			
Proconsul nyanzae	1	36.26			
Pierolapithecus catalaunicus	1	23.60			
Dryopithecus fontani	1	44.65			
Hispanopithecus laietanus	1	20.66			
Ankarapithecus metai	1	21.31			
Sivapithecus indicus	1	11.76			
OAH					
Hylobates spp.	22	62.45	7.24	(59.24, 65.66)	(48.78, 78.48)
Pongo pygmaeus	21	91.24	9.68	(86.84, 95.65)	(70.52, 108.06)
Pan spp.	41	113.10	10.12	(109.91, 116.29)	(90.00, 135.52)
Gorilla gorilla	26	112.50	14.66	(106.58, 118.43)	(86.96, 145.02)
Aegyptopithecus zeuxis	1	64.29			
Afropithecus turkanensis	1	93.37			
Proconsul heseloni	1	69.16			
Proconsul nyanzae	1	77.70			
Pierolapithecus catalaunicus	1	90.56			
Dryopithecus fontani	1	101.48			
Hispanopithecus laietanus	1	96.49			
Ankarapithecus metai	1	89.42			
Sivapithecus indicus	1	130.78			
NMH					
Hylobates spp.	22	80.48	10.16	(75.98, 84.99)	(62.25, 97.66)
Pongo pygmaeus	21	89.93	10.33	(85.23, 94.63)	(71.64, 112.90)
Pan spp.	41	105.19	11.33	(101.61, 108.76)	(82.22, 131.22)
Gorilla gorilla	26	84.35	9.97	(80.33, 88.38)	(61.05, 102.72)
Aegyptopithecus zeuxis	1	72.50			
Afropithecus turkanensis	1	67.87			
Proconsul heseloni	1	80.69			
Proconsul nyanzae	1	84.61			
Pierolapithecus catalaunicus	1	82.25			
Dryopithecus fontani	1	93.16			
Hispanopithecus laietanus	1	82.64			
Ankarapithecus metai	1	81.97			
Sivapithecus indicus	1	96.08			
ZRH					
Hylobates spp.	22	23.27	6.25	(20.50, 26.04)	(12.47, 38.92)
Pongo pygmaeus	21	34.93	7.00	(31.74, 38.11)	(21.75, 48.39)
Pan spp.	41	53.71	10.85	(50.29, 57.14)	(27.08, 75.15)
Gorilla gorilla	26	57.98	17.09	(51.08, 64.89)	(33.33, 100.45)
Aegyptopithecus zeuxis	1	7.14			
Afropithecus turkanensis	1	28.51			
Proconsul heseloni	1	15.56			
Proconsul nyanzae	1	29.14			
Pierolapithecus catalaunicus	1	42.02			
Dryopithecus fontani	1	34.50			
Hispanopithecus laietanus	1	47.52			
Ankarapithecus metai	1	33.23			
Sivapithecus indicus	1	56.86			

N, sample size; SD, standard deviation; CI, confidence interval.

and right parts of the NAC are completely fused in IPS35026. The area of the suture is preserved throughout its complete length but there is neither a septal groove (as occurs in *Morotopithecus*) nor any other trace of attachment of a nasal septal cartilage (NSC, as occurs in *Pierolapithecus*). This indicates that the point of attachment for the NSC recesses into the nasal cavity as in *Gorilla*, and does not reach the base of the nasal aperture, contrary to the pattern observed in *Pierolapithecus*, *Morotopithecus* and the other African Miocene taxa, as well as in extant *Hylobates*, *Pongo*, and *Pan*. In these taxa, the NSC does frequently even surpass the lower margin of the nasal aperture (Ward and Kimbel, 1983; McCollum and Ward, 1997). As in *Hispanopithecus* from Rudabánya and many other Miocene hominoids (Ward and Kimbel, 1983; Moyà-Solà et al., 2004), IPS35026 shows a stepped nasal floor; *Gorilla* also shows a stepped nasal floor, but contrary to all these fossil specimens, the

TABLE 4. *ANOVA results and post-hoc multiple comparisons (Bonferroni method) for the four variables employed in the discriminant analysis*

NML	ANOVA	$F = 59.1$	$P < 0.001$
Bonferroni	*Pongo*	*Pan*	*Gorilla*
Pan	NS ($P = 0.103$)		
Gorilla	$P < 0.001$	$P < 0.001$	
Hylobates	$P < 0.001$	$P < 0.001$	$P < 0.001$
OAH	ANOVA	$F = 123.6$	$P < 0.001$
Bonferroni	*Pongo*	*Pan*	*Gorilla*
Pan	$P < 0.001$		
Gorilla	$P < 0.001$	NS ($P = 1.000$)	
Hylobates	$P < 0.001$	$P < 0.001$	$P < 0.001$
NMH	ANOVA	$F = 34.5$	$P < 0.001$
Bonferroni	*Pongo*	*Pan*	*Gorilla*
Pan	$P < 0.001$		
Gorilla	NS ($P = 0.457$)	$P < 0.001$	
Hylobates	$P < 0.05$	$P < 0.001$	NS ($P = 1.000$)
ZRH	ANOVA	$F = 51.2$	$P < 0.001$
Bonferroni	*Pongo*	*Pan*	*Gorilla*
Pan	$P < 0.001$		
Gorilla	$P < 0.001$	NS ($P = 0.831$)	
Hylobates	$P < 0.01$	$P < 0.001$	$P < 0.001$

NS, non-significant.

premaxilla overlaps to some degree the maxilla, thus lacking an open palatine fenestra. The NAC is elongated posteriorly, has an ovoid section, and the posterior limit is situated very close to the anterior pole of the maxilla. The NAC does not overlap the palate at the midline but only at the most lateral rims of the palatine fenestra.

Morphometric analysis of facial morphology

To evaluate the similarities in facial morphology (muzzle and orbital region) between IPS35026 and both extant and other fossil taxa, we employed four different indices measurable in this fossil specimen, and which define the basic architecture of the lower face (see Supporting Information Table 2 for individual data of extant and fossil specimens). These indices were computed by standardizing four metrical variables among postcanine tooth row length (in %), which is a reasonably methodology to correct for size differences, given the available fossil material: NML (nasomaxillary length: distance between anteriormost point of nasomaxillary suture and projection of lowermost point of orbital rim, parallel to the alveolar plane); OAH (orbitoalveolar height: distance between lowermost point of orbital rim and alveolar plane); NMH (nasomaxillary height: distance between anteriormost point of nasomaxillary suture and alveolar plane); and ZRH (zygomatic root height: distance between lowermost point of zygomatic and alveolar plane). Linear measurements were taken as projections on the sagittal plane, either orthogonal or parallel to the tooth row, on the basis of photographs taken in lateral view.

With regard to the extant comparative sample, many of the employed photographs were taken by the authors at the Koninklijk Museum voor Midden-Africa (Tervuren, Belgium) and at the Anthropologisches Institut und Museum (Zürich, Switzerland), while the remaining ones were taken from the "Mammalian Crania Photographic Archive" Second Edition, which is available from the Internet (http://1kai.dokkyomed.ac.jp/mammal/en/mammal.html). Data from extant hominoid genera were taken from 21 orangutans (*Pongo*), 41 chimpanzees and

TABLE 5. *Main results of the discriminant analysis*

	CA1	CA2	CA3
	Discriminant functions (canonical axes)		
Eigenvalues	5.766	2.718	0.235
% of variance	66.1	31.2	2.7
Cumulative %	66.1	97.3	100
Canonical correlation	0.923	0.855	0.436
	Unstandardized canonical discriminant function coefficients		
NML	−0.02	0.146	0.076
OAH	0.137	−0.030	−0.058
NMH	−0.099	−0.051	0.097
ZRH	0.014	0.036	0.042
Constant	−4.558	2.291	−7.066
	Functions at group centroids		
Pongo	−0.748	−1.280	−0.892
Pan	0.940	−1.455	0.403
Gorilla	2.645	2.239	−0.114
Hylobates	−4.164	1.288	0.236
	Discriminant scores		
Dryopithecus fontani	−0.219	2.286	0.931
Ankarapithecus meteai	−0.323	−0.237	−1.290
Hispanopithecus laietanus	0.800	−0.057	−1.087
Aegyptopithecus zeuxis	−4.272	7.777	2.203
Proconsul heseloni	−3.626	2.648	0.516
Afropithecus turkanensis	0.610	7.053	0.509
Pierolapithecus catalaunicus	−0.112	0.368	−0.789
Sivapithecus indicus	4.496	−2.718	−2.057
Proconsul nyanzae	−2.551	2.007	0.612

bonobos (*Pan*), 26 gorillas (*Gorilla*), and 22 gibbons and siamangs (*Hylobates*). Regarding fossil specimens, the following taxa were included in the study: the propliopithecid *Aegyptopithecus zeuxis*; the proconsulids *Proconsul heseloni* and *P. nyanzae*; the afropithecid *Afropithecus turkanensis*; and the great apes *Pierolapithecus catalaunicus*, *Hispanopithecus laietanus*, *Ankarapithecus meteai* and *Sivapithecus indicus*. Photographs of these extinct taxa were taken by one of the authors on the original specimens (*Pierolapithecus* and *Hispanopithecus*) or on good quality casts, except in the case of *Ankarapithecus*, for which a photograph kindly provided by John Kappelman (personal communication to SMS) was employed. Distortion of photographic images due to the parallax effect does not preclude their use in morphometric analyses, but requires a standardized methodology in which the camera is always oriented in the same way (Mullin and Taylor, 2002). Given the different sources of the photographs employed in this paper, the methodology for capturing the images could not be standardized regarding focus length. However, we minimized the parallax bias by employing photographs in which the crania were situated on the center of the photograph, with the camera lens parallel to the midsagittal plane.
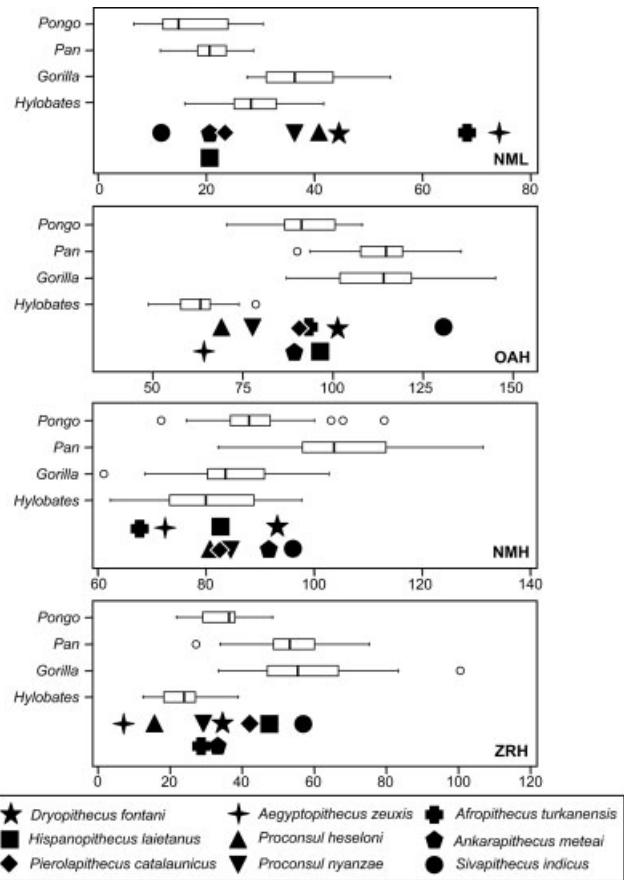
The four aforementioned indices were evaluated individually by means of analysis of variance (ANOVA), and also simultaneously by means of a multivariate discriminant (canonical) analysis. In the case of univariate analyses, differences between extant taxa were evaluated by means of *post-hoc* multiple comparisons (Bonferroni method), whereas for fossil specimens, available indices
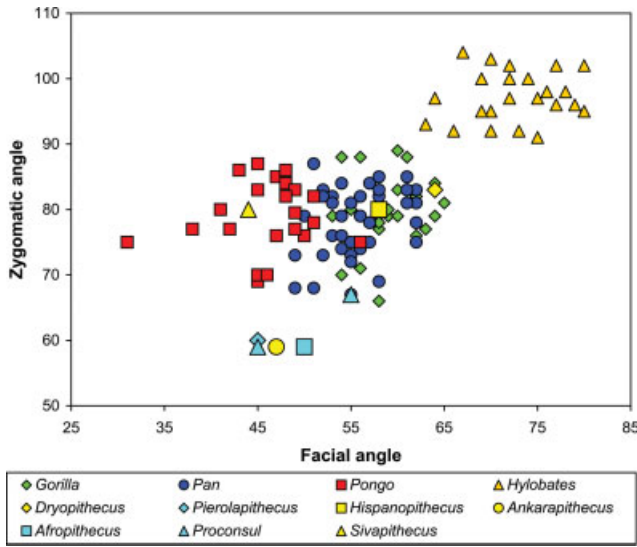
Fig. 8. Bivariate plot of the zygomatic angle (measured as the angle between the teeth row and the line joining the lower-most point of the zygomatic process and the midpoint of the frontozygomatic suture) and the lower facial angle (measured as the angle between the tooth-row and the line joining the pre-maxilla/maxilla suture between the C1/ and I2/, and the most anterior contact between the nasals and the maxilla). These angles were measured from sagittal projections taken from photographs, on the basis of the same sample employed in the multivariate analysis (see Text for further details). In the *D. fontani* specimen (IPS35026), the zygomatic angle was estimated by taking into account the preserved portion of the zygomatic, since the frontozygomatic suture is missing.

were compared with the 95% confidence interval (CI) for the mean and maximum-minimum ranges of extant taxa. Boxplots showing the median, quartiles, and extreme values of extant taxa have been employed in order to show the position of fossil taxa. In the case of the multivariate analysis, discriminant functions (canonical axes, CA) were derived by grouping extant taxa into four different genera, and then fossil taxa were classified on the basis of squared Mahalanobis distances from group centroids. Similarities have been represented by means of a bivariate plot of CA2 vs. CA1, as well as an UPGMA cluster based on Euclidean distances computed on the basis of the three canonical axes by using discriminant scores (in the case of fossils) and group centroids (in the case of living genera). ANOVA, boxplots and discriminant analyses were performed with SPSS v. 15.0,

Fig. 9. Boxplots for the four indices (NML, OAH, NMH and ZRH) employed in the discriminant analysis. Vertical line: median; box: interquartile range (i.e., the difference between the 75th and 25th percentiles); whiskers: extreme values; circles: outliers.

Fig. 10. Results of the canonical (discriminant) analysis performed on the basis of four indices (NML, OAH, NMH and ZRH) reflecting facial morphology (muzzle and orbital regions) in extant hominoid genera. (**A**): Bivariate plot of second against first canonical axes (CA2 vs. CA1), which explain together more than 97% of total variance (66% the first one and 31% the second one); the centroids of extant genera are represented by the same symbols than individuals, in black; the depicted polygons represent the range of extant taxa. (**B**): UPGMA cluster on the basis of Euclidean distances computed from centroids (for extant genera) and discriminant scores (for fossil taxa); at the right, the portion of the UPGMA cluster based on individual discriminant scores where *Dryopithecus* is nested; only two *Gorilla* individuals are nested outside this cluster (see supplementary Fig. 5).

TABLE 6. Classification results of the discriminant analysis

	Classification of fossil taxa			
	Predicted group (first)	Squared Mahalanobis distance to centroid	Predicted group (second)	Squared Mahalanobis distance to centroid
Dryopithecus fontani	*Gorilla*	9.30	*Pan*	15.62
Ankarapithecus meteai	*Pongo*	1.43	*Pan*	5.95
Hispanopithecus laietanus	*Pongo*	3.93	*Pan*	4.20
Aegyptopithecus zeuxis	*Hylobates*	45.98	*Gorilla*	83.89
Proconsul heseloni	*Hylobates*	2.22	*Pongo*	25.70
Afropithecus turkanensis	*Gorilla*	27.71	*Hylobates*	56.10
Pierolapithecus catalaunicus	*Pongo*	3.13	*Pan*	5.85
Sivapithecus indicus	*Pan*	20.30	*Pongo*	30.92
Proconsul nyanzae	*Hylobates*	3.26	*Pongo*	16.32
	Classification of original cases (extant taxa)			
	Pongo	*Pan*	*Gorilla*	*Hylobates*
Pongo	20 (95.2%)	1 (4.8%)	0 (0%)	0 (0%)
Pan	4 (9.8%)	37 (90.2%)	0 (0%)	0 (0%)
Gorilla	1 (3.8%)	0 (0%)	25 (96.2%)	0 (0%)
Hylobates	0 (0%)	0 (0%)	0 (0%)	22 (100%)

Squared Mahalanobis distance of *D. fontani* to extant centroids and fossil taxa

Pongo	*Pan*	*Gorilla*	*Hylobates*	*A. metai*	*H. laietanus*
16.32	15.62	9.30	17.04	11.31	10.60
A. zeuxis	*P. heseloni*	*A. turkanensis*	*P. catalaunicus*	*S. indicus*	*P. nyanzae*
48.20	11.91	23.59	6.65	56.20	48.20

bivariate plots with Excel 2000, and cluster analyses with PAST v. 1.54 (Hammer et al., 2001).

The descriptive statistics for the four indices employed in the multivariate analysis have been reported in Table 3 (see also Fig. 9), while ANOVA results are reported in Table 4. There are significant differences between extant taxa for the four indices, although *post-hoc* multiple comparisons indicate that 21% of the comparisons between pairs of extant genera are not significant (Table 3): *Pan-Pongo* for NML; *Pan-Gorilla* for OAH and ZRH; and *Gorilla-Pongo* and *Gorilla-Hylobates* for NMH. In short, as reflected by both OAH and ZRH, great apes differ from hylobatids by the higher faces of the former, while African apes further differ from orangutans by showing even higher values. There are however some differences between chimpanzees and gorillas: while the former are characterized by very high values of NMH, gorillas uniquely display very long faces (as reflected by NML). Thus, gorillas display higher values of NML than hylobatids and, especially, other extant great apes; only *Aegyptopithecus* and *Afropithecus* display even higher values, reflecting their extremely long muzzles. *Dryopithecus* differs from hylobatids and resembles extant great apes by its relatively high face (albeit less so than in African apes), differing from chimpanzees by its intermediate NMH, but resembling gorillas by its high NML. Thus, while *Pierolapithecus* and Late Miocene great apes are comparable to chimps and orangs with regard to NML (with somewhat lower values in *Sivapithecus*), *Proconsul* and, uniquely among fossil great apes, *Dryopithecus*, are on the contrary more comparable to gorillas by the possession of a considerably long face (albeit less so than in afropithecids and propliopithecids).

Although none of these four indices separately permits to adequately evaluate the similarity between particular fossil taxa and each of the extant hominoid genera included in the analysis, this can be readily accomplished by means of the multivariate analysis reported in Tables 5 and 6 (see also Fig. 10). This canonical analysis correctly classifies 94.5% of the original cases (individuals of living genera included in the analysis) (Table 6), with all erroneous attributions occurring between different great ape genera (mainly between orangs and chimps). The analysis discriminates well between hylobatids and living great apes, and although there is some overlap between orangs and chimps, gorillas can be also clearly distinguished (Fig. 10A). Hylobatids are characterized by uniquely low scores on CA1 (mainly due to low OAH), as well as relatively high scores on CA2 (mainly due to relatively high NML, which is nevertheless lower than in gorillas). This facial configuration of hylobatids, characterized by low and moderately long faces, is likely to be primitive for crown hominoids. This is confirmed by the very similar configuration of the putative stem ape *Proconsul* (which clusters with hylobatids), and also by the similarly low faces of *Afropithecus* and, especially, *Aegyptopithecus*, which further display extremely long muzzles that set them apart from the remaining taxa (Fig. 10B). All fossil great apes included in the analysis, except for *Sivapithecus* and *Dryopithecus*, are classified as orangutans (Table 6) and cluster with this taxon (Fig. 10B), albeit they are neither far from the chimpanzee centroid (Fig. 10A; Table 6). *Sivapithecus* is set apart by its extremely short midface and very high face, thus displaying just the opposite condition to *Aegyptopithecus*. Interestingly, *Dryopithecus* is classified as a gorilla (Fig. 10B; Table 6), even when gorilla outliers are removed from the sample. Although this taxon falls outside the gorilla range of variation, it is closest to the gorilla centroid. In fact, *Dryopithecus* is virtually indistinguishable from the gorilla centroid with regard to CA2, due to the considerably long faces displayed by both taxa (longer than in hylobatids, and most comparable to proconsulids).

Fig. 11. Partial left femur (IPS41724) of *Dryopithecus fontani* from ACM/C3-Az, (**A**): superior view; (**B**): medial view; (**C**): anterior view; (**D**): lateral view; (**E**): posterior view. [Color figure can be viewed in the online issue, which is available at www.interscience. wiley.com.]

When the distance between *D. fontani* and other fossil taxa is taken into account (Table 6), it emerges that the former is closer to the gorilla centroid than to other fossil taxa, with the only exception of *Pierolapithecus*. The latter, however, is much closer to the centroids of both chimps and orangs, whereas *D. fontani* is much closer to several gorilla individuals than to *Pierolapithecus*. This is illustrated by the cluster analysis when individual data from extant hominoid genera, instead of centroids, are employed (Fig. 10B and Supporting Information Fig. 5). The results are generally comparable to the former analysis, but permit to more fully appreciate the degree of variation and overlap between extant taxa, as well as the degree of similarity between fossil and living individuals. *Aegyptopithecus* and *Afroptihecus* are so divergent that cluster together apart from the remaining taxa. Something similar happens with *Sivapithecus*, which nevertheless clusters with other great apes. All the remaining fossil taxa, on the contrary, cluster with individuals from extant genera. Interestingly, the two *Proconsul* species cluster with one another well within the hylobatid cluster, which shows no overlap with great apes. With regard to the latter, there are three main clusters, corresponding to *Gorilla*, *Pan* and *Pongo*. Chimpanzees and orangutans are more similar to one another; and four orangs and six chimps cluster incorrectly, thus reflecting the overlap also reflected in Figure 10A. On the contrary, only two gorillas cluster incorrectly with orangutans. *Pierolapithecus*, *Hispanopithecus*, and *Ankarapithecus* cluster with orangutans, presumably reflecting a generalized or primitive great-ape condition characterized by short and moderately high faces. Unlike any other fossil taxon, *Dryopithecus* not only clusters with the gorilla centroid, but it is also nested well within the gorilla cluster (Fig. 10B and Supporting Information Fig. 5). Although this morphometric analysis does not necessarily reflect phylogenetic relationships, the unique similarity between *Dryopithecus* and gorillas remains intriguing and deserves further consideration.

Description of the femur and body mass estimates

A well-preserved proximal half of a left femur (IPS41724) from ACM/C3-Az (see Fig. 11) is also tentatively attributed to *D. fontani*. To estimate body mass (BM) from this specimen, we employed several measurements of the femoral head, which is functionally related with weight-bearing. Revised BM estimates have been also provided for *H. laietanus*, on the basis of average values taken from the two (right and left) partial femora (IPS18800) from Can Llobateres. Two femoral variables were employed as BM estimators (see Ruff, 1990, 2002, for details on variable definition and measurement): femoral head superoinferior breadth (FHSI, in mm); and femoral head surface area (FHSA, in mm^2). According to Ruff (2003), articular breadths are always equal or superior to articular areas in precision when estimating BM. In this particular case, however, the percent standard error of estimate for the hominoid regressions of the two aforementioned variables is very similar (12.9 for FHSA and 12.0 for FHSI: Ruff, 2003). Accordingly, the two variables were employed. Regression equations of ln BM vs. ln FHSI and ln FHSA were derived from the sex/species means reported by Ruff (2003: Appendix Table 1A), because this author only reports the regression equation for the former of the two selected estimators. A correction factor, based on the quasimaximum likelyhood estimator (QMLE), was applied to BM estimates in order to correct for the detransformation bias. Following Ruff (2003), this correction factor was computed as QMLE = $\exp(SEE^2/2)$, where SEE is the standard error of estimate. Although confidence intervals can be computed on the basis of the SEE and a two-tail Student's *t* distribution, in this particular case, both 95 and 50% CI were directly computed by means of SPSS v. 15.0.

Femoral head measurements taken on the partial femur from ACM (IPS41724) permit us to infer an estimated male body mass of 44 kg for *D. fontani* (Table 7), as compared to the 39 kg that can be inferred for male

TABLE 7. Femoral head measurements and body mass estimates of D. fontani (IPS41724) and H. laietanus (IPS18800)

	Femoral measurements and BM estimators			
	FHSI (mm)	FHAP (mm)	FHDP (mm)	FHSA (mm^2)
H. laietanus	30.7	29.6	21.6	2044.9
D. fontani	31.7	31.4	23.5	2328.1
	BM estimates (based on FHSI)			
	BM (kg)	50% CI	95% CI	
H. laietanus	39.6	(36.4, 43.1)	(30.2, 52.0)	
D. fontani	43.6	(40.1, 47.4)	(33.2, 57.3)	
	BM estimates (based on FHSA)			
H. laietanus	37.5	(34.3, 41.1)	(27.9, 50.4)	
D. fontani	45.2	(41.2, 49.5)	(33.6, 60.8)	
	Average BM estimate and combined CI			
H. laietanus	38.6	(34.3, 43.1)	(27.9, 52.0)	
D. fontani	44.4	(40.1, 49.5)	(33.2, 60.8)	

BM, body mass; FH, femoral head; SA, surface area; SI, superoinferior diameter; AP, anteroposterior diameter; DP, depth. FHSA computed as 1.57 FHDP (FHSI + FHAP), following Ruff (2002). The measurements of *H. laietanus* are the mean value of the right and left sides, except in the case of FHAP, which could be only realiably measured on one side.

H. laietanus on the basis of the same measurements (Table 7), and the 34 kg that have been inferred for the (male) holotype of *P. catalaunicus* on the basis of other postcranial measurements (Moyà-Solà et al., 2004). All these specimens are unambiguously attributable to male individuals on the basis of canine size and morphology, so that they are fully comparable to one another irrespective of body size sexual dimorphism. Although there is some overlap in the CI for the mean between *D. fontani* and *H. laietanus* (Table 7), the larger body mass inferred for the former is in agreement with the larger dental size of *D. fontani*, thus suggesting that IPS42724 must be attributed to the former taxon. The isolated partial femur from ACM cannot be sexed; however, if it belonged to a female, given some degree of dimorphism, it must belong to an even larger taxon as compared to both *Hispanopithecus* and *Pierolapithecus*.

An attribution of the partial femur IPS41724 to the genus *Hispanopithecus* can be further discarded on the basis morphological considerations. The absence of crista trochanterica, the anteroposterior compressed shaft, and a femoral head that is large in relation to the neck and situated roughly over the greater trochanter, clearly indicate modern ape affinities. However, IPS42724 differs from the two partial femora of *H. laietanus* (IPS18800) from Can Llobateres (Köhler et al., 2002) in several important features, such as the shorter and less steep femoral neck (123° contra 132° in *H. laietanus*), the relatively low position of the head relative to the greater trochanter, and the more posterior situation of the lesser trochanter. These traits suggest a more quadrupedal locomotor repertoire for *D. fontani*, different from the more suspensory, *Pongo*-like locomotion inferred for *Hispanopithecus* (Köhler et al., 2002; Almécija et al., 2007). This further strengthens the contention that *D. fontani* is distinct at the genus level from Late Miocene specimens previously attributed to the same genus. However, it should be taken into account that, due to the lack of comparable postcranial remains, the attribution

of IPS42724 to *Pierolapithecus* is merely discarded on the basis of the smaller estimated BM of the former. Given the large uncertainty associated to BM estimation (see 95% CI in Table 7, and Ruff, 2003, for further discussion), and the impossibility to evaluate intraspecific body size variation with the currently available material, the attribution of this partial femur to *D. fontani* must remain tentative.

DISCUSSION
Taxonomic and nomenclatural implications

The new facial and dental evidence of *Dryopithecus fontani* discussed in this article shows that this taxon is distinct at the genus level from the Late Miocene European taxa previously attributed to *Dryopithecus*, suggesting that this genus must be restricted to Middle Miocene specimens. Differences in femoral morphology between the ACM specimen and *Hispanopithecus* further suggest that differences are not restricted to the cranium. Considering that the type species of the genus *Dryopithecus* Lartet 1856 is *D. fontani*, the recognition of these two different morphological patterns in the Miocene of Europe raises the question of the generic attribution of the Late Miocene species. For the Late Miocene taxa previously included in *Dryopithecus*, the name *Neopithecus* Abel, 1902 is available; the holotype of the type species, *Neopithecus brancoi* (Schlosser, 1901), is an isolated lower third molar from Salmendingen (Germany). This specimen is currently named as *D. brancoi* and considered conspecific with the abundant material from Rudabánya (Szalay and Delson, 1979; Begun and Kordos, 1993). However, the selection of a type species based on a single lower molar is extremely problematic, especially taking into account the previously unexpected diversity of Miocene European taxa (Moyà-Solà et al., 2004) and the limited information provided by isolated teeth (Begun and Kordos, 1993). This point is illustrated by the claim of some investigators (Andrews et al., 1996) that the Salmendingen tooth might even belong to a pliopithecid, a taxonomic controversy that is still under discussion (Begun et al., 2006).

Whatever the affinities of the Salmendingen specimen finally prove to be, the essential question is whether a single molar with a very limited hypodigm from the same locality (another single lower molar, probably a second one) can be diagnostic of a genus and a species. Given these taxonomic uncertainties and the lack of general agreement about its hominoid affinities, due to the limited diagnostic information provided by the type specimen and associated material, both *Neopithecus* and *N. brancoi* are best considered nomina dubia (see Mones, 1989, for a discussion on this concept). We therefore resurrect *Hispanopithecus* Villalta and Crusafont, 1944 as the genus name for Late Miocene European "*Dryopithecus*." This genus had been formerly considered a junior synonym of *Dryopithecus*, and has priority over *Rudapithecus* Kretzoi, 1969. There have been some previous attempts to resurrect the genus *Hispanopithecus*, albeit with a different meaning, i.e. restricted to the Catalan material (Cameron, 1997). More recently, Almécija et al. (2007) have referred to the material from Can Llobateres as *Hispanopithecus laietanus*, without further justification. In this article, we formally reassign the Spanish Late Miocene taxa to *H. laietanus* Villalta and Crusafont, 1944 and *H. crusafonti* (Begun, 1992) comb. nov. The Hungarian taxon from Rudabánya should be

reassigned to *H. hungaricus* (Kretzoi, 1969) comb. nov., since we do not accept the synonymy (Andrews et al., 1996) of this material with *D. fontani carinthiacus* Mottl, 1957, a taxon considered a junior synonym *of D. fontani* by Begun et al. (2006) and Begun (2007). The latter author (Begun, 2006, 2007) has recently asserted that *Pierolapithecus* is quite similar to *Dryopithecus* s.l., further suggesting that *P. catalaunicus* might be a junior subjective synonym of *D. fontani*. This possibility is contradicted by the new fossil evidence reported in this paper. Begun (2007) further considers that the teeth from La Grive might correspond to *Pierolapithecus*, if not synonymous with *D. fontani*. As already discussed previously in this paper, the evidence available from La Grive, albeit limited, indicates that these teeth cannot belong to the same species than the BCV1 specimen. To sum up, our taxonomic opinion is that two hominoid taxa, distinct at the genus level—*Pierolapithecus* and *Dryopithecus*, have been sampled from Middle Miocene localities, whereas Late Miocene taxa previously assigned to *Dryopithecus* must be reassigned to *Hispanopithecus*.

Phylogenetic inferences

The IPS35026 specimen shows an interesting association of facial features that may help to interpret the phylogenetic relationships of *D. fontani* within the Hominoidea. Thus, on the one hand, *D. fontani* shows a large nasal aperture widest at the base, with the edges of the nasal aperture formed by the maxillae, a wide palate, a moderately high zygomatic root, and a distinctly vertical nasomaxillary suture (NMS). These are clearly derived hominid features indicating that this taxon is a member of the great ape and human clade (Moyà-Solà et al., 2004). On the other hand, *D. fontani* exhibits an assemblage of primitive hominoid characters not present in extant great apes. The maxillary sinus is small and does not penetrate into the zygomatic root, while the zygomatic arch is upwardly inclined and not horizontal (with respect to the alveolar plane) as in the great apes, thus resembling Early Miocene hominoids such as *Afropithecus*. Moreover, as previously discussed, the intrinsic size proportions of the teeth are primitive, resembling *Proconsul* (see Fig. 7). Like all the Miocene Hominidae currently described, *D. fontani* shows a mosaic of derived great ape characters and primitive hominoids features (Rae, 1999).

Furthermore, the lower face of *D. fontani* displays an unusual combination of features of more difficult phylogenetic interpretation that deserves a more detailed analysis. As we stated previously, the anterior nasomaxillary contact is very anteriorly placed, over the P3/. The nasomaxillary suture is thus long and less vertically oriented than the lateral rims of the nasal aperture, shaping a gorilla-like midfacial prognathism. In this pattern, the upper nasal aperture, situated at the level of P3/, closely approaches the posterior pole of the nasoalveolar clivus (NAC). The lower orbital rim is situated high above the tooth row and anteriorly to the zygomatic root (situated over M2/) at the level of the M1/. The multivariate analysis of muzzle shape in IPS35026 as compared to extant and fossil hominoids confirms that, uniquely among fossil great apes and stem hominoids, *D. fontani* most closely resembles gorillas. *D. fontani* further differs from stem hominoids and *Pierolapithecus* by the higher and less posteriorly inclined face (orbits, zygomatic and

nasal aperture) of the former, with an anterior nasomaxillary contact also more anteriorly placed.

Fossil evidence of the initial Middle Miocene great ape radiation is still scarce and fragmentary (Pilbeam, 1996; Moyà-Solà et al., 2004), and considering the pervasive presence of homoplasy in hominoid evolution, it is currently difficult to assess the real phylogenetic signal provided by the *D. fontani* morphological pattern. However, considering that the gorilla-like steep facial pattern of *D. fontani* is absent in stem Miocene hominoids and primitive hominids, the facial pattern of IPS35026 is likely to be derived with respect to these forms. However, considering the limited evidence provided by a lower face, with a relatively minor number of utilizable characters, it is very difficult to provide a robust and conclusive phylogenetic hypothesis. In fact, several alternatives must be considered:

(a) The combination of facial characteristics of *D. fontani* is homoplastic with *Gorilla*.
(b) The facial pattern of *D. fontani* is homologous with *Gorilla* and represents a synapomorphy of the Homininae.
(c) The facial pattern of *D. fontani* is homologous with *Gorilla* but symplesiomorphic for crown hominids.

The latter hypothesis is highly unlikely, since, as stated above, a similar facial configuration is unknown among Lower and Middle Miocene hominoids. Furthermore, as *P. catalaunicus* shows (Moyà-Solà et al., 2004), stem hominids are facially more primitive, retaining an array of stem hominoid features. Thus, *D. fontani* and *Gorilla* lower facial pattern can be hardly considered to represent the primitive hominid condition. This fact indicates that the gorilla-like facial pattern of *D. fontani* is derived relative to stem hominids, but two different alternative phylogenetic hypotheses are possible. The alternative that argues that the facial pattern of *D. fontani* is homologous with that of *Gorilla* might indicate that *D. fontani* would be a stem Homininae. Although the hypothesis that taxa with derived African-great-ape features were present in the European Miocene genera *Hispanopithecus* and *Ouranopithecus* is not new, it has proven to be highly problematic (Begun, 1992b; de Bonis et al., 1990). The characters claimed to support this view, in particular the homology of frontal torus and frontal sinus, the clivus/palate pattern, and the dental morphology of *Hispanopithecus* and *Ouranopithecus* are hotly debated and there is no consensus on their phylogenetic significance (Moyà-Solà and Köhler, 1995; Köhler et al., 2001a,b; Rae and Koppe, 2004; Rossie, 2005).

On the other side, the absence of fossil evidence of apes in the African Late Miocene has been used to indicate that apes were not present in Africa during this period of time, thus supporting an out-of-Africa origin of the Homininae (Stewart and Disotell, 1998; Begun, 2001; Begun et al., 2003, 2006; Begun and Nargolwalla, 2004). However, various authors consider this claim as premature (Moya-Solà et al., 1999; Pilbeam, 2002; Ward and Duren, 2002; Cote, 2004) and suggest that this presumed absence of apes in the Late Miocene of Africa is biased by small sampling sizes, poor preservation or inappropriate habitat sampling (Cote, 2004). The finding of *Kenyapithecus* in Turkey (Kelley et al., 2008) gives plausibility to the dispersal of hominoids from Eurasia to Africa (Andrews and Kelley, 2007), but is consistent with great apes having originated in any of these conti-

nents. Recent findings in Ethiopia (Suwa et al., 2007) and Kenya (Kunimatsu et al., 2007) suggest that putative hominines were present in Africa by 10.5–10 Ma, i.e. earlier than suspected by some advocates of an European origin of this subfamily. These findings strongly support that, as previously suggested (Moya-Solà et al., 1999; Pilbeam, 2002; Ward and Duren, 2002; Cote, 2004), the presumed absence of apes in the Late Miocene of Africa is possibly due a sampling bias (Cote, 2004) and not evidence that the origin of the hominines took place out of Africa in the European continent. Considering this evidence, it is also currently possible (if not probable) that *D. fontani* represents an independent offshoot from stem hominids in the European continent, convergent with the lower facial pattern of gorillas. Unfortunately, with the currently limited evidence provided by the present meager fossil record, it is not possible to choose between these two competing hypothesis. We expect that future discoveries in the Mediterranean region, and particularly in the area of Els Hostalets de Pierola (Catalonia, Spain), may help us to understand the complex and elusive question of the initial radiation of great apes and help to test, based on new and more complete fossils, the phylogenetic meaning of the gorilla-like facial morphology of the seminal taxon *Dryopithecus fontani*.

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