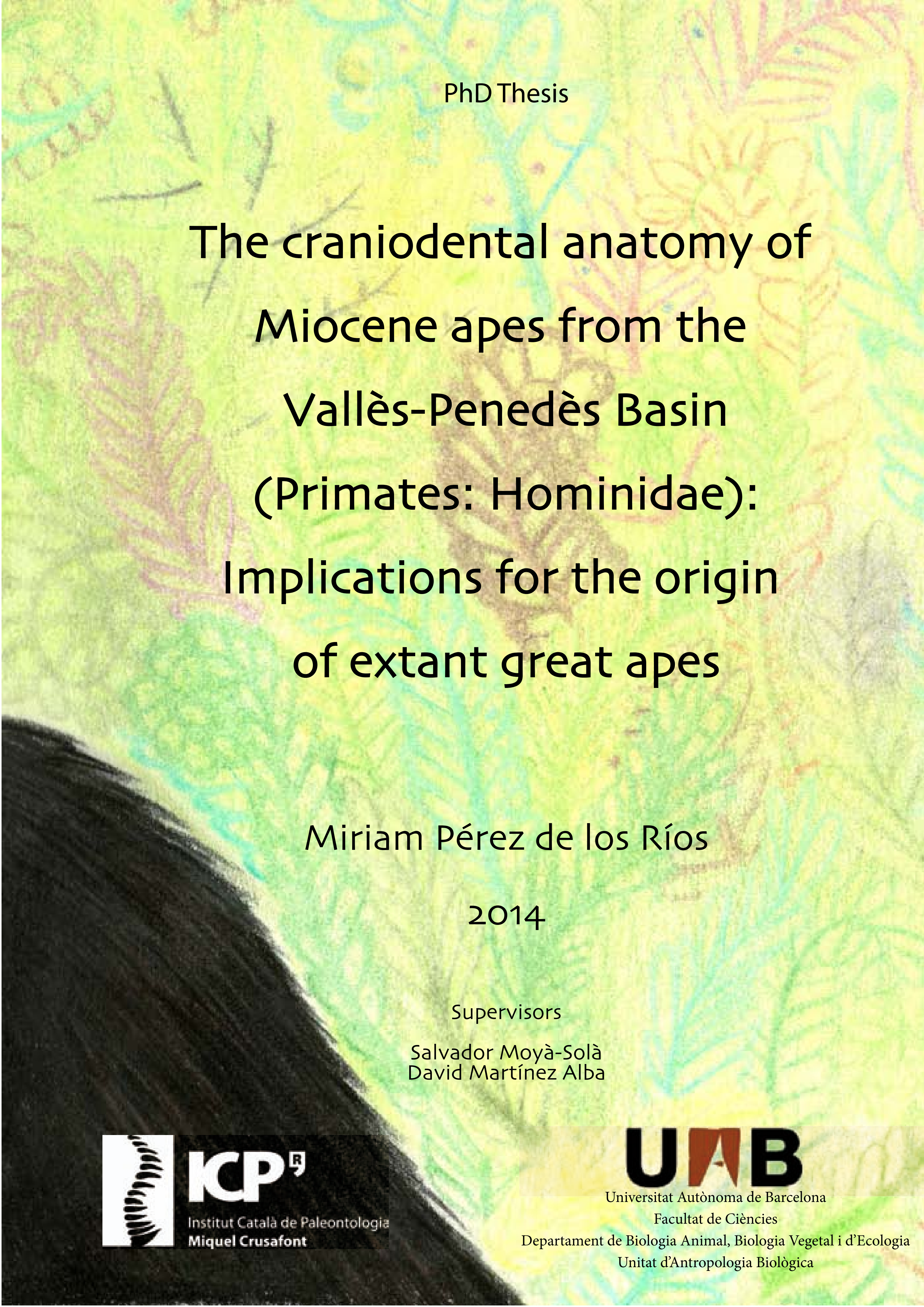

PhD Thesis

The craniodental anatomy of Miocene apes from the Vallès-Penedès Basin (Primates: Hominidae): Implications for the origin of extant great apes

Miriam Pérez de los Ríos

2014

Supervisors

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Memoria presentada por Miriam Pérez de los Ríos para optar al título de Doctor con Mención Internacional por la *Universitat Autònoma de Barcelona*, programa de doctorado en *Biodiversitat* del *Departament de Biologia Animal, Biologia Vegetal i d'Ecologia* (BABVE). Investigación dirigida por el Doctor Salvador Moyà Solà, ICREA en el *Institut Català de Paleontologia Miquel Crusafont* y en la *Unitat d'Antropologia Biològica* del BABVE en la *Universitat Autònoma de Barcelona*, y por el Doctor David Martínez Alba, investigador Ramón y Cajal en el *Institut Català de Paleontologia Miquel Crusafont* en la *Universitat Autònoma de Barcelona*.

Doctoranda
Miriam Pérez de los Ríos

Directores
Salvador Moyà Solà **David Martínez Alba**

El hombre es enemigo de lo que ignora

La paciencia es la llave de la solución

Proverbios árabes

A mi familia, por apoyarme en cada paso del camino

A Stefano, por recorrerlo a mi lado

Chapter 3. New dental remains of *Anoiapithecus* and the first appearance datum of hominoids in the Iberian Peninsula 161

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CHAPTER 1

Introduction

Aims and structure of this dissertation

This dissertation is devoted to the study of the craniodental remains of Miocene hominoids. Hominoids are an extant group of primates (superfamily Hominoidea) including humans and its closest relatives, the apes. In particular, the dissertation is focused on the hominoid remains from the Vallès-Penedès Basin (NE Iberian Peninsula), which are customarily included in the Dryopithecinae (or dryopithecines). The latter are an extinct subfamily of putative stem hominids from the Middle to Late Miocene of Europe, represented by two subfamilies: Dryopithecini and Hispanopithecini. The need to carry out this work is justified by the abundant and remarkably complete cranial dryopithecine remains recovered during the last decade in the Vallès-Penedès Basin, which at the beginning of this dissertation project were still unpublished or had not yet been described in detail in the literature. This study has, as a first goal, to contribute to the clarification of the taxonomy of dryopithecines. The second objective is to compare the dryopithecine cranial morphology with both extant and extinct hominoids from elsewhere in Europe, Africa and Asia, in order to explore the phylogenetic and paleobiological implications of the investigated material. Although no formal cladistic analysis is performed, the descriptions accomplished in this work provide a firm basis for developing such phylogenetic analyses in the future.

This work can be subdivided into several more specific goals, corresponding to the various chapters that constitute the main body of this dissertation:

1. Chapter 2: Detailed description of the external morphology of the skull (cranial and mandibular) remains of dryopithecines from the Vallès-Pendès Basin and nearby areas (Seu d'Urgell Basin), and comparison with those of other hominoids (with particular emphasis on extinct taxa from both Africa and Eurasia), in order to evaluate contrasting taxonomic schemes and phylogenetic hypotheses.

2. Chapter 3: Description of the oldest hominoid remains from the Iberian Peninsula, and discussion about their taxonomic allocation, with the aid of non-invasive technologies based on CT scans.

3. Chapter 4: Description of the internal morphology of the holotype cranium of

Pierolapithecus catalaunicus with the aid of CT scans, with emphasis on the study of the morphology of paranasal sinuses, in order to enlighten the phylogenetic affinities of this taxon with other hominoids.

4. Chapter 5: Re-evaluation of the taxonomic affinities of the dryopithecine dental remains from the French site of La Grive, in the light of the evidence provided by the finds from the Vallès-Penedès Basin, and discussion of the implications for their taxonomy.

Besides these chapters, this dissertation includes an Introduction (Chapter 1) and two final chapters of Discussion and Conclusions. The Introduction provides the necessary background on the systematics, craniomandibular anatomy and evolutionary history of hominoids (with emphasis on dryopithecines), and further summarizes the material and general methods employed in this dissertation. The Discussion (Chapter 6) and the Conclusions (Chapter 7) discuss the results reported in the preceding chapters, and which further summarizes the main conclusions of this dissertation. The work ends with a list of References cited in Chapters 1, 6 and 7, since Chapters 2 to 5 have references lists on their own. Chapters 3 to 5 correspond to papers published in journals, whereas the Chapter 2 corresponds to an unpublished manuscript submitted to be published as a book chapter.

Hominoids

Content and systematics

The superfamily Hominoidea Gray, 1825 constitutes a clade of catarrhine primates that includes the extant lesser apes (family Hylobatidae Gray, 1870) as well as the great apes and humans (family Hominidae Gray, 1825), together with their extinct relatives that are more closely related to them than to the hominoid's sister-taxon, the Old World monkeys (superfamily Cercopithecoidea Gray, 1821; see Table 1.1). As defined here, the Hominoidea include the total group, i.e., not only crown hominoids, but also the members of their stem lineage. Thus, the clade constituted by crown hominoids includes all of the extant hominoids as well as those extinct taxa that are more closely related to either hylobatids or hominids. In contrast, stem hominoids are a paraphyletic array of extinct taxa that precede the hylobatid-hominid split, and which are consequently equally related to both hylobatids and hominids. These cladistic concepts of crown group and stem lineage are most useful for discussing the phylogenetic affinities of extinct taxa, being customarily applied not only to hominoids, but also to hominoid subclades (e.g., stem Hominidae vs. crown Hominidae).

Table 1.1. Classification of extant and extinct hominoids to the genus rank. Extinct taxa are denoted with a dagger (†). Vallès-Penedès taxa are in bold type. Modified from Alba (2012a: Table 2), and further incorporating new data from Stevens et al. (2013), Kelley and Gao (2012) and Ji et al. (2013).

- Superfamily incertae sedis
    - Genus *Kamoyapithecus*†
    - Family Dendropithecidae†
        - Genus *Dendropithecus*†
        - Genus *Kamoyapithecus*†
    - Family Dendropithecidae†
        - Genus *Dendropithecus*†
        - Genus *Micropithecus*†
        - Genus *Simiolus*†
- Superfamily **Hominoidea**
    - Family Proconsulidae†
        - Subfamily Proconsulinae†
            - Genus *Proconsul*†
        - Subfamily Nyanzapithecinae†
            - Genus *Nyanzapithecus*†
            - Genus *Mabokopithecus*†
            - Genus *Rangwapithecus*†
            - Genus *Turkanapithecus*†
            - Genus *Xenopithecus*†
            - Genus *Rukwapithecus*†
        - Subfamily incertae sedis
            - Genus *Samburupithecus*†
    - Family Afropithecidae†
        - Subfamily Afropithecinae†
            - Genus *Afropithecus*†
            - Genus *Morotopithecus*†

- Genus *Heliopithecus*†
- Subfamily incertae sedis
  - Genus *Otavipithecus*†
- Family Hylobatidae
  - Genus *Hylobates*
  - Genus *Symphalangus*
  - Genus *Nomascus*
  - Genus *Hoolock*
- Family **Hominidae**
  - Subfamily Kenyapithecinae†
    - Tribe Equatorini†
      - Genus *Equatorius*†
      - Genus *Nacholapithecus*†
    - Tribe Kenyapithecini†
      - Genus *Kenyapithecus*†
      - Genus*Griphopithecus*†
  - Subfamily **Dryopithecinae**†
    - Tribe **Dryopithecini**†
      - Genus ***Dryopithecus***†
        - **[*Dryopithecus fontani*†]**
      - Genus ***Pierolapithecus***†
        - **[*Pierolapithecus catalaunicus*†]**
      - Genus ***Anoiapithecus***†
        - **[*Anoiapithecus brevirostris*†]**
      - Genus **incertae sedis**
        - **[“*Sivapithecus*” *occidentalis*† nomen dubium]**
    - Tribe **Hispanopithecini**†
      - Genus ***Hispanopithecus***†
        - **[*Hispanopithecus* (*Hispanopithecus*) *laietanus*†]**
        - **[*Hispanopithecus* (*Hispanopithecus*) *crusafonti*†]**
        - **[*Hispanopithecus* (*Rudapithecus*) *hungaricus*†]**
    - Tribe Ouranopithecini†
      - Genus *Ouranopithecus*†
    - Tribe incertae sedis
      - Genus ?*Udabnopithecus*†
  - Subfamily Ponginae
    - Tribe Sugrivapithecini†
      - Genus *Sivapithecus*†
      - Genus *Ankarapithecus*†

        - Genus *Indopithecus*†
        - Genus *Gigantopithecus*†
    - Tribe Pongini
        - Genus *Pongo*
        - Genus *Khoratpithecus*†
- Subfamily Homininae
    - Tribe Gorillini
        - Genus *Gorilla*
    - Tribe Panini
        - Genus *Pan*
    - Tribe Hominini
        - Genus *Homo*
        - Genus *Australopithecus*†
        - Genus *Paranthropus*†
        - Genus *Ardipithecus*†
        - Genus *Orrorin*†
    - Tribe incertae sedis
        - Genus *Nakalipithecus*†
        - Genus *Chororapithecus*†
        - Genus *Sahelanthropus*†
- Subfamily incertae sedis
    - Tribe Lufengpithecini†
        - Genus *Lufengpithecus*†
    - Tribe Oreopithecini†
        - Genus *Oreopithecus*†

Currently, hominoids exhibit a relatively restricted diversity and geographic distribution, since only eight different genera are distinguished. In particular, they include four hylobatid genera from Southeastern Asia (*Hylobates* Illiger, 1811; *Symphalangus* Gloger, 1841; *Hoolock* Mootnick and Groves, 2005; and *Nomascus* Miller, 1933), as well as four hominid genera, one from Asia (*Pongo* Lacépède, 1799), two from Africa (*Pan* Oken, 1816; *Gorilla* I. Geoffroy Saint-Hilaire, 1852) and *Homo* Linnaeus, 1758 worlwide (Mootnick and Groves 2005; Mittermeier et al., 2013). In the past, however, hominoids were much more diverse (Table 1.1) and widely distributed throughout Africa and Eurasia, since their emergence (probably in the Late Oligocene) and subsequent radiation in the Early Miocene of Africa and the Middle to Late Miocene of

Eurasia (Begun 2002a, 2007, 2010; Kelley 2002; Harrison 2002, 2010; Ward and Duren 2002; Alba 2012a,b). Taken overall, extinct hominoids displayed a greater morphological disparity, a higher taxonomic diversity, and a wider range of locomotor behaviors and dietary preferences than their extant counterparts. Following Alba (2012a), putative stem hominoids are here included into two distinct extinct families (Proconsulidae L.B.S. Leakey, 1963 and Afropithecidae Andrews, 1992; Table 1.1), although there are other alternative taxonomic schemes available from the literature (Harrison 2002, 2010; Begun et al. 2010, 2013; Zalmout et al. 2010).

Anatomy of crown hominoids

Extant hominoids differ from its closest living relatives, the Old World monkeys (cercopithecoids), by numerous cranial and postcranial features (e.g., see Fleagle 2013), which are summarized below.

Postcranial body plan. The postcranium of extant hominoids is characterized by an orthograde ('upright') body plan, which provides increased mobility to the limbs and is suitable for performing orthograde (or antipronograde; Stern 1975) positional behaviors (which are characterized by vertical trunk positions and the frequent use of the forelimbs under tension). This orthograde body plan contrasts with the pronograde body plan of most other primates and mammals (Benton 1974; Ward 1993, 2007; Moyà-Solà and Köhler 1996; Larson 1998), in which the limbs are restricted to parasagittal movements and the spine is much more flexible, being most suitable for quadrupedalism along (sub)horizontal supports, with the trunk held horizontally and the limbs being under compression.

Orthogrady-related features are reflected in both the axial skeleton (ribs and vertebrae) and the appendicular skeleton (limbs and girdles), as previously noted by many authors (Keith 1903, 1923; Aiello and Dean 1996; Madar et al. 2002; Sarmiento et al. 2002; Moyà-Solà et al. 2004; Ward 2007; Alba et al. 2012a; Fleagle 2013; Almécija et al. 2013; Susanna et al., 2014). Thus, in extant hominoids the thorax (ribcage) is craniocaudally short, mediolaterally broad and dorsoventrally shallow, due to the marked curvature of ribs. The scapulae are dorsally situated (with a long and wide acromion process and a more lateral and cranially positioned glenoid fossa) and the clavicles are long and robust. The vertical column is relatively short and ventrally situated with respect to the ribcage, and not very flexible, with a particularly short and stiff lumbar region, and the tail being reduced to a few fused internal vertebrae (coccyx). In accordance to the thorax, the pelvis (hipbone) is broad, with expanded and dorsally-rotated iliac blades. The forelimbs (expecially the forearms and hands) are longer than the hind limbs (except in humans), resulting in high intermembral indices. Due to the dorsal position of the scapula, the humeral head is torsioned. In turn, the elbow joint is characterized by several features (such a reduced olecranon) enabling high ranges of pronation/supination while providing stability, whereas the lack of ulnocarpal articulation provides an increased range of ulnar deviation at the wrist. The femur is characterized by a spherical head and a highly angled neck, enabling a wide degree of mobility at the hip joint. Among the above-mentioned features, taillessness (i.e., the lack of an external tail) is the first one to be recorded in the hominoid fossil record (Ward et al. 1991; Nakatsukasa et al. 2003, 2004), being associated to a pronograde body plan and thus suggesting that this condition is not necessarily associated to orthogrady.

In spite of sharing an orthograde body plan, extant hominoid taxa differ from one another in the frequency and types of practiced positional (postural and locomotor) behaviors (Hunt 2004), having in common both vertical climbing and below-branch suspension (with the exception of humans, which are almost obligated bipeds). Orthogrady has been therefore variously interpreted as an adaptation to all forelimb-dominated arboral behaviors (Ward 1993), to suspensory behaviors only (Gebo 1996), or to slow and cautious climbing and clambering (Cartmill and Milton 1977; Cartmill 1985; Sarmiento 1995). Based on the information provided by the fossil record, including some of the dryopithecines investigated in this dissertation (Moyà-Solà and Köhler 1996; Moyà-Solà et al. 2004; Almécija et al. 2009; Alba et al. 2010, 2012a), it has been suggested that the body plan of the last common ancestor of extant hominoids would have been probably more primitive than inferred based on the living forms alone, by lacking suspensory adaptations and displaying instead powerful-grasping capabilities for above-branch quadrupedalism. Powerful-grasping capabilities are probably related to the need to maintain balance in a relatively large, tailless, and quadrupedal arboreal primate with climbing but no suspensory adaptations (Sarmiento 1995; Kelley 1997; Ward 2007; Almécija et al. 2009; Alba et al. 2010, 2012a). In turn, vertical climbing would have probably been the main target of selection favoring the evolution of orthogrady, with suspensory adaptations having evolved independently several times in various hominoid lineages

(Larson 1998; Moyà-Solà et al. 2004; Alba 2012a). In particular, from tailless and climbing-adapted ancestors, suspension might have evolved as a more efficient way of traveling when body mass surpassed a particular threshold, with orthograde adaptations originally evolved as adaptations to climbing being subsequently co-opted for suspension (Cartmill 1985).

Cranial morphology. The most disctinctive cranial features of extant hominoids include the flat nasals, the deep palate, the projecting nasals, the high nasoalveolar clivus, the high zygomatic root, the lack of subarcuate fossa, the premaxillary suture that does not contact the nasals, the non-projecting interorbital region and the relative wide anterior palate (Rae 1999; Shea 2013). Among extant hominoids, hylobatids are characterized by the following features (Fleagle 2013; Shea 2013): shallow palate; short face with marked midfacial prognathism; moderately high nasoalveolar clivus; moderately wide nasal aperture wider at midheigth; extensive maxillary sinus; absence of frontal sinus; open palatine fenestra with two incisive foramina; shallow subarcuate fossa; and a broad interorbital pillar. In turn, extant hominids are characterized by the following features (Moyà-Solà et al. 2004; Fleagle 2013; Shea 2013): relatively short face with a high midface; extensive maxillary sinus; frontal processes of the maxillae, nasals and orbits in the same plane; high zygomatic root; high nasoalveolar clivus; deep palate; robust premaxilla; nasals projecting anteriorly beneath the level of the inferior orbital rims; absence of subarcuate fossa; wide nasal aperture widest at the base; closed palatine fenestra due to some degree of overlap between the premaxilla and the hard palate, resulting in an incisive canal that links the palate to the nasal cavity.

Biology of crown hominoids

Distribution and habitat. With the exception of modern humans, which are cosmopolitan and can inhabit almost any habitat on Earth thanks to the possession of culture and technology, extant hominoids are currently restricted to tropical areas of Africa and Southeastern Asia. The dozen or so species of hylobatids are distributed through southern China, Thailand, Cambodia, Myanmar and Malaysia (including the islands of Sumatra and Borneo). In contrast, orangutans are currently absent from mainland Asia, being restricted to Sumatra and Borneo. African great apes, in turn, are distributed exclusively through Equatorial Africa. The two species of gorillas occupy different areas of Central Africa, whereas chimpanzees are distributed throughout Eastern and Central Africa, and bonobos are restricted to Central Africa south of the Congo River.

All the living apes preferentially live in primary and/or secondary rain forests, and are to some degree arboreal. Both hylobatids and orangutans live in primary rain forests and usually do not descend to the ground (except for large male orangutans). African apes, in contrast, have a wider range of tolerance to different environmental conditions, thereby not being restricted to primary rain forests, but also occupying secondary forests, bamboo forests, and even grasslands and savannah, depending on each particular species.

Positional behavior. From the viewpoint of positional behaviors (posture and locomotion), the orthograde body plan allows for very versatile movements, as shown by the diversity of locomotor modes displayed by extant hominoids. The arboreal and moderately-sized hylobatids frequently employ vertical climbing as well as suspensory behaviors (for feeding and horizontal travel). Suspension in gibbons is very acrobatic and displays a phase of free flight (ricochetal brachiation), and they are also capable of leaping to cross discontinuities in the canopy. The similarly-arboreal, but larger-bodied, orangutans also employ vertical climbing and suspensory behaviors, but the latter are less acrobatic than in gibbons, and further include quadrumanous suspension. In orangutans, canopy and discontinuities are frequently solved by means of deliberate clambering and bridging behaviors, since they do not leap. Only rarely they move quadrupedally over branches, or over the ground in the case of large males or in captivity (Tuttle 1969).

Unlike the Asian apes, African apes are semiterrestrial, by combining arboreal locomotion (for feeding and nesting) with terrestrial locomotion for traveling. When on the ground, African apes employ a specialized type of quadrupedal locomotion known as knucke-walking, in which body weight is supported by the dorsal aspect of the middle phalanges, which displays specialized skin pads as an adaptation. When on the canopy, chimpanzees and bonobos may employ vertical climbing and below-branch suspensory behaviors (arm-swinging), although depending on the support diameter they may alternatively use knuckle-walking or palmigrady. Gorillas are more terrestrial than chimpanzees, so that their climbing and suspensory behaviors and less acrobatic and mostly restricted to juvenile and female individuals.

Humans, unlike other hominoids, are commited bipeds, although facultatively they can practice other types of locomotion, in the same way that apes can be facultatively bipedal. Gibbons and orangutans, in fact, practice to some extent arboreal bipedalism, although it frequently assited by their forelimbs (Thorpe and Crompton 2005; Crompton et al. 2010; Chivers et al. 2013). African apes can be also facultatively bipedal on the ground during short locomotor bouts, especially for display or when a hand is used for manipulation or other locomotor tasks. Unlike Asian apes and humans, however, African apes cannot fully extend the knee joint (Crompton et al. 2010; Fleagle 2013), which coupled with the lack of bipedal adaptations precludes a more frequent use of bipedal postures and locomotion in these taxa. Only humans, in any case, are capable of bipedal running, which involves a phase in which none of the two hind limbs contacts the ground.

Diet. From a dietary viewpoint, extant apes have a general preference for ripe fruit, although there are significant differences in dietary preferences between the various species (ranging from folivory to frugivory to omnivory), all of which consume a wide array of different food items. Siamangs tend to be more folivorous than the smaller-bodied gibbons, whereas, among great apes, gorillas are the most folivorous. Both orangutans and chimpanzees are generally considered frugivorous, by displaying a preference for soft and ripe fruit, although in fact orangutans habitually consume hard food items (such as nuts and unripe fruit) more habitually than other apes, especially as fallback foods. Chimpanzees and bonobos are essentially soft-frugivores, although they tend to consume leaves or herbaceous vegetation as fallback foods (when soft fruits are not available), and they further complement their diet with other food items (sporadically including animal prey). Humans, finally, consume a high variety of food items and habitually consume meat, thus being best considered omnivores.

Body size, life history and cognition. Extant hominoids differ from other primates by displaying a slow life-history profile, the latter including aspects related to the maximization of reproductive effort in relation to the timing of sexual and somatic maturation. Body size is one of the most fundamental life-history variables, and considerable differences can be found between hylobatids (with a medium body size for primate standards between 5-12 kg) and the much larger great apes and humans (ranging from about 35-40 kg in chimpanzees to more than 200 kg in male gorillas).

However, even when scaling effects are removed, it is clear that life history is slower in all hominoids compared to the remaining primates, although this is more accentuated in great apes and, especially, humans than in hylobatids. This is reflected in relatively longer gestation periods, as well as later ages of weaning and attainment of sexual maturation, among others, which imply an intensive parental care of the immature descendants. The slow life history profile of extant hominoids is generally related to their higher cognitive capacities (especially in great apes and humans) compared to other primates, which in turn depend to a large extent on their larger brain size relative to body size, or encephalization (Alba 2010). In the latter regard, hylobatids are essentially comparable to monkeys, whereas all great apes are more encephalized than both monkeys and hylobatids, although less than humans.

Sociosexual behavior and sexual dimorphism. Hominoids are diurnal primates with a wide range of social organization and sociosexual behaviors, which in turn are related to different patterns of sexual dimorphism. Leaving the complex human societies apart, the social organization of great apes is generally characterized by lack of philopatry, and fission-fusion groups are common in many species (Fleagle 2013). Hylobatids live in monogamous pairs that lack a definite breeding season and constitute small nuclear families. In relation to this, they display almost no body size or dental sexual dimorphism, although some species show sexual dichromatism. Great apes and humans are more sexually dimorphic than hylobatids, with males tending to be larger and display better-developed canines than females. Such sexual dimorphism is more accentuated in the larger species (gorillas and orangutans, in which males are about twice the body size of females), and less so in the smaller species (especially, bonobos and humans). This must be related to differences in sociosocial structure as well as patterns of agonistic behavior. In orangutans, the males are generally solitary and overlap in range with several females, which live with their immature offpring, although males lacking a territory display an arrested development of secondary sexual features. Gorillas live in relatively small groups with one or a few alfa male(s), a higher number of females, and their offspring. The lesser degrees of body size and canine sexual dimorphism in chimpanzees would be related to the fact that they live in larger fission-fusion groups of multiple males and females, whereas bonobos have a similar social organization but display important differences in sexual and agonistic behaviors.

Dryopithecines and other extinct hominoids

The hominoid fossil record

Possible oldest hominoids and other early catarrhines. The oldest putative stem catarrhine is the genus *Saadanius* Zalmout et al., 2010, based on a partial cranium from the Late Oligocene of Saudi Arabia (Zalmout et al. 2010). This taxon displays some primitive cranial features shared with the early stem catarrhine *Aegyptopithecus* from the Oligocene of Egypt (Simons et al. 2007), such as the non-protuding glabella, the anterior position of bregma or the long and concave nasal bones (Zalmout et al. 2010). However, *Saadanius* also displays some derived features of crown catarrhines (cercopithecoids and hominoids; Leakey et al. 1988; Teaford et al. 1988; Begun 2001), in particular, the presence of atrioturbinals and the tubular and fused ectotympanic (Zalmout et al. 2010; Harrison 2013).

The representatives of family Dendropithecidae Harrison, 2002, including at least the genera *Dendropithecus* Andrews and Simons, 1977, *Micropithecus* Fleagle and Simons, 1978 and *Simiolus* R.E. Leakey and M.G. Leakey, 1987, have been also considered stem catarrhines by some authors (Harrison 1987, 2002, 2005, 2010, 2013; Rose 1997; Stevens et al. 2013). Alternatively, other authors have recently considered them to be more closely related to hominoids than to cercopithecoids (Kelley 1997; Rae 1997, 1999, 2004; Zalmout et al. 2010). During the mid 20th century, these extinct small catarrhines were considered to be early representatives of the Hylobatidae (Leakey 1946; Le Gros Clark 1949; Le Gros Clark and Leakey 1950,1951; Andrews 1978). However, during the 1980s it was already recognized that these taxa were too primitive to be direct ancestors of gibbons (e.g., Fleagle 1984), being currently considered stem catarrhines by most researchers (e.g., Harrison 2010). Harrison (1982), in particular, suggested that *Dendropithecus* was more derived than pliopithecoids, so that the former genus should be considered as the most derived sister group of extant catarrhines. The absence of complete cranial remains makes the phylogenetic status of dendropithecids difficult to assess, although the loss of the entepicondylar foramen in the distal humerus is a clearly derived catarrhine feature already present in dendropithecids (Harrison 1987). Moreover, some studies (Rae 1999) have considered dendropithecids as members of the Hominoidea, as the former display some hominoid putative derived characters. The same applies to other small-bodied catarrhines from the Late Oligocene-Early Miocene of East Africa, such as *Limnopithecus* Hopwood, 1933 and *Lomorupithecus* Rossie and MacLatchy, 2006, which might be dendropithecids as well (Harrison 2010)—*Lomorupithecus* was originally suggested to be a pliopithecoid (Rossie and MacLatchy 2006), but this has been refuted by other authors (Harrison 2010; Pickford et al. 2010).

Another putative hominoid, *Kamoyapithecus* Leakey et al., 1995 from the Late Oligocene of Kenya, has been considered either a basal hominoid (Leakey et al. 1995) or a stem catarrhine (Harrison 2002, 2010; Harrison and Andrews 2009; Stevens et al. 2013). Only part of two right maxillae and a left mandibular body fragment with two isolated teeth have been recovered (Leakey et al. 1995). *Kamoyapithecus* retains some primitive stem catarrhine dental features shared with propliopithecoids, such as among others the short stout canines and the broad upper molars with strong flare (Harrison and Gu 1999), indicating that it might be the sister taxon of dendropithecids plus crown catarrhines (Harrison 2010). *Kamoyapithecus* represents the oldest known catarrhine from the East African fossil record, together with the presumed hominoid *Rukwapithecus* Stevens et al., 2013 and the putative cercopithecoid *Nsungwepithecus* Stevens et al., 2013 from the Oligocene of Tanzania, which unfortunately are known based on scarce dental remains (Stevens et al. 2013).

Systematics of the hominoid total group. As stated above, the superfamily Hominoidea is here understood as including not only crown hominoids, but also their stem lineage. Thus, in the systematic scheme adopted here, four hominoid families are distinguished: two extinct ones, Proconsulidae L.S.B. Leakey, 1963 and Afropithecidae Andrews, 1992, for putative stem hominoids; and two extant ones, Hylobatidae and Hominidae, for crown hominoids.

Of course, alternative taxonomic schemes can be found in the literature. Thus, Harrison (2010) removed proconsulids and afropithecids from the Hominoidea and classified them into a separate superfamily Proconsuloidea. This, however, is due to Harrison's (2010) view that proconsulids and afropithecids are stem catarrhines instead of stem hominoids, so that his scheme is not followed here. Another different proposal is that by Begun (2001, 2005), who informally distinguished the Eohominoidea and the Euhominoidea, to refer to stem and crown hominoids, respectively. Following Moyà-Solà et al. (2009a), however, it is here considered that these groups are unnecessary, especially because the concepts of stem lineage and crown group have a long tradition and are much more easily understandable. Subsequently, Begun (2007, 2013) distinguished two distinct superfamilies (Proconsuloidea and Hominoidea) within the 'magnafamily' Hominidea BEGUN, 2007, which would be equivalent to superfamily Hominoidea as customarily conceived. Again, however, this distinction seems rather unnecessary, for the "Hominidea" are equivalent to the total group Hominoidea, and additing the rank of magnafamily merely complicates the systematics of the group.

Stem hominoids. Proconsulids and afropithecids are restricted to the Early and Middle Miocene of Afro-Arabia (Harrison 2002, 2010). Two subfamilies are distinguished within the Proconsulidae: Proconsulinae L.S.B. LEAKEY, 1963 (including only the polytypic genus *Proconsul* HOPWOOD, 1933) and Nyanzapithecinae HARRISON, 2002 (including the genera *Nyanzapithecus* HARRISON, 1986, *Mabokopithecus* VON KOENIGSWALD, 1969, *Rangwapithecus* ANDREWS, 1974, *Turkanapithecus* R.E. LEAKEY AND M.G. LEAKEY, 1986a, *Xenopithecus* HOPWOOD, 1933 and *Rukwapithecus* STEVENS ET AL., 2013). With regard to the Afropithecidae ANDREWS, 1992, as conceived here they only comprise the nominotypical subfamily (Afropithecinae ANDREWS, 1992), represented by three genera: *Afropithecus* R.E. LEAKEY AND M.G. LEAKEY, 1986b, *Morotopithecus* GEBO ET AL., 1997 and *Heliopithecus* ANDREWS AND MARTIN, 1987. These taxa are customarily considered stem hominoids by most researchers (e.g., Rose 1983, 1997; Andrews 1992; Kelley 1997; Rae 1997, 1999; Ward 1997; Begun et al. 1997; Singleton 2000; M oyà-Solà et al. 2004, 2009a; Alba 2012a; Begun 2012), although other authors have considered them to be crown hominoids (Ward et al. 1991; Kelley 1997) or even stem catarrhines (Harrison 1987, 1988, 1993, 2002; Walker 1997; Harrison and Rook 1997, Harrison and Gu 1999). The content of this family therefore varies among authors, since the genera *Nacholapithecus* ISHIDA ET AL., 1999 and *Equatorius* S.C. WARD et al., 1999 are considered afropithecids by some (Ward and Duren 2002; Moyà-Solà et al. 2009a,b; Harrison 2010) but not all (S.C. Ward et al. 1999; Cameron 2004; Nakatsukasa and Kunimatsu 2009; Alba 2012a; Alba et al. 2012a) authors.

Most critical regarding the phylogenetic position of afropithecids is *Morotopithecus*, which has been considered a junior subjective synomym of *Afropithecus* by some authors (Pickford 2002; Harrison 2010), a stem hominoid of the (sub)family Afropithecidae (Harrison 2005), or even a stem hominid (Young and MacLatchy 2004), given the possession of several orthograde features that, if homologous, would link it to crown hominoids (Ward 1993; Sanders and Bodenbender 1994; Gebo et al. 1997; MactLatchy et al. 2000). *Morotopithecus* displays several postcranial hominoid synapomorphies with an orthogradry (MacLatchy 2004; Ward 2007), although other authors (Harrison 2010; Alba 2012a) further argue that the orthogrady of *Morotopithecus* has evolved in parallel with that of hominoids, and the dental similarities with afropithecids are enough to consider *Morotopithecus* a stem hominoid rather than a stem hominid. The primitive cranial morphology of proconsulids and afropithecids, lacking hominid derived features, supports a stem hominoid status for *Morotopithecus*. The members of these two families display several hominoid cranial synapomorphies, such as the lower location of contact of the premaxillary suture in the nasal cavity, the flat nasals with a sligth projection below the orbital margins, the relatively wide anterior palate, and the high nasoalveolar clivus (Rae 1999). Postcranially, *Proconsul* and *Nacholapithecus* are already characterized by the lack of external tail (Corruccini et al. 1976; C.V. Ward et al. 1999; Nakatsukasa et al. 2003, 2004), thereby suggesting that this was one of the earliest crown-hominoid synapomorphies to evolve (Kelley 1997).

The phylogenetic relationships of *Otavipithecus* Conroy et al., 1992 and *Samburupithecus* Ishida and Pickford, 1997 are still under discussion due to the scarcity of material. *Otavipithecus*, from the Middle Miocene of Namibia, is only represented by a mandibular (symphyseal) fragment, a partial frontal, an atlas, a phalanx and an ulna (Pickford 1982; Conroy et al 1992; Pickford et al. 1997). This taxon been variously interpreted as a close relative of *Afropithecus* (Andrews 1992; Singleton 1998, 2000; Harrison 2010), or as a stem hominid sister taxon of extant great apes and humans (Conroy 1994; Pickford et al. 1994), the former alternative being favored here based on dental and mandibular features. Regarding *Samburupithecus*, only a left palate fragment with premaxilla and maxilla is preserved (Ishida and Pickford 1997). This taxon has been considered a member of the African ape and human clade (Ishida et al. 1984), a stem hominid (Ward and Duren 2002), or a late surviving stem hominoid (probably proconsulid) (Begun 2001; Harrison 2010). The latter view is favored here due to the primitive features shared between *Samburupithecus* and proconsulids, coupled with the lack of clear derived hominid features in the former.

Hylobatids. With regard to crown hominoids, the fossil record of hylobatids, currently restricted to Southeastern mainland Asia and the islands of Sumatra, Borneo and Java (Chivers et al. 2013), is very scarce. The oldest putative fossil hylobatid remains are those of *Yuanmoupithecus xiaoyuan* Pan, 2006, from the Late Miocene of the Yuanmou Basin of China (Pan 2006; Harrison et al. 2008; Fleagle 2013). This species was initially related with *Micropithecus* and *Limnopithecus* (Pan 2006), but subsequently Harrison et al. (2008) noted its hylobatid affinities based on dental similarities. Unfortunately, these are the only Miocene remains currently attributable to hylobatids.

Also noteworthy are the more recent fossil hylobatid remains of *Bunopithecus sericus* Matthew and Granger, 1923, a species based on a mandibular fragment with attached M_2-M_3 from the Middle Pleistocene of Sichuan, in China (Matthew and Granger 1923, Mootnick and Groves 2005). After its description, this taxon was considered a subspecies of the hoolock gibbon (Groves 1967, 1972), by then included in genus *Hylobates* s.l., so that *Bunopithecus* Matthew and Granger, 1923 was widely employed for the hoolock gibbon, i.e., *Hylobates* (*Bunopithecus*) *hoolock* Harlan, 1834 (e.g., Prouty et al. 1983). Most recently, however, the holotype of *Bunopithecus sericus* was considered to be out of the range of variation of extant hylobatids (Mootnick and Groves 2005). This taxonomic problem was corrected by Mootnick and Groves (2005), who erected a new genus (*Hoolock* Mootnick and Groves, 2005) for the two extant species currently distinguished of hoolock gibbons. Fossil *Hylobates* sp. have been identified in the Pliocene of China (Wu and Poirier 1995), as well as from the Pleistocene of Sumatra, Java and Borneo (Hooijer 1960; Gu 1989; Tyler 1993; Chatterjee 2009; Jablonski and Chaplin 2009), Vietnam (Long et al. 1996) and Southern China (Gu 1989).

Putative stem hominids. Hominids display a much better fossil record than hylobatids, although there are controversies regarding what taxa must be considered stem hominids instead of stem hominoids. This is the case of the taxa included here in the subfamily Kenyapithecinae Andrews, 1992, from the Middle Miocene of Africa and Eurasia, which have been variously considered afropithecids (Andrews 1992; Begun 2002a; Kelley 2002; Ward and Duren 2002; Moyà-Solà et al. 2009a,b; Harrison 2010; Fleage 2013) or as the basal-most members of the Hominidae

(Pickford 1986; Harrison 2002; Begun et al. 2010; Alba 2012a). Two tribes are distinguished here among kenyapithecines: the Equatorini Cameron, 2004 and the Kenyapithecini Andrews, 1992. Equatorins, which include the genera *Equatorius* S.C.Ward et al., 1999 and *Nacholapithecus* Ishida et al., 1999, from the Middle Miocene of Africa, retain more primitive features than the kenyapithecins (Ward et al. 1999; Ward and Duren 2002; Harrison 2010), especially in the case of *Equatorius*, since *Nacholapithecus* apparently displays a more derived subnasal morphology (Nakatsukasa and Kunimatsu 2009). The Middle Miocene kenyapithecins, in turn, include the earliest hominoids from Eurasia, represented by the genera *Griphopithecus* Abel, 1902 and *Kenyapithecus* L.S.B. Leakey, 1962, the latter recorded both in Africa and Turkey (Alpagut et al. 1990; Martin and Andrews 1993; Begun 2002; Ward and Duren 2002; Kelley et al. 2008; Moyà-Solà et al. 2009a; Alba 2012a). Some authors have used the family name Griphopithecinae Begun, 2001, either at the subfamily (Kelley 2002) or family (Begun 2013) rank, to refer to *Griphopithecus* and allied forms. However, as noted by Moyà-Solà et al. (2009a), this nomen is merely a junior synonym of Kenyapithecinae (or Kenyapithecini) when both *Kenyapithecus* and *Griphopithecus* are classified within it.

Kenyapithecins display a mosaic of primitive and derived features, combining several hominoid primitive features (such as the narrow nasal aperture, widest at midheight, and the low zygomatic root) with the derived subnasal morphology of crown hominids displayed by *Nacholapithecus* (Nakatsukasa and Kunimatsu 2009). Accoringly, kenyapithecines have been considered the most plausible sister-taxon of the European Dryopithecinae Gregory and Hellman, 1939 (Moyà-Solà et al. 2009a; Alba 2012a; Begun et al. 2012). The taxa included in the subfamily Dryopithecinae, from the Middle and Late Miocene of Europe, are customarily considered at least stem hominids more derived than kenyapithecines (Moyà-Solà et al. 2009a; Alba 2012a), although many uncertainties remain regarding their phylogenetic relationships, with some authors considering them crown hominids (e.g., Begun 2009, 2010; Begun et al. 2012; see below).

Crown hominids. With regard to undoubted crown hominids, they include the subfamilies Ponginae Elliot, 1913 and Homininae Gray, 1825. Pongines include the single extant genus *Pongo* Lacépède, 1799, which is currently restricted to the islands of Borneo and Sumatra, although in the past it displayed a wider distribution in mainland Asia (Harrison et al. 2014; Wang et al. 2014). Undisputable extinct pongines are exclusively distributed in Asia, including *Ankarapithecus* Ozansoy, 1955 from the Late Miocene of Anatolia, *Sivapithecus* Lyddeker, 1879 from the Middle to Late Miocene of India, China and Pakistan (Pilgrim 1910; Kelley 1988), *Khoratpithecus* Chaimanee et al., 2004 from the Late Miocene of Thailand (Chaimanee et al. 2004, 2006), *Indopithecus* von Koenigswald, 1950 from the Late Miocene of Pakistan (Madden and Lewis 1980; Cameron and Patnaik 2003), scarce remains of fossil *Pongo* from the Pleistocene of China (Wang et al. 2014), and *Gigantopithecus* von Koenigswald, 1935 from the Late Miocene of India and Pakistan (Pei and Woo 1956).

The taxonomy of extinct pongines is currently not very well resolved, being here distributed into the tribes Sugrivapithecini Simoneta, 1957 (*Sivapithecus*, *Ankarapithecus Gigantopithecus* and *Indopithecus*, the latter being sometimes considered a junior subjective synonym of *Gigantopithecus*, e.g., Begun et al. 2012) and Pongini Elliot, 1913 (*Pongo* and *Khoratpithecus*,). The Lufengpithecini Alba, 2012 have been customarily included in the Ponginae (e.g., Begun et al. 2010; Alba 2012), but they are excluded here following recent finds and analyses (see below). Unlike lufengpithecins, both *Sivapithecus* and *Ankarapithecus* display clear pongine-like cranial features, including their subnasal morphology (smooth subnasal floor with overlap between the premaxilla and maxilla), the anteriorly-orientated zygomatic, and the presence of supraorbital costae (Benefit and McCrossin 1995; Ward 1997; Andrews 2000). The postcranial morphology of these taxa, however, is more primitive than in extant orangutans, with *Sivapithecus* apparently displaying a mainly pronograde locomotor repertoire with only a few orthograde behaviors and no suspensory adaptations (Madar et al. 2002)—thereby being more primitive in this regard than the clearly orthograde, Middle Miocene dryopithecine *Pierolapithecus* (Moyà-Solà et al. 2004; Almécija et al. 2009). This is more uncertain in the case of *Ankarapithecus*, whose postcranial remains are very scarce. Among the Ponginae, the putative pongin *Khoratpithecus* is the only taxon that displays an exclusive synapomorphy of extant orangutans, namely the lack of impression of the anterior digastric muscles insertion, thus being considered as the closest relative of orangutans by some authors (Chaimanee et al. 2004, 2006).

In turn, with the exception of humans and their closest extinct relatives, hominines are restricted to Africa, where their members display a relatively abundant fossil record from the Late Miocene onwards (Wood and Harrison 2011; Strait 2013). Two early Late Miocene forms, *Chororapithecus* Suwa et al., 2007 and *Nakalipithecus* Kunimatsu et al., 2007, have been considered hominines (Kunimatsu et al. 2007; Suwa et al. 2007), although their phylogenetic affinities, due to the scarcity of the available material, are very uncertain (being hence left as tribe incertae sedis). Most of the hominine fossil record, in fact, is attributed to members of the tribe Hominini Gray, 1825, which includes humans and those forms more closely related to them than to African great apes.

Three Late Miocene genera may be interpreted as the earliest known members of the Hominini, although there is no consensus as to which is more closely related to humans: *Sahelanthropus* Brunet et al., 2002 from Chad; *Orrorin* Senut et al., 2001 from Kenya; and *Ardipithecus* White et al., 1994 from Ethiopia. *Sahelanthropus* is purportedly the oldest one of these genera (7-6 Ma), being represented by a complete but distorted cranium, a mandible and several isolated teeth. This taxon has been considered to be more closely related to humans than to extant African apes based on dental morphology, the horizontal and anteriorly positioned foramen magnum, the continuous supraorbital torus, and the reduced subnasal prognathism (Brunet et al. 2002, 2005), further being interpreted as a biped on the basis of the position of the foramen magnum (Brunet 2002; Brunet et al. 2002, 2005; Zollikofer et al. 2005). The interpretation of *Sahelanthropus* as a hominin, however, is controversial (e.g., Wolpoff et al. 2002), being here left unclassified at the tribe rank.

The slightly younger *Orrorin* (ca. 6 Ma), known from both craniodental and postcranial remains (Senut et al. 2001), is more securely interpreted as a hominin, in spite of being represented by more fragmentary and less informative remains than *Sahelanthropus*. Interpreted as a closer relative of hominins or even humans by the original describers, *Orrorin* displays in fact more similarities in dental morphology and enamel thickness with apes than with humans (Fleagle 2013). However, the femur displays morphological traits indicating a bipedal locomotion as in hominins (Senut et al. 2001; Richmond and Jungers 2008; Almécija et al. 2013). Finally, *Ardipithecus* is the most completely known of the three genera of putative earliest hominins. Being recorded by two species, one from the Late Miocene (5.8-5.2 Ma) and the other from the Early Pliocene (4.4 Ma), the latter—*Ardipithecus ramidus* (White et al., 1994)—is known from abundant craniodental remains, including a partial skeleton (Lovejoy et al. 2009a,b,c; Suwa et al. 2009a,b; White et al. 2009). Dentally, *Ardipithecus* resembles australopiths but already displays a reduced canine honing complex. Postcranially, *Ardipithecus* is much more primitive than australopiths, by displaying a mosaic of locomotion adaptations that purportedly range from arboreal quadrupedalism to terrestrially bipedalism (Lovejoy et al. 2009a,b,c,d; White et al. 2009). Based on currently available evidence, it cannot be completely discounted that *Sahelanthropus*, *Orrorin* and *Ardipithecus* genera might finally prove to belong to a single genus (White et al. 2009), although this seems unlikely given the striking morphological differences between one another (Pickford 2012).

The closer relatives to humans (included in genus *Homo*) are australopiths. The latter are included in two genera: the 'gracile' australopiths, belonging to the genus *Australopithecus* Dart, 1925 (4-2 Ma), which is recorded from Central, Eastern and Southern Africa (Reed et al. 2013); and the 'robust' australopiths, included in the genus *Paranthropus* Broom, 1938, from the Late Pliocene to Early Pleistocene of Eastern and Southern Africa. Species of *Australopithecus* generally show a somewhat intermediate morphology between that of extant great apes and that of modern humans, with clear adaptations to terrestrial bipedalism but further retaining some arboreal traits (McHenry 2002; White 2002; Fleagle 2013). *Paranthropus*, in turn, is customarily considered a more derived form displaying a more massive skeleton and particular craniodental adaptations, but further displaying clear bipedal adaptations (White 2002; Fleagle 2013; Wood and Schroer 2013). The genus *Homo* (2 Ma-present), finally, originated in Africa but spread from there to Eurasia during the Early Pliocene, and, subsequently to the rest of continents in the Late Pleistocene-Holocene. Except for the earliest species, members of *Homo* are terrestrial obligated bipeds and display a highly derived cranial morphology, with marked reduction of canine size and that of the postcanine dentition, coupled with slender mandibles and a very enlarged neurocranium (McHenry 2002; Fleagle 2013; Strait 2013).

With regard to African great apes (*Gorilla* and *Pan*), they are here attributed to two different tribes (Gorillini Frechkop, 1943 and Panini Delson, 1977, respectively for gorillas and chimpanzees plus bonobos). They are restricted to Equatorial Africa, thereby contrasting with the ubiquitous distribution of modern humans (*Homo*). The only evidence of a fossil chimpanzee comes from the Middle Pleistocene of the Kapthurin Formation from Lake Baringo (McBrearty & Jablonski 2005). Unfortunately, the absence of an older fossil record of apes in Central and Western Africa (probably due to a preservational bias in the tropical rainforests that are currently inhabited by African apes; Cote 2004) makes it difficult to interpret their ancestral morphology (i.e., that of the last common ancestor of apes and humans before their divergence). However, the primitive postcranial morphology of *Ardipithecus* and *Orrorin* suggests that the ancestral great-ape morphotype must be more primitive (i.e., more Miocene ape-like) than previously hipothesized based on extant forms alone (White et al. 2009; Almécija et al. 2013).

Hominids incertae sedis. Among the Hominidae, two monotypic tribes of uncertain phylogenetic affinities are here left as incertae sedis at the subfamily rank: the Oreopithecini Schwalbe, 1915, including the genus *Oreopithecus* Gervais, 1872 from the Late Miocene of Italy; and the Lufengpithecini, including the genus *Lufengpithecus* Wu, 1987 from the Late Miocene of Southeastern Asia. Over the years, the phylogenetic relationships of *Oreopithecus* have been thoroughly discussed, having been even considered a cercopithecoid (Delson 1979; Szalay and Delson 1979). However, after the reviews by Harrison (1986) and Sarmiento (1987), the hominoid status of *Oreopithecus* has been firmly established, especially based on postcranial grounds (e.g., Gervais 1872; Harrison 1986, 1991; Sarmiento 1987; Rook et al. 1996; Moyà-Solà and Köhler 1997; Alba et al. 2001). In spite of this fact, the precise phylogenetic relationships of *Oreopithecus* have proven most elusive. Thus, some authors have considered it to be an endemic insular descendant of a *Dryopithecus* s.l.-like (i.e., currently *Hispanopithecus*-like) mainland ancestor (Harrison and Rook 1997; Moyà-Solà and Köhler 1997, 2000; Alba et al. 2001). Other authors, in contrast, have stressed its apparently primitive (stem hominoid-like) cranial features (e.g., Begun 1997) or its dental similarities with African nyanzapithecines (Harrison 1985, 1986; Benefit and McCrossin 1997).

With regard to *Lufengpithecus*, this taxon has been customarily considered a pongine by many researchers during the last decades (Schwartz 1990; Begun and Kordos 1997; Kelley et al. 2002; Begun 2009; Alba 2012a), although more recent studies (Kelley and Gao 2012; Ji et al. 2013) tend to favor the alternative view that it is best interpreted as a stem hominid preceding the pongine-hominine split (e.g., Begun 1992; Andrews et al. 1996; Harrison and Rook 1997), having been most recently included in the Dryopithecinae by Fleagle (2013). Although plausible, the latter view is not formally adopted here, however, pending formal cladistic analysis supporting it.

Dryopithecine discoveries through time

The first discovery of a dryopithecine fossil remain corresponds to a partial humerus and mandible from the Middle Miocene of Saint-Gaudens (France). These fossils were employed by Lartet (1856) to erect the genus and species *Dryopithecus fontani* LARTET, 1856. Several decades later, additional mandibular remains attributed to the same taxon were discovered in the same site (Gaudry 1890; Harlé 1898, 1899), while Depéret (1911) further attributed to *D. fontani* an upper molar from fissure L3 or L5 of La Grive-Saint-Alban (France; Casanovas-Vilar et al. 2011a). Many years later, Andrews et al. (1996) further reported an upper incisor from La Grive fissure M, being since then customarily attributed to *D. fontani* (but see Pickford 2002 for a different interpretation, as well as further discussion in Chapter 5). More or less simultaneously with the classical discoveries of *D. fontani*, Branco (1898) reported an isolated molar from Salmendingen (Germany), which was employed by Schlosser (1901, 1902) to erect the genus and species *Anthropodus brancoi* SCHLOSSER, 1901, although *Anthropodus* was soon replaced by *Neopithecus* ABEL, 1902.

Neopithecus brancoi (SCHLOSSER, 1901) was subsequently reassigned to *Dryopithecus* LARTET, 1856, being employed by Begun and Kordos (1993; see also Begun, 2002a) to subsume the dryopithecine material from Rudabánya (Hungary). Remains from the latter locality had been originally attributed to *Rudapithecus hungaricus* KRETZOI, 1969 and *Bodvapithecus altipalatus* KRETZOI, 1975. The attribution of the Hungarian remains to *Dryopithecus brancoi* (SCHLOSSER, 1901) was not universally accepted, being alternatively ascribed by Andrews et al. (1996) to *Dryopithecus carinthiacus* MOTTL, 1957, which had been originally described as a subspecies of *D. fontani* based on a female mandible from St. Stefan (Austria). Currently, *Neopithecus brancoi* is considered a nomen dubium (Moyà-Solà et al. 2009b), the material from Austria is attributed to *D. fontani* without distinguishing subspecies (Begun 2002a; Begun et al. 2006; Moyà-Solà et al. 2009b; Casanovas-Vilar et al. 2011a), and the remains from Rudabánya are attributed to *Hispanopithecus* (*Rudapithecus*) *hungaricus* (Moyà-Solà et al. 2009b; Casanovas-Vilar et al. 2011a; Alba 2012a; Alba et al. 2012b, 2013) or *Rudapithecus hungaricus* (Begun 2009, 2010, 2013; Begun et al. 2012; Fleagle 2013).

Other dryopithecine taxa are further known from Eastern Europe: *Graecopithecus freybergi* von Koenigswald, 1972 from Pyrgos (Greece) and *Ouranopithecus macedoniensis* de Bonis and Melentis, 1977 from Ravin de la Pluie and other Greek localities (de Bonis et al, 1975; de Bonis and Koufos 1993, 1995, 1997; Koufos 1993, 1995). Although some authors (Andrews et al. 1996; Cameron 1997) have considered *Ouranopithecus* de Bonis and Melentis, 1977 to be a junior subjective synonym of *Graecopithecus* von Koenigswald, 1972, the fact is that the holotype of *G. freybergi* is not informative enough as to be considered as taxonomically valid, thereby being best considered a nomen dubium (Casanovas-Vilar et al. 2011a).

With regard to hominoid finds from the Iberian Peninsula, the first hominoid ever discovered there corresponds to the mandible from Teuleria del Firal (Seu d'Urgell Basin; Vidal 1913a,b, 1914; Woodward 1914), which was originally attributed to *D. fontani*, but more recently (albeit with some doubts) to *Dryopithecus crusafonti* Begun, 1992 (Begun 1992, 2002) or *Hispanopithecus crusafonti* (Begun, 1992) (see Moyà-Solà et al. 2009b; Casanovas-Vilar et al. 2011a; Alba et al. 2012b; Alba 2012a). All the subsequent hominoids finds from the Iberian Peninsula, in contrast, correspond to various localities from the Vallès-Penedès Basin (Alba 2012a). Thus, during the 1920s, an isolated upper molar was recovered from the area of els Hostalets de Pierola, although its identification as a hominoid was not established until much later (van der Made and Ribot 1999), being assigned to *Dryopithecus*. Additional hominoid mandibular remains were later recovered from the site of Can Vila, also in the area of els Hostalets de Pierola, being initially attributed to *D. fontani* (Villalta Comella and Crusafont Pairó 1941), but subsequently employed to erect a new taxon, *Sivapithecus occidentalis* Villalta Comella and Crusafont Pairó, 1944, which is currently considered a nomen dubium (Moyà-Solà et al. 2004; Alba 2012a). Within the same paper, another genus and species, *Hispanopithecus laietanus* Villalta Comella and Crusafont

Pairó, 1944, were also established based on the dentognathic remains from La Tarumba 1, in the area of Viladecavalls (Villalta Comella and Crusafont Pairó 1944; Crusafont 1958; Crusafont Pairó and Hürzeler 1961).

Relatively abundant finds, but mostly consisting in isolated teeth or fragmentary dentognathic remains, were recovered from other localities of the Vallès-Penedès Basin from the 1950s to the 1970s (Villalta Comella and Crusafont Pairó 1950; Crusafont 1958; Crusafont Pairó and Hürzeler 1961, 1969; Crusafont and Golpe-Posse 1974). The most important collections come from the sites of Can Llobateres 1 (Villalta Comella and Crusafont Pairó 1944; Crusafont 1958; Golpe Posse 1982, 1993; Begun et al. 1990; Harrison 1991) and Can Poncic (Crusafont and Golpe-Posse 1974; Golpe Posse 1974, 1982, 1993; Begun 1992; Harrison 1991). At some point, Crusafont and Hürzeler (1961, 1969) intended to erect two additional taxa, *Dryopithecus piveteaui* and *Rahonapithecus sabadellensis*. These nominal taxa, however, were never formally described and must be hence considered nomina nuda (Simons and Pilbeam 1965; Szalay and Delson 1979; Begun et al. 1990; Alba and Moyà-Solà 2012; Alba et al. 2012a).

Until relatively recently (Golpe Posse 1993), some authors still recognized the presence of two taxa (*Hispanopithecus laietanus* and *Sivapithecus indicus*) at Can Llobateres 1, although following Begun (1987; Begun et al. 1990; Harrison 1991) a single species has been customarily recognized at this locality (e.g., Alba et al. 2012b). Until recently, the species recorded at Can Llobateres and most other Late Miocene Vallès-Penedès localities was assigned by most authors to the genus *Dryopithecus* (i.e., *Dryopithecus laietanus*), until Moyà-Solà et al. (2009b) resurrected the genus *Hispanopithecus* (see also Cameron 1997, 1998, 1999; Alba 2012a; Alba et al. 2012b). Based on the remains from Can Poncic, Begun (1992) erected the species *Dryopithecus crusafonti*, to which the remains from Teuleria del Firal were also tentatively assignated. The taxonomic validity of this species has been doubted (Andrews et al. 1996) or even challenged (Ribot et al. 1996) by some authors, although it is generally accepted by most current authors, being assigned to genus *Hispanopithecus* (Moyà-Solà et al. 2009b; Alba 2012a; Alba et al. 2012b). Additional isolated finds of hominoids from other Vallès-Penedès localities correspond to those from Trinxera del Ferrocarril (=Sant Quirze; Golpe-Posse 1982), Can Poncic (Crusafont-Pairó and Hürzeler 1961, 1969; Golpe-Posse 1974, 1982, 1993; Crusafont and Golpe-Posse 1974; Begun 1992), and Can Mata 1 (Crusafont and Golpe-Posse 1973; Golpe-Posse 1974).

During the 1990s, more complete hominoid remains, including postcranials, were discovered from the localities of Can Llobateres 2 (Moyà-Solà and Köhler 1993, 1994, 1995, 1996; Köhler et al. 2001a,b) and Can Feu (Alba et al. 2012a), being currently attributed to *H. laietanus*. However, the most spectacular hominoid discoveries from the Vallès-Penedès have been made at various localities of the Abocador de Can Mata (ACM) local stratigraphic series, in the framework of the constructive works of a landfill (Alba et al. 2006a,b, 2009, 2011). These discoveries have led to the description of two genera and species (*Pierolapithecus catalaunicus* MOYÀ-SOLÀ ET AL., 2004 and *Anoiapithecus brevirostris* MOYÀ-SOLÀ ET AL., 2009a), as well as to the recognition of *D. fontani* in the Vallès-Penedès Basin (Moyà-Solà et al. 2004, 2009a,b). The distinction of these taxa is based on differences in cranial morphology, although the holotype of *P. catalaunicus* further preserves an associated partial skeleton, with profound implications for our current understanding of the radiation of hominoid primates in Eurasia (Moyà-Solà et al. 2004; Alba 2012a). The recognition of as many as three different hominoid genera in the Middle Miocene of such a small geographical area has raised some skepticism, with Begun and co-authors arguing that *P. catalaunicus* and *A. brevirostris* should be considered junior synonyms of *D. fontani*, at least at the species level (Begun, 2009; Begun et al. 2012; but see Alba 2012a and Pickford 2012 for different views).

Dryopithecine systematics and phylogeny

Dryopithecines are here considered an extinct subfamily of putative stem hominids from the Middle to Late Miocene of Europe (see Table 1.1), following Alba (2012a). Three different tribes are distinguished within this subfamily: the Dryopithecini GREGORY and HELLMAN, 1939; the Hispanopithecini CAMERON, 2004; and the Ouranopithecini DE BONIS AND MELENTIS, 1977. Dryopithecins include several genera (*Pierolapithecus*, *Dryopithecus* and *Anoiapithecus*) and are recorded from the Middle Miocene of Spain (Moyà-Solà et al. 2004, 2005, 2009a,b; Alba 2012a; Alba et al. 2012a,b; 2013), France (Lartet 1856; Gaudry 1890; Harlé 1898, 1899; Abel 1902; Déperet 1911; Andrews et al. 1996) and Austria (Mottl 1957, Begun 2002a). Hispanopithecins, in turn, include the (sub)genera *Hispanopithecus* VILLALTA COMELLA AND CRUSAFONT PAIRÓ, 1944 and *Rudapithecus* KRETZOI, 1969, and are recorded from the Late Miocene of Hungary (Kretzoi 1969; Kelley and Pilbeam 1986; Begun and Kordos 1993; Begun 1994a, 2002a, 2007, 2009, 2010, 2013; Kordos 2000; Kordos and Begun 1994, 1997, 2001, 2002) and Spain (Villalta Comella and Crusafont Pairó 1941, 1944; Crusafont 1958; Crusafont-Pairó and Hürzeler 1961, 1969; Crusafont-Pairó and Golpe-Posse 1973, 1974; Begun 1992; Moyà-Solà and Köhler 1993, 1994, 1995; Köhler et al., 2001a,b; Alba et al. 2012a,b). Finally, ouranopithecins include a single genus (*Ouranopithecus*) from the Late Miocene of Greece (de Bonis and Melentis 1977; de Bonis et al. 1990; de Bonis and Koufos 1993, 1995, 1997; Cameron 1997; Begun 2009; Alba 2012a), Turkey (Güleç et al. 2007) and, tentatively, Bulgaria (Spassov et al. 2012).

As explained above, the taxonomic affinities of the material from Salmendingen and other German localities (Schlosser 1901, 1902; Abel 1902), termed *Neopithecus brancoi*, is still unclear, having been synonymized with *Dryopithecus* (Simons and Pilbeam 1965; Szalay and Delson 1979; Begun and Kordos 1993; Begun 1994a, 2002, 2007), but here considered a nomen dubium, with the material form Rudabánya being currently included into *Hispanopithecus hungaricus* (Moyà-Solà et al. 2009b) or *Rudapithecus hungaricus* (Begun 2009). Another dryopithecine nominal taxon, "*Sivapithecus*" *occidentalis* from Can Vila, is further considered a nomen dubium (Moyà-Solà et al. 2004, 2009a; Casanovas et al. 2011a; Alba 2012a), although as noted by Alba (2012a) it is likely to be senior synomym of one of the various genera currently recognized from the Middle Miocene of the Vallès-Penedès Basin.

Dryopithecines display a mosaic of crown-hominid synapomorphies as well as more plesimorphic features already present in kenyapithecines (McCrossin and Benefit 1993, 1997; Ward et al. 1999; Begun 2005; Kelley et al. 2008; Moyà-Solà et al. 2009a). Thus, dryopithecines share with kenyapithecines the following primitive features: a high zygomatic root relative to the alveolar plane of the maxilla; a reduced facial prognathism; a stepped subnasal floor with an open palatine fenestra; the lack of frontal sulcus and supraorbital tori; a posteriorly situated glabella; a broad interorbital pillar; a strong mandibular inferior torus; a very strongly proclined mandibular symphysis; and a shallow genioglossal fossa. On the other hand, dryopithecines more clearly display crown hominid synapomorphies, which are absent or not ascertainable in kenyapithecines;

they include: a wide nasal aperture widest at the base; the palate widest anteriorly; the lacrimal fossa visible anteriorly; the deep palate; the edges of the nasal aperture formed by the maxillae; the strong mandibular tori; the frontal process of the maxilla, the nasals and orbits in the same plane; the lack of subarcuatte fossa; the high zygomatic root; and the short premaxilla. Given this mosaic of features, the phylogenetic status of this group is still uncertain, with several hypotheses being potentially valid: (a) dryopithecines constitute a clade of stem hominids; (a) dryopithecines are a paraphyletic assemblage of stem hominids; (c) dryopithecines are indeed crown hominids, being more closely related to either pongines and/or hominines. Thus, several authors have considered that some or all dryopithecines are best considered stem hominids (Moyà-Solà et al. 2004, 2005, 2009a,b; Alba and Moyà-Solà 2009; Alba 2012a; contra Begun and Ward 2005) and/or stem pongines (Schwartz 1990, Moyà-Solà and Köhler 1993, 1995, 1996; Köhler et al. 2001a; Cameron 1997; Alba 2012a; Pérez de los Ríos et al. 2012), whereas other authors have favored the view that they are indeed stem hominines (de Bonis et al. 1990; de Bonis and Koufos 1993; Begun 1994a, 2002a, 2007, 2009, 2010; Begun and Kordos 1997; Kordos and Begun 2001, 2002; Begun and Ward 2005; Begun et al. 2012).

Hominoid craniodental anatomy

A succinct description of the bones of the skull (cranium and mandible) in hominoids, including general descriptions of the teeth (after Sobotta 2000; Swindler 2002; Aiello and Dean 1996; Ankel Simons 2007; White et al. 2012), is given below so as to provide the necessary background to follow the descriptions provided in this dissertation.

Cranium

The primate cranium consists of 29 different bones (Fig. 1.1), which conform the splanchnocranium (face) and neurocranium (braincase, including the calvarium and basicranium), as well as three tiny bones of the middle ear. The cranial bones are connected with one another through the cranial sutures (which are serrate bony structures that initially consist in fibrous joints but become fused in adults). The cranium serves various functions, by enclosing and protecting the brain and other sense organs, and further playing an important role during mastication.

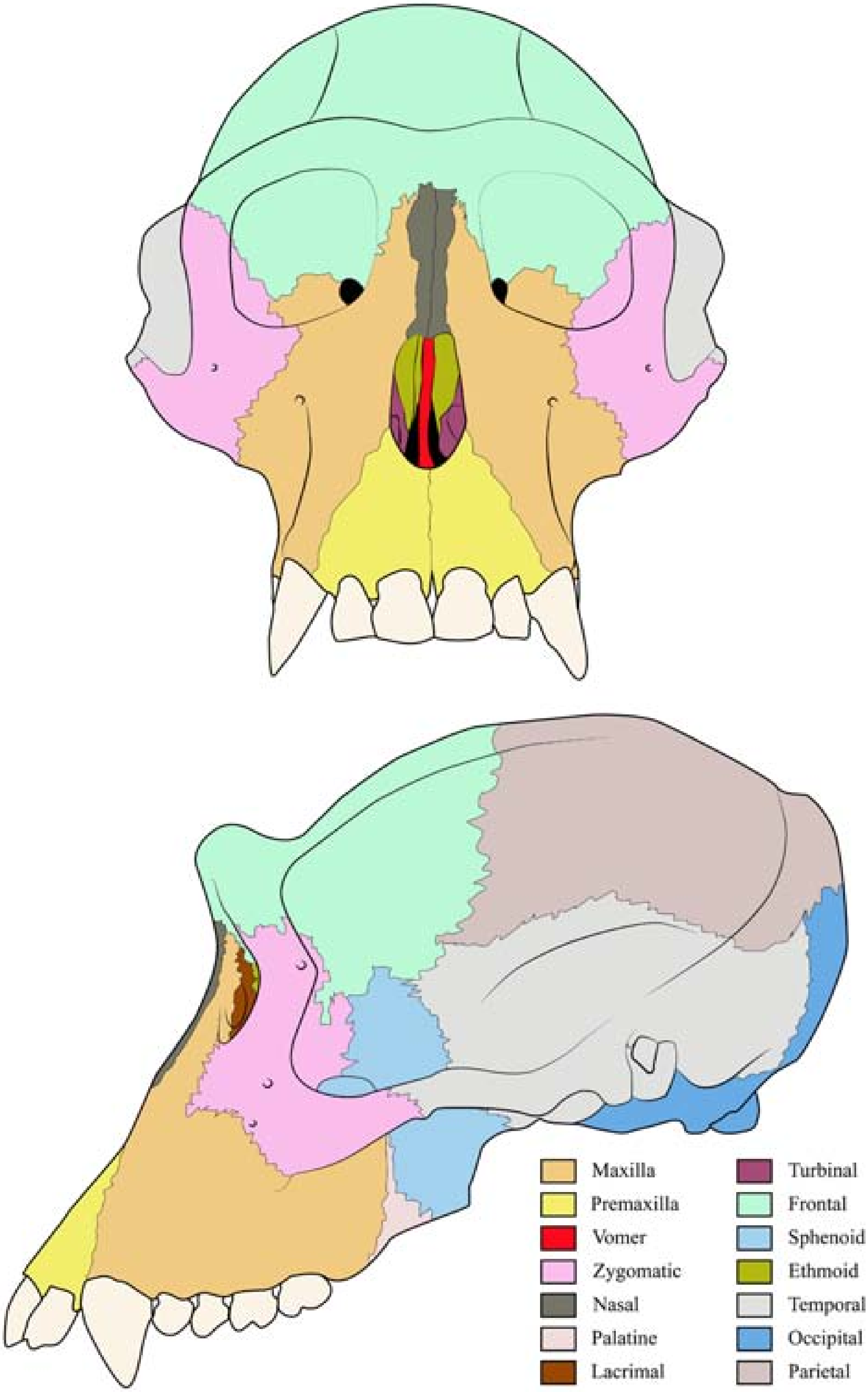

Figure 1.1 Frontal (top) and left lateral (bottom) views of a chimpanzee cranium, with the various cranial bones denoted by different colors.

Premaxilla. The premaxilla is a paired bone connected by the inter-premaxillary suture in the sagittal plane. It bears the alveoli of the upper incisors, and constitutes the anteriormost part of the hard palate and the subnasal floor, running until the palatine fenestra or canal. It limits posteriorly with the maxilla through the premaxilla-maxillary suture (which is not observable in humans due to the fusion of these two bones).

Maxilla. The maxilla is a paired bone, whose alveolar process harbors the alveoli of the upper canine cheek teeth and conforms the basal portion of the nasal aperture, further constituting part of the hard palate and the orbit. In particular, the superior portion of the maxilla conforms the infraorbital rim and inferior orbital wall. It displays one of the largest foramina in the splachnocranium (the infraorbital foramen), as well as the largest pneumatization of the face (the maxillary sinus), which is located over the dentition and sometimes spreads through the zygomatic and frontal recess of the maxilla. The maxilla also shows an anterior process in the sagittal plane (the anterior nasal spine). The two maxillae contact inferiorly with one another through the medial palatine suture. Furthermore, the maxilla contacts ten other different bones: the premaxilla by through the premaxilla-maxillary suture, the frontal through the frontomaxillary suture, the nasals through the nasomaxillary suture, the lacrimals through the lacrimomaxillary suture, the ethmoid through the ehtmoid-maxillary suture, the sphenoid through the sphenomaxillary suture, the zygomatic through the zygomaticomaxillary suture, the palatine through the transverse palatine suture, the vomer (on the nasal crest) through the vomer-maxillary suture, and the inferior nasal concha (one of the turbinals) through the turbinal crest of the maxilla.

Palatine. The palatine is a paired bone located between the pterygoid plate of the sphenoid and the posterior portion of the maxilla. It forms the posterior-most part of the hard palate, and displays two foramina (the greater and lesser palatine foramina). It displays an orbital process that takes part of the orbital cavity, and which articulates with the sphenoid bone (originating the sphenopalatine foramen, which is a passage for the sphenopalatine and maxillary arteries). The medial wall of the palatine displays a crest that articulates with the inferior turbinal, whereas its posterior-most process is the posterior nasal spine. The palatine contacts the maxilla throught the transverse platine suture, the sphenoid through the sphenopalatine suture, and the vomer througth the vomer-palatine suture.

Vomer. The vomer is a non-paired bone that runs througth the saggital plane in the nasal cavity, dividing its posterior part in two (right and left) moieties. The vomer consists in a flat bony plate that articulates with the nasal crest of the maxilla by through the vomer-maxillary suture inferiorly, with the palatine bone throught the vomer-palatine suture inferoposteriorly, with the sphenoid bone through the vomer-sphenoidal suture superiorly, and with the ethmoid througth the vomer-ethmoidal suture superiorly.

Nasal: The nasal is a paired bone of long, narrow, thin and trapezoidal shape, which conforms the nasal bridge and the upper border of the nasal aperture. The nasals are located among the frontal processes of the maxillae. They contact the frontal bone superiorly through the frontonasal suture, the maxillae laterally through the nasomaxillary sutures, and one another through the internasal suture.

Lacrimal. The lacrimal is a paired bone of oval morphology, situated behind the orbital rim on the internal medial wall of the orbits (under the interorbital region of the frontal bone). This bone conforms the posterior wall of the lacrimal fossa, which is delimited by the posterior lacrimal crest. Within the lacrimal fossa, the lacrimal sac and the lacrimal duct (or canal) are located.

Turbinals. The turbinals (or turbinates, or nasal conchae) are long and thin paired bones that curl and run through the nasal cavity and support the olfactory epithelium. There are three types of turbinals: the inferior ones, the medial ones, and the superior ones. The inferior turbinals are attached to the maxilla, whereas the medial and superior turbinals are part of the sphenoid.

Zygomatic: The zygomatic (or malar) is a paired bone located superolaterally relative to the maxilla. It contacts the maxilla anteriorly through the zygomaticomaxillary suture, the frontal and sphenoid superiorly through the frontozygomatic and zygomaticosphenoid sutures (respectively), and the temporal posteriorly through the zygomaticotemporal suture. The temporal process of the zygomatic bone, together with the zygomatic process of the temporal bone, constitute the zygomatic arch on each side of the cranium. The zygomatic displays several zygomaticofacial foramina on its anterior portion (in the outer part of the inferolateral orbital rim), which are related to the passage of nerves and blood vessels of the cheek region.

Frontal: The frontal is a non-paired bone (although ontogenetically it originates from two intramembranous ossification centers that are separated by the metopic suture, which becomes completely fused and disappears during infancy). This bone constitutes the superior-most portion of the splanchnocranium and the anterior-most portion of the neurocranium, further defining the superior and superolateral portions of the orbital rim as well as the roof of the orbit. The posterior (inner) portion of the frontal displays the anterior cranial fossa, in which the frontal lobe of the brain is located, being divided by the frontal crest along the sagittal plane. Internally, the frontal may display a pneumatization (frontal sinus), generally behind the glabella, although it can also spread throughout the supraorbital rims. The frontal contacts the parietals posteriorly through the frontoparietal sutures, the sphenoid laterally through the sphenofrontal sutures, and the zygomatics anteriorly through the frontozygomatic sutures. The frontal further contacts the lacrimals, the ethmoid, the nasals, and the frontal processes of the maxillae in the interorbital area.

Sphenoid. The sphenoid bone is a non-paired bone situated in the central area of the cranium, being surrounded by most of the other bones that conform it. This bone constitutes the posterior portion of the orbital wall, the anterior portion of the temporal fossa and the posterior portion of the palate, as well as the wings of the pterygoid plate (or the pterygoid processes). The sphenoids are connected with the vomer, the palatine and the maxilla inferiorly through the vomer-sphenoidal, the sphenoid-palatine and the sphenomaxillary sutures, respectively. They also contact the zygomatics, the frontal and the ethmoid in the orbital area, by through the sphenozygomatic, the sphenofrontal and the sphenomaxillary sutures, respectively.

Ethmoid. The ethmoid is a non-paired bone situated at the level of the orbits above the nasal cavity. It constitutes part of the internal wall of the orbits and further holds the superior and medial turbinals. The ethmoid also separates the nasal cavity from the brain. This bone limits with the frontal, the sphenoid, the nasals, the maxilla, the lacrimals, the palatines and the vomer throught the ethmofrontal, the sphenoethmoidal, the ethmonasal, the ethmomaxillary, the ethmolacrimal, the ethmopalatine and the vomer-ethmoidal sutures, respectively. The ethmoid sometimes displays an internal pneumatization (ethmoidal sinus), which from a developmental viewpoint is considered to constitute the origin of the frontal sinus.

Temporal: The temporal is a paired bone that constitutes the lateral portion as well as the base of the neurocranium. It further contains the tympanic bulla and the auditive meatus. The temporal bone is actually formed by the fusion of five bones (the squamous, the zygomatic process, the tympanic, the styloid process and the petromastoid). As explained above, together with the temporal process of the zygomatic, the zygomatic process of the temporal constitutes the zygomatic arch. The temporal is connected to the parietal superiorly through the temporoparietal suture, with the sphenoid anteriorly through the sphenosquamosal suture, and with the occipital posteriorly though the occipitomastoid suture.

Occipital. The occipital is a non-paired bone located in the posteroinferior portion of the cranium. It constitutes the portion of the basicranium in which the foramen magnum (the largest foramen of the cranium) is located, as well as the occipital squama (which is the posterior-most portion of the bone). The occipital, in fact, constitutes the posterior-most part of the cranium (termed the external occipital protuberance). Under this protuberance, the external occipital crest runs inferiorly until reaching the foramen magnum, whereas laterally the superior nuchal crest runs around the bone and conforms the attachment of the nuchal and suboccipital muscles. At each side of this foramen, and somewhat anterolaterally from it, the occipital condyles are located, constituting the area of articulation with the atlas (the first cervical vertebra). Under the anterior facet of the condyles, the hypoglossal or condylar canal runs anteroposteriorly towards the foramen magnum. The internal aspect of the occipital displays an internal occipital protuberance (as the inner expression of the external one) at the midline of the internal occipital crest, the cerebellar fossa at each side of this crest, and the transverse groove (as the inner expresion of the external nuchal crest). The occipital contacts the parietals superoanteriorly through the lamboidal suture, the temporals inferoanteriorly through the occipitomastoid and the petro-occipital sutures, and the ethmoidal inferoanteriorly through the occipitoethmoidal suture.

Parietal. The parietal is a paired bone of quadrangular shape that is located at each side of the neurocranium. On their external surface, the parietals display part of the inferior and superior temporal lines. On their internal surface, the grooves for the middle meningeal vessels can be discerned. The parietals contact each other superiorly by through the sagittal suture, the frontal bone anteriorly through the coronal suture, the occipital posteriorly through the lamboidal suture, and the temporals inferiorly through the parietomastoideal and the squamosal sutures.

Middle ear bones. These small bones (or ossicles) are located in the middle ear, which is the cavity that links the external acoustic meatus with the inner ear. They include the malleus ("hammer"), incus ("anvil") and stapes ("stirrup"). They are the smallest bones in the cranium, being involved in hearing by transmitting sound. The malleus receives the vibrations of the sound through the eardrum or tympanic membrane, and transmits it to the incus and to the stapes. The latter is a tiny bone that contacts the membrane of the fenestra ovalis, which connects the middle ear with the fluid-filled inner ear and thus allows hearing. The malleus articulates with the incus by through the incudomalleolar joint, whereas the incus and the stapes articulate by through the incudostapedial joint.

Mandible

The mandible (Fig. 1.2) is not attached by any suture to the remaining skull bones, being articulated with the cranium through the temporomandibular joint. It is formed by two hemimandibles fused on their anterior-most portions (mandibular symphysis) in early developmental stages. Each hemimandible is composed by the mandibular corpus (the horizontal bony portion that bears the teeth) and the mandibular ramus (a more verticalized portion that terminates in the mandibular condyle, for articulation with the glenoid fossa of the skull). Anteriorly from the condyle, there is the coronoid process, which is the attachment area of the masseter, the temporalis and the medial and lateral pterygoid muscles. On the outer portion of the mandibular corpus, the mental foramen can be usually discerned below the premolars, consisting in a passage for nerves and blood vessels. The internal side of the corpus displays a marked ridge (the mylohyoid line), where the mylohyoid muscle attaches, and which delimits the sublingual fossa from the submandibular fossa. In the internal surface of the symphysis, the mandibular transverse tori (superior and inferior) may be present. These are shelf-like thickenings of the bone, which may be more or less developed, so that in some cases ony one of them is present. When the inferior transverse torus is very well developed, it projects posteriorly, thus creating the "simian shelf" that is characteristic of several groups of primates. The depression present in most taxa between the superior and inferior transverse tori, where the digastric muscles attach, is termed digastric fossa. In some cases, such as humans, the digastric fossa is located almost in the inferior border of the symphysis, since the inferior transverse torus is absent.

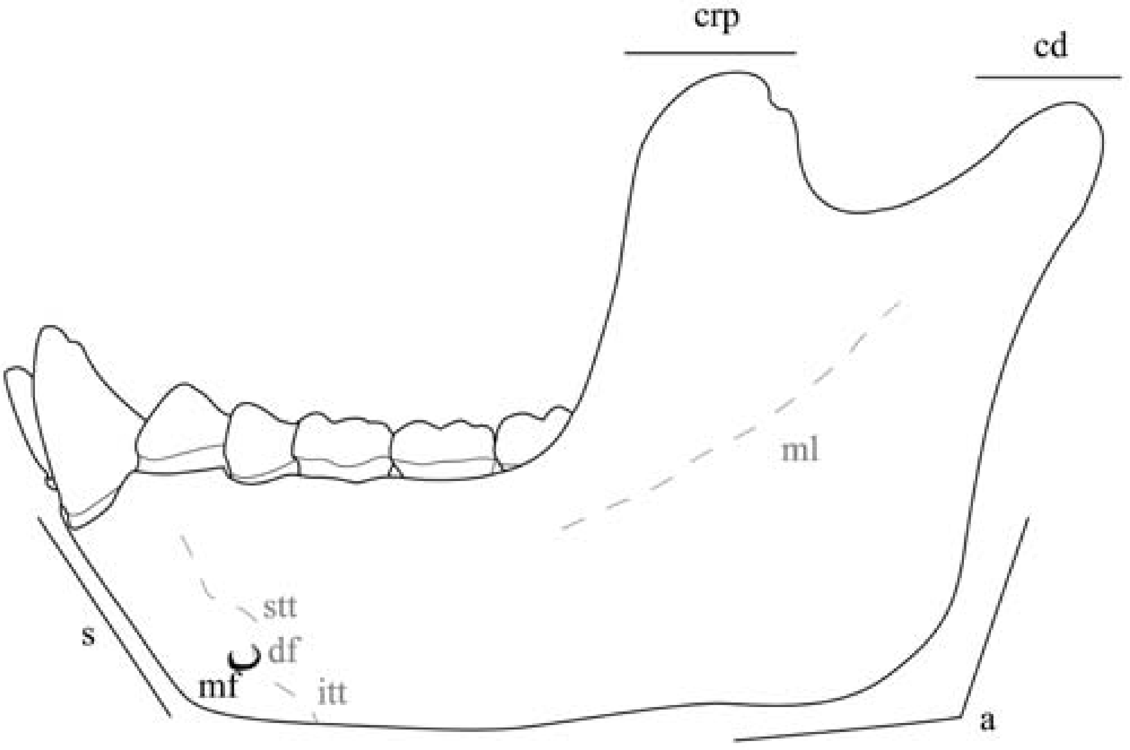

Figure 1.2 Lateral view of a chimpanzee mandible. The dashed line and gray letters indicate internal morphologies. Abbreviations: a, angle of the mandible; crp, coronoid process; cd, condyle; df, digastric fossa; itt, inferior transverse torus; mf, mental foramen; ml, mylohyoid line; s, symphysis; stt, superior transverse torus.

Dentition

The decidual and permanent dentition of hominoids is characterized by the same dental formula as the rest of catarrhines: 2dI-1dC-2dP/2dI-1dC-2dP (for the deciduous teeth) and 2I-1C-2P-3M/2I-1C-2P-3M (for the permanent teeth), being I, incisors; C, canines; P, premolars; and M, molars. There are thus two incisors in each tooth row, the central one (I1) and the lateral one (I2); there is only a single canine (C1), and two premolars, which are considered to be the third (P3) and the fourth (P4) ones; finally, there are three molars, the first (M1), the second (M2) and the third (M3).

The incisors are spatulated and high-crowned, with the upper ones being heteromorphic to some degree, so that the upper central incisor is larger and generally displays a more complex lingual morphology than the lateral one. The lower incisors are narrower and homomorphic, i.e., with the central and lateral ones being more similar to one another in both size and morphology.

The canines generally display a marked sexual dimorphism, with the male ones being larger and higher-crowned than those of females, with the exception of those of hylobatids, which are not dimorphic at all. In hominids, the upper and lower male canines are rather tusk-like, with a pointed shape, and slighlty rotated relative to the postcanine dentition; a marked mesiolingual sulcus is present in the upper canines of some taxa. In contrast, hylobatids display markedly mediolaterally-compressed and dagger-like upper canines. A diastema is present between the upper canine and the upper lateral incisor, and between the lower canine and the lower third premolar. Except in humans and extinct relatives, the upper and lower canines show an extensive distolingual wearing facet, due to wear against the lower third premolar and the upper canine, respectively, thereby conforming a well-developed honing complex.

The premolars and molars are collectively referred to as postcanine dentition or cheek teeth. The upper premolars are bicuspid and similar in shape to one another, with two main cusps: the higher paracone and the lower protocone. The lower premolars are highly heteromorphic in most taxa, with the P_3 displaying a triangular shape in buccal view (with the protoconid much higher and sharper than the variably developed metaconid), and the P_4 displaying an oval occlusal outline with four cuspids, the mesial ones (protoconid and metaconid) being linked by a transverse crest and better developed than the distal cuspids (hypoconid and the entoconid).

The upper molars are generally four-cusped, with the trigon constituted by three cusps (the mesial paracone and protocone, and the distal metacone) and the talon formed by another additional distal cusp (hypocone), although the development of the distal cusps is variable in M3. The protocone is generally the most extensive cusp and the hypocone the least, although both are lower than the paracone and metacone. The buccal cusps (paracone and metacone) are more mesially situated than the lingual ones (protocone and hypocone). A diagonal crest (crista obliqua) links the protocone with the metacone, and an additional transverse crest linking the metacone and the hypocone may be present. The lower molars display five cusps, with the trigonid constituted by two cusps (protoconid and metaconid), and the talonid formed by the remaining three cusps (entoconid, hypoconid and hypoconulid). The buccal protoconid and the lingual metaconid are linked by a transverse crest (constituted by the hypoprotocristid and hypometacristid), which separates the mesial fovea (trigonid basin) from the central fovea (talonid basin). The entoconid is situated behind the metaconid on the lingual side, whereas the hypoconid is situated behind the protoconid on the buccal side. The two latter crests are linked by a relatively straight cristid obliqua (constituted by the postprotocristid and the prehypocristid). The fifth cusp (hypoconulid) is situated closer to the hypoconid towards the buccal moiety of the crown. The hypoconulid and the entoconid can be linked by a composite crest formed by the hypoentocristid and the postcristid, which (if present) delimits a distal fovea from the remaining portion of the trigonid basin. The occlusal pattern of the lower molars of most hominoids is known as the Y5-pattern, due to the presence of five cusps and the disposition of the grooves between them, which shape a horizontal Y groove pattern (with the stem of the Y being situated between the bases of the metaconid and entoconid).

Basic anthropometric landmarks

Anthropometric landmarks are commonly used points from the skull that are employed to define measurements or in craniomandibular descriptions (e.g., Aiello and Dean 1996). The main landmarks employed in this dissertation are the following (Fig. 1.3):

- Alveolare: Midline point of the inferior-most edge of the alveolar plane between the upper central incisors.
- Basion: Point in the sagittal plane located on the anterior margin of the foramen magnum.
- Bregma: Meeting point of the sagittal and coronal sutures.
- Glabella: Anterior-most point in the sagittal plane of the cranium between the supraorbital rim. Located in the frontal bone.
- Inion: Point of the sagittal plane of the cranium when that crosses the superior nuchal crest.

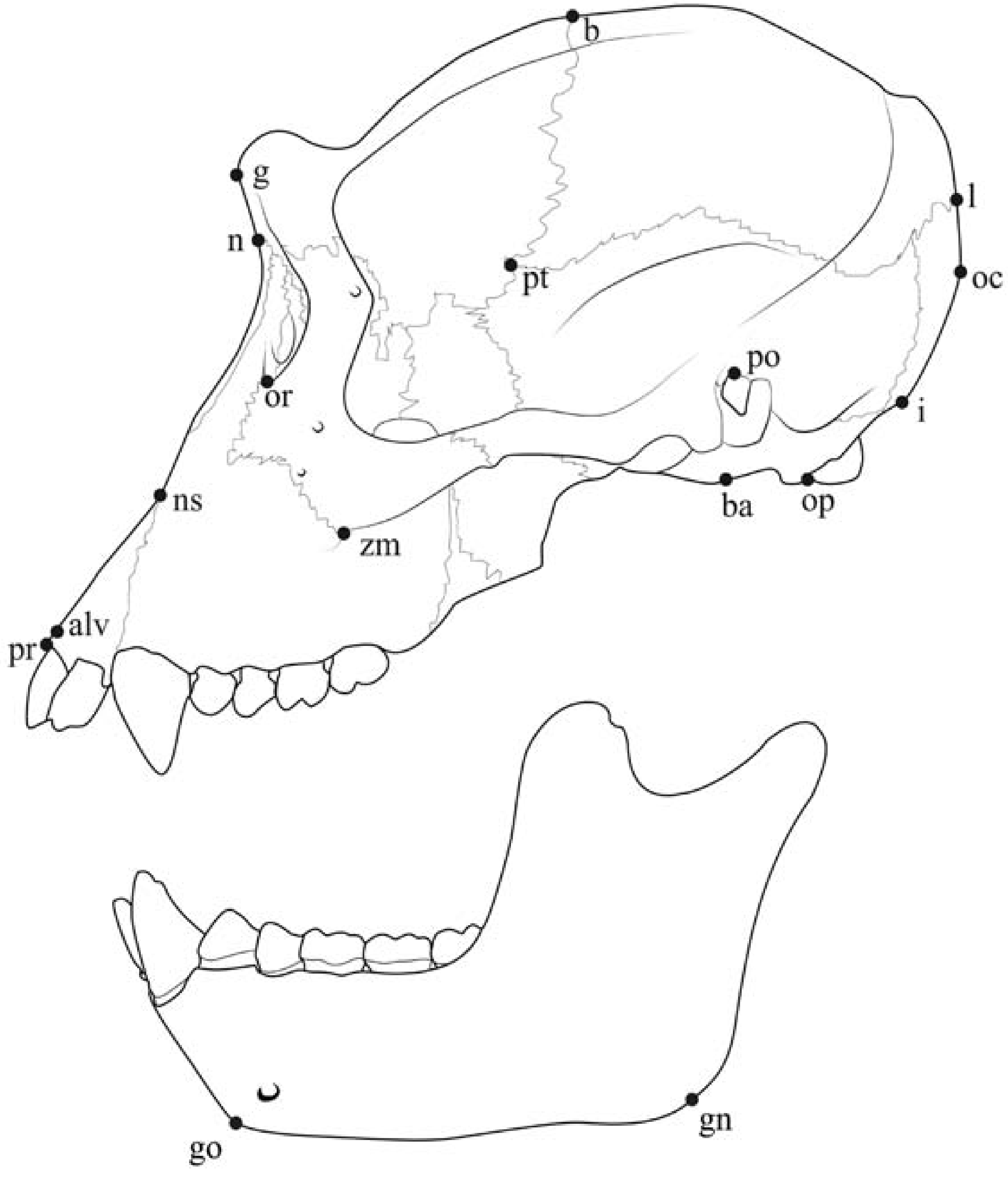

Figure 1.3 Basic anthropometric landmarks of the cranium and mandible, indicated on a chimpanzee skull. Abbreviations: alv, alveolare; ba, basion; b, bregma; g, glabella; gn, gnathion; go, gonion; i, inion; l, lambda; n, nasion; ns, nasospinale; op, opisthion; oc, opisthocranium; or, orbitale; pt, pterion; po, porion; pr, prosthion; zm, zygomaxillare Gonion: Point of maximun curvature at the madibular angle.• Gnathion: Inferior-most point of the mandible in the saggital plane.

- Lambda: Meeting point of the lambdoid and sagittal sutures in the saggital plane.
- Nasion: Meeting point between the frontonasal and the internasal sutures.
- Nasospinale: Superior and anterior-most point of the premaxilla at the saggital plane plane, marked by the presence of the anterior nasal spine.
- Opisthion: Midline point on the posterior border of the foramen magnum.
- Opisthocranion: Posterior-most midline point of the cranium. Located in the occipital bone.
- Orbitale: Inferior-most point of the infraorbital margin.
- Pterion: Confluence of the sutures of the frontal, parietal, temporal and sphenoid bones.
- Porion: Lateral and superior-most point of the external auditory meatus.
- Prosthion: Anterior-most point of the premaxilla-premaxilla suture between the upper central incisors.
- Zygomaxillare: Inferior-most point of the zygomaticomaxillary suture.

Besides the landmarks above, some of the planes defined by lines linking some of them are also important antropometric tools. One of the most used reference planes is the Frankfurt Horizontal, which is defined by the lines connecting porion and orbitale at each side of the cranium.

Material and general methods

Each of the main chapters of this dissertation have its own detailed materials and methods section, so just some general considerations on the methodology employed are provided below.

Studied remains

All the fossils studied in the framework of this dissertation, and described in Chapter 2, Chapter 3 and Chapter 4, are housed in the Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, with the exception of a couple of specimens that are deposited in the Museu de Geologia del Seminari Conciliar de Barcelona. Fossils and skeletal remains of extant taxa included in the comparative sample come from the following institutions: American Museum of Natural History (New York, USA); Nairobi National Museum (Kenyan National Museums, Nairobi, Kenya); Magyar Állami Földtani Intézet [Geological Museum] (Budapest, Hungary); Museum of Comparative Zoology (Harvard University, Cambridge, USA); Muséum National d'Histoire Naturelle (Paris, France); Magyar Természettudományi Múzeum [Hungarian Natural History Museum] (Budapest, Hungary); Naturhistorisches Museum Basel (Switzeland); Naturhistorisches Museum Wien (Austria); Peabody Museum of Archaeology and Ethnology (Harvard University, Cambridge, USA); and Université Claude Bernard Lyon 1 (France). This dissertation describes for the first time all of the craniomandibular remains of Miocene hominoids from the Vallès-Penedès Basin, including not only the remains found by Crusafont and collaborators during the 1940s to 1970s (Villalta Comella and Crusafont Pairó 1941, 1944; Crusafont 1958; Crusafont-Pairó and Hürzeler 1961, 1969; Crusafont-Pairó and Golpe-Posse 1973, 1974), but also the new collections recovered towards the end of the 20th Century by Moyà-Solà and collaborators (Moyà-Solà and Köhler 1993, 1995; Moyà-Solà et al. 1999; Köhler et al. 2001a,b; Alba et al. 2012a,b), as well as those recovered from Abocador de Can Mata during the 2000s (Moyà-Solà et al. 2004, 2005, 2009a,b; Alba 2012a; Alba et al. 2013).

Description and measurements

For the description of cranial material, anatomical nomenclature follows White et al. (2012) for the external morphology (Figs. 1.1-1.2), and mostly Rossie (2008) for internal anatomy (see also Chapter 3). In turn, dental terminology (Fig. 1.4) mostly follows Harrison and Gu (1999) and Alba et al. (2010a; see also Swindler 2002, and Chapters 3 and 5).

Craniomanibular and dental measurements were taken with a digital caliper to the nearest 0.1 mm. The measurements and indices employed for the cranial and mandibular specimens are detailed in Chapter 2. With regard to dental specimens, three measurements were taken: labiolingual/buccolingual breadth (BL), mesiodistal length (MD) and labial/buccal maximum height (H). Based on these variables, two indices were computed: breadth/length index (BLI = BL / MD x 100) and relative crown height (RCH = H/MD x 100).

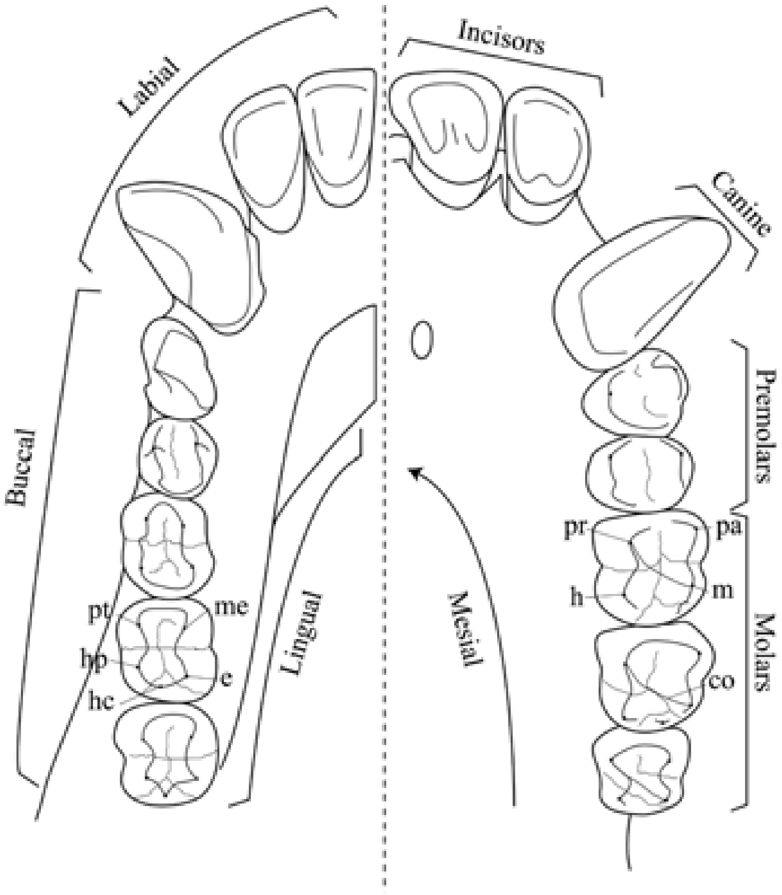

Figure 1.4. Lower (left) and upper (rigth) permanent dentition of a chimpanzee, further indicating the main axes within the oral cavity as well as the molar cusps. Abbreviations: co, crista obliqua; e, entoconid; h, hypocone; hp, hypoconid; hc, hypoconulid; m, metacone; me, metaconid; pa, paracone; pr, protocone; pt, protoconid.

Iconography

Photographs of the fossil remains figured in this dissertation were taken with a reflex digital camera Nikon D3000 with a 10.2 megapixels resolution, using a 18–55 mm zoom Nikkor lens for the larger (cranial and mandibular) specimens, and a 60 mm macro Nikkor lens for the smaller (mostly dental) remains as well as details of the remaining material. Photographs were processed with Photoshop CS4 11.0.2 in order to balance the contrast, color and brigthness, as well as to remove the background. Neither alterations nor reinterpretations of the remains were performed with this software.

Computed tomography

Besides photographs, non-invasive computed tomography (CT) techniques were employed to study the internal cranial morphology as well as tooth enamel and enamel-dentine junction (EDJ) morphology. Thus, several teeth were scanned with an X-ray microCT at the Multidisciplinary Laboratory of the International Centre for Theoretical Physics of Trieste in Italy (Tuniz et al. 2013), using the parameters detailed in Chapter 3. The slices of the dental images were reconstructed with Cobra v.7.4 (Exxim) and processed into ImageJ 1.46r software, and fhe final reconstruction was done with Avizo 7.1 software (VSG). Relative enamel thickness (RET) was computed as specified in Chapter 2. CT techniques were also employed to obtain images of the internal cranial anatomy of *Pierolapithecus* in Chapter 4. Given the relatively large size of the specimen, a high-resolution industrial CT (Yxlon Compact 225) from Burgos University (Spain) was used (see Chapter 4 for further details on the parameters employed). The obtained CT images were processed with the software MIMICS (Materialise, Belgium).

Phylogenetic mapping

The mapping of the presence/absence of the frontal sinus in catarrhines over previously-published cladograms (the ‘Begun’ and ‘Horowitz’ trees published by Rossie 2008) performed in Chapter 4 was runned with the MacClade 4.08a OSX software.

Geological context

The Vallès-Penedès Basin is a small Tertiary Basin (around 100 km in length and 12-14 km in width) of a roughly NE-SW orientation and situated in the northeastern area of the Iberian Peninsula. It is delimited by the Catalan Coastal Ranges (Littoral and Prelittoral), which are roughly parallel to the coastline. It is delimited on its NW margin by the Vallès-Penedès fault, and on the SE one by the Garraf-Montnegre horst, which confere a half-graben morphology to the basin (Anadón et al. 1979; Cabrera and Calvet 1990; Bartrina et al. 1992; Roca and Desegaulx 1992; Roca and Guimerà 1992; Cabrera et al. 2004). This characteristic morphology results in an irregular deposition of the sediments, being the highest accumulation rate in the NW area due to the main fault activity.

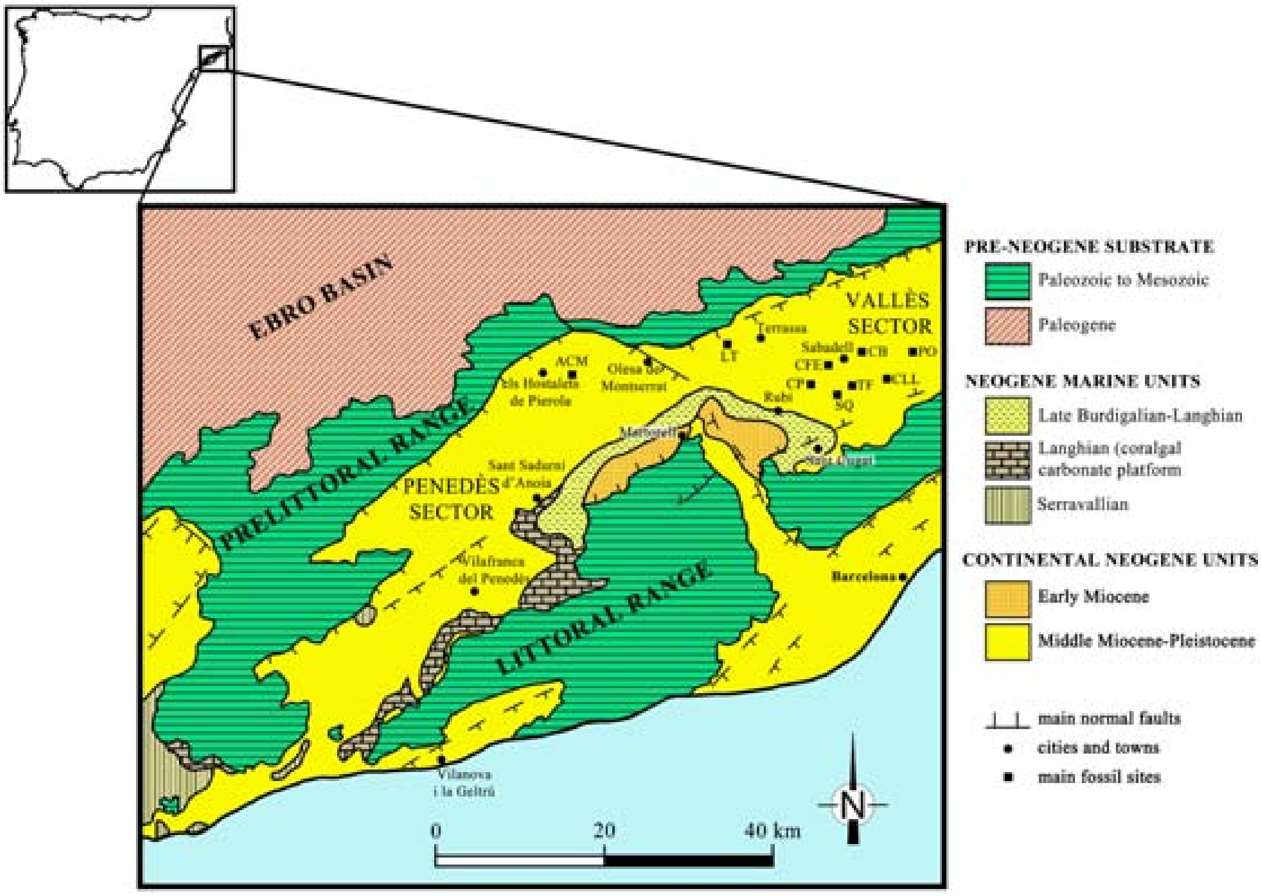

Figure 1.5 Simplified geological map of the Vallès-Penedès Basin, showing the hominoid-bearing fossil sites. Modified from an original kindly provided by Isaac Casanovas Vilar. Abbreviations: ACM, Abocador de Can Mata; CB, Castell de Barberà; CFE, Can Feu; CLL, Can Llobateres; CP, Can Poncic; LT, La Tarumba; PO, Polinyà; SQ, Sant Quirze; TF, Trinxera del Ferrocarril.

The stratigraphic subdivision of the Vallès-Penedès Basin during the Miocene is based on the sedimentary context (Cabrera 1981; Agustí et al. 1985, 1990; de Gibert and Casanovas-Vilar 2010). Deposition in the basin was initially colluvial during the Ramblian, but in the Early Miocene it became an area of alluvial fan systems, with some lake carbonate deposits showing gypsum intercalations. During the late Burdigalian, several marine transgressions took place, resulting in some evaporitic units, whereas in the Langhian, sequences of marine deposits of sandstones and mudstones, with a considerable stratigraphic thickness, were deposited. Finally, from the middle Aragonian to the middle Turolian, continental sedimentation was resumed in this area, after a regression of the sea level.

Accordingly, the Miocene deposits of the Vallès-Penedès Basin are subdivided into four different sedimentary units (Cabrera 1981; Cabrera et al. 1991; Agustí et al. 1985, 1990; Cabrera and Calvet 1996): (1) the Unit of Basal Breccias (Aquitanian–Burdigalian); (2) the Inferior Continental Complexes (Aquitanian-late Burdigalian); (3) the Marine-Transitional Complexes (late Burdigalian–Serravalian); and (4) the Superior Continental Complexes (Serravalian–Late Tortonian). The hominoid-bearing sites are situated within the Superior Continental Complexes, being characterized by a lithology mainly composed by detritic facies, sandstones and mudstones with intercalations of conglomerates. The sediments from the hominoid-bearing sites generally correspond to medial to distomarginal facies of the fan systems (such as those of els Hostalets de Pierola, Olesa-Les Fonts, Terrassa-Viladecavalls and Castellar del Vallès; Casanovas-Vilar et al. 2008; Fig. 1.5), in which alluvial plains with flooding events, canal deposits and/or small lakes and ponds were developed. Given that the source of material for these fans is situated on the mountain chains at the norhwestern area of the basin, the depositional sequence becomes narrower towards its southern portion, where the fossil localities are located (Cabrera and Calvet 1990; Garcés 1995). Both Middle Miocene and Late Miocene localities can be distinguished.

Middle Miocene. The classical Middle Miocene (late Aragonian) hominoid-bearing sites from the Vallès-Penedès Basin are Trinxera del Ferrocarril (Sant Quirze), from the late Aragonian (late MN7+8, 11.9-11.6 Ma; Bataller 1918, 1928; Golpe Posse 1982, 1993; Casanovas-Vilar et al. 2011a); and Can Mata 1 and Can Vila, both situated in the area of els Hostalets de Pierola (Bataller 1938; Villalta and Crusafont 1941, 1944; Crusafont and Truyols 1954; Crusafont and Golpe 1973; Golpe-Posse 1974). The two latter localities have been traditionally grouped, together with other Middle Miocene localities from els Hostalets, in “Hostalets inferior” (Crusafont and Truyols 1954; Golpe-Posse 1974; Agustí et al. 1985, 1997, 2001), due to the lack of precise stratigraphic control. This situation therefore dramatically contrasts with the local stratigraphic series of Abocador de Can Mata (ACM), exposed during the last decade thanks to building works of a landfill in this area (Alba et al. 2006a,b, 2009, 2011a,b,c; Moyà-Solà et al. 2009b; Casanovas-Vilar et al. 2011a).

More than 250 fossil vertebrate localities have been formally defined along the composite section of ACM, which has a thickness of about 250 m and ranges from about 12.6 to 10.5 Ma (Alba et al. 2006a,b, 2009, 2011a,b,c; Moyà-Solà et al. 2009a; Casanovas-Vilar et al. 2008, 2011a;

updated age estimates provided by David M. Alba, pers. comm. 2014). Several of these localities, which can be accurately dated thanks to detailed litho-, magneto- and biostratigraphic correlation (Moyà-Solà et al. 2009b; Casanovas-Vilar et al. 2011a), have yielded primate remains, including those of hominoids; they are the following (updated age estimates, following Hilgen et al. 2012, provided by David M. Alba, pers. comm. 2014): ACM/BCV1, with an estimated age of 12.0 Ma and correlated to the early MN7+8 (Moyà-Solà et al. 2009a; Casanovas-Vilar et al. 2011a; Alba 2012a; Alba et al. 2012c); ACM/C3-Aj, with an estimated age of 12.0 Ma correlated to the early MN7+8 (Moyà-Solà et al. 2009a; Casanovas-Vilar et al. 2011a; Alba 2012a; Alba et al. 2012c); ACM/C3-Ae, with an estimated age 11.9 Ma and correlated to the MN7+MN8 (Moyà-Solà et al. 2009b; Alba 2012a; Alba et al. 2012c); ACM/C1-E*, with an estimated age of 12.4–12.3 Ma and correlated to the early MN7+8 (Casanovas-Vilar et al. 2011a; Alba 2012a; Alba et al. 2012c).

Late Miocene. The Late Miocene (early and late Vallesian) hominoid-bearing localities of the Vallès-Penedès Basin are situated in the Vallès sector of the basin, since none of the Hostalets localities (situated in the Penedès sector) has thus far provided fossil remains of hominoids. All these localities are in the area of the Terrassa-Viladecavalls and Castellar del Vallès alluvial fan systems. They are the following: Castell de Barberà (Barberà del Vallès), previously considered to be late Aragonian (late MN7+8; e.g., Casanovas-Vilar et al. 2011a), but most likely attributable to the earliest Vallesian (11.2-10.5 Ma; Crusafont and Golpe-Posse 1973, 1974; Golpe-Posse 1974; Almécija et al. 2011; Alba 2012a; Alba and Moyà-Solà 2012); Can Poncic (Sant Quirze), from the early Vallesian (MN9; 10.4-9.9 Ma; Golpe-Posse 1974; Crusafont and Hartenberger 1975; Crusafont and Golpe-Posse 1974; Casanovas-Vilar et al. 2011a); Polinyà 2 (Polinyà), from the late Vallesian (MN10; 11.1-9.7 Ma Golpe-Posse 1982,1993; Alba 2012a); Can Feu (Sant Quirze), from the early Vallesian (MN9; 10.0–9.7; Alba et al. 2012b; Casanovas et al. 2012); Can Llobateres 1 (Sabadell), from the early Vallesian (MN9; 9.7 Ma; Garcés et al. 1996; Agustí et al. 1996, 1997; Alba et al. 2011b,c, 2012b; Casanovas-Vilar et al. 2011a); Can Llobateres 2 (Sabadell), from the late Vallesian (MN10, 9.6 Ma; Agustí et al. 1996, 1997, 2001; Casanovas-Vilar et al. 2011a; Alba et al. 2011a); and La Tarumba 1 (Viladecavalls), from the late Vallesian (MN10, 9.5 Ma; Villalta Comella and Crusafont Pairó 1944; Agustí et al. 1997; Casanovas-Vilar et al. 2011b).

CHAPTER 2

Cranial and mandibular remains
(pp. 63-160)

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Chapter 3

New dental remains of *Anoiapithecus* and the first appearance datum of hominoids in the Iberiam Peninsula

Reproduced from: Alba, D.M., Fortuny, J., **Pérez de los Ríos, M.**, Zanolli, C., Almécija, S., Casanovas-Vilar, I., Robles, J.M & Moyà-Solà, S. (2013). New dental remains of *Anoiapithecus* and the first appearance datum of hominoids in the Iberian Peninsula. *Journal of Human Evolution, 65,* 573–584.

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New dental remains of *Anoiapithecus* and the first appearance datum of hominoids in the Iberian Peninsula

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ABSTRACT

New dental remains of the fossil great ape *Anoiapithecus brevirostris* are described from the Middle Miocene local stratigraphic series of Abocador de Can Mata (ACM) in els Hostalets de Pierola (Vallès-Penedès Basin, NE Iberian Peninsula). These specimens correspond to maxillary fragments with upper teeth from two female individuals from two different localities: left P^3–M^1 (IPS41712) from ACM/C3-Aj (type locality; 11.9 Ma [millions of years ago]); and right M^1–M^2 and left P^4–M^2 (IPS35027) from ACM/C1-E* (12.3–12.2 Ma). Relative enamel thickness is also computed in the latter individual and re-evaluated in other Middle Miocene hominoids from ACM, in order to better assess their taxonomic affinities. With regard to maxillary sinus development, occlusal morphology, molar proportions and enamel thickness, the new specimens show greater resemblances with the (male) holotype specimen of *A. brevirostris*. They differ from *Pierolapithecus catalaunicus* in displaying less inflated crests, a more lingually-located hypocone, and relatively lower-crowned molars; from *Dryopithecus fontani*, in the relatively thicker enamel and lower-crowned molars; from *Hispanopithecus* spp., in the more inflated crown bases, less peripheral cusps and more restricted maxillary sinus; and from *Hispanopithecus laietanus* also in the thicker crests, more restricted occlusal foveae, and relatively lower-crowned molars. The new specimens of *A. brevirostris* show some slight differences compared with the holotype of this species: smaller size (presumably due to sexual size dimorphism), and less distally-tapering M^2 occlusal contour (which is highly variable in both extant and extinct hominoids). The reported remains provide valuable new evidence on dental intraspecific variation and sexual dimorphism in *Anoiapithecus*. From a taxonomic viewpoint, they support the distinction of this taxon from both *Dryopithecus* and *Pierolapithecus*. From a chronostratigraphic perspective, IPS35027 from ACM/C1-E* enlarges the known temporal distribution of *Anoiapithecus*, further representing the oldest record (first appearance datum) of hominoids in the Iberian Peninsula.

Introduction

In the Iberian Peninsula, Miocene apes are only recorded from Catalonia, where five different species from four different genera are recognized (Alba, 2012, and references therein): *Pierolapithecus catalaunicus*, *Anoiapithecus brevirostris* and *Dryopithecus fontani*, from different late Aragonian (Middle Miocene) sites of Abocador de Can Mata (ACM; Vallès-Penedès Basin); *Hispanopithecus* (*Hispanopithecus*) *crusafonti*, from the early Vallesian (Late Miocene) of

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Teuleria del Firal (Seu d'Urgell Basin) and Can Poncic 1 (Vallès-Penedès Basin); and *Hispanopithecus* (*Hispanopithecus*) *laietanus*, from early to late Vallesian sites of the Vallès-Penedès Basin (La Tarumba 1, Polinyà 2, Can Llobateres 1 and 2, and EDAR 13).

The distinction of four different hominoid genera in a three million-years span within the Vallès-Penedès Basin reveals a previously unsuspected paleobiodiversity for this group in the European Miocene (Alba, 2012; Alba and Moyà-Solà, 2012a; Pickford, 2012). This has led some authors to question the distinct generic/species status of *Pierolapithecus* and *Anoiapithecus* (Begun, 2009; Begun et al., 2012). The small sample sizes currently available for most of the taxa seriously hamper a proper evaluation of their alpha-taxonomy, which is further complicated by the generally considerable degree of sexual dimorphism in Miocene apes. These difficulties have led to various taxonomic disagreements, specifically whether the La Grive hominoid incisor should (Begun, 2009; Pickford, 2012) or should not (Pérez de los Ríos et al., 2013) be attributed to the same taxon as the holotype of *Pierolapithecus*, whether the Can Poncic hominoid (*H. crusafonti*) is (Begun, 1992; Alba, 2012; Alba et al., 2012a) or is not (Harrison, 1991; Ribot et al., 1996) a different species from that of Can Llobateres (*H. laietanus*), and whether the Teuleria del Firal hominoid is *H. crusafonti* (Begun, 1992, 2002; Alba, 2012; Alba et al., 2012a) or *D. fontani* (Harrison, 1991; Andrews et al., 1996; Ribot et al., 1996).

In the Vallès-Penedès Basin, hominoid fossil remains are usually very scarce compared with most other mammals, and hence their recovery generally requires a large sampling effort. In this sense, enlarging the available samples for the various described taxa—even by a few individuals—represents a valuable addition for refining and/or revising their alpha-taxonomy, chronostratigraphic range and degree of sexual dimorphism. Here we describe and figure unpublished upper dentognathic hominoid remains from two ACM localities: ACM/C1-E*, with an estimated age of 12.3–12.2 Ma (millions of years ago) (Casanovas-Vilar et al., 2011; Alba, 2012; Alba et al., 2012b); and ACM/C3-Aj (the type locality of *A. brevirostris*), with an estimated age of 11.9 Ma (Moyà-Solà et al., 2009a; Casanovas-Vilar et al., 2011; Alba, 2012; Alba et al., 2012b). These specimens are compared below with other maxillary remains from the same basin, leading us to conclude that the former are attributable to female individuals of *A. brevirostris*.

Materials and methods

Dental terminology

The dental terminology employed in this paper (see Fig. 1) generally follows Harrison and Gu (1999; see also Alba et al., 2010b), except that, as in Pérez de los Ríos et al. (2013), we follow Swindler (2002) in using 'protoconule' instead of its synonym 'paraconule', also frequently used by other authors (e.g., Szalay and Delson, 1979; Harrison and Gu, 1999).

Studied sample

The hominoid specimen from ACM/C1-E* (IPS35027) includes a right maxillary fragment with P^3–P^4 roots and M^1–M^2 implanted crowns (Fig. 2A–E) as well as a left maxillary fragment with P^4–M^1 and detached M^2 crown with partial roots (Fig. 2F–J). Both specimens were found in anatomical position within a single block of sediment, but the portion of maxillary bone connecting both fragments was already missing before burial. The left maxillary fragment from ACM/C3-Aj (IPS41712) preserves the P^3–M^1 series (Fig. 2K–M) and associated detached canine root (Fig. 2N–P). It was found during the screen-washing of the sediments excavated from the type locality of *A. brevirostris*.

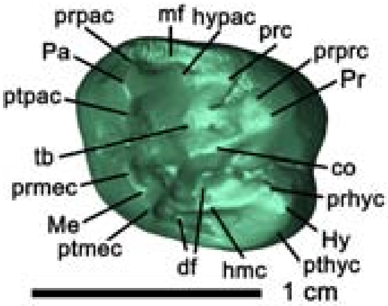

Figure 1. Dental terminology employed in this paper, based on a virtual model of the right M^2 of *Anoiapithecus brevirostris* IPS35027 described in this paper in occlusal view. Abbreviations: co, crista obliqua (postprotocrista + hypometacrista); df, distal fovea; hmc, hypocone metacone crista; Hy, hypocone; hypac, hypoparacrista; Me, metacone; mf, mesial fovea; Pa, paracrista; Pr, protocone; prc, protoconule; prhyc, prehypocrista; prmec, premetacrista; prpac, preparacrista; prprc, preprotocrista; pthyc, posthypocrista; ptmec, postmetacrista; ptpac, postparacrista; tb, trigon basin.

These specimens, housed at the Institut Català de Paleontologia Miquel Crusafont (ICP), are compared with the sample of upper dental hominoid remains from the Vallès-Penedès Basin deposited at the same institution. They include the holotypes of *Pierolapithecus catalaunicus* from ACM/BCV1 (IPS21350; Moyà-Solà et al., 2004), *A. brevirostris* from ACM/C3-Aj (IPS43000; Moyà-Solà et al., 2009a) and *Hispanopithecus crusafonti* from Can Poncic 1 (IPS1798; Begun, 1992), together with remains of *Dryopithecus fontani* from ACM/C3-Ae (Moyà-Solà et al., 2009b), *H. crusafonti* from Can Poncic 1 (Begun, 1992; Golpe-Posse, 1993) and *H. laietanus* from Can Llobateres 1 (Begun et al., 1990; Golpe-Posse, 1993; Alba et al., 2012a [1]) and 2 (Moyà-Solà and Köhler, 1995). The isolated M^2 from Hostalets de Pierola (MLGSB 48486; Made and Ribot, 1999), deposited at the Museu del Seminari Conciliar de Barcelona, was further included in the comparative sample.

Relative enamel thickness

Teeth of the new specimen IPS35027, as well as of the holotype of *A. brevirostris* (IPS43000), the holotype of *Pierolapithecus catalaunicus* (IPS21350) and a specimen of *Dryopithecus fontani* (IPS35026) were scanned by X-ray microCT at the Multidisciplinary Laboratory of the International Centre for Theoretical Physics of Trieste, Italy (Tuniz et al., 2013). The following parameters were used: 120 kV (IPS43000 left), 140 kV (IPS35027 and IPS43000 right), 149 kV (IPS35026) and 150 kV (IPS21350) voltage; 62 μA (IPS35027 and IPS43000 right), 83 μA (IPS43000 left), 200 μA (IPS21350) and 201 μA (IPS35026) current; 2400 projections. The slices were reconstructed using Cobra v.7.4 (Exxim), obtaining an isotropic voxel size ranging from 13.33 to 18.18 μm. Slices were processed and processed into ImageJ 1.46r software (developed at the U.S. National Institutes of Health and available from the internet at http://rsb.info.nih.gov/ij/) and a semi-automatic threshold-based segmentation was carried out with Avizo 7.1 software (VSG).

Two-dimensional relative enamel thickness (2D RET) was computed on the basis of virtual coronal buccolingual sections passing through the tips of the mesial dentine horns in order not to overestimate RET due to obliquity (Smith et al., 2003). Image stacks

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[1] Alba et al. (2012a) reported a partial P^3 (IPS58334) from Can Llobateres 1, but subsequently the missing fragment was recovered while screen-washing the excavated sediments (Fig. 2I), so that now it is possible to include reliable measurements of this specimen: MD 7.2 mm (estimated, although only very small portion of enamel are missing); BL 11.1 mm.

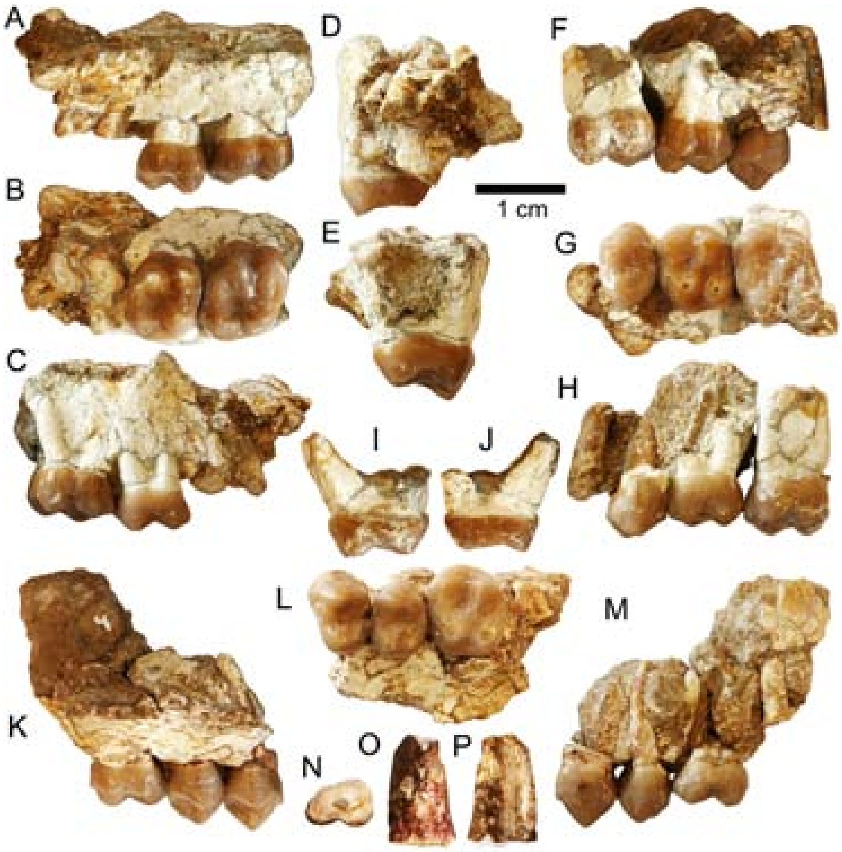

Figure 2. New remains of *Anoiapithecus brevirostris* from ACM. A–E, Right maxillary fragment with M^1–M^2 IPS35027 from ACM/C1-E*, in lingual (A), occlusal (B), buccal (C), mesial (D) and distal (E) views; F–J, left dental series with P^4–M^2 IPS35027 from ACM/C1-E*, in lingual (F), occlusal (G) and buccal (H) views, and details of the M^2 in distal (I) and mesial (J) views; K–P, left dental series with P^3–M^1 IPS41712 from ACM/C3-Aj, in lingual (K), occlusal (L) and buccal (M) views, as well as associated female canine root of the same individual, in occlusal (N), buccal (O) and lingual (P) views.

were three-dimensionally oriented parallel to the plane defined by three dentine horn tips, and a perpendicular plane was then passed through the mesial ones (Olejniczak, 2006). According to Smith et al. (2012b), this method does not yield significantly different results from that used by Smith et al. (2010), which is more similar to that employed in physical sectioning (e.g., Smith et al., 2005). The formula to compute RET, after Martin (1983, 1985), is summarized by Smith et al. (2005; see also footnotes in Table 2 and Alba et al., 2010a). Enamel thickness categories follow Martin (1985). As previously done by other authors (e.g., Smith et al., 2005), for several of the analyzed teeth it was necessary to correct RET measurements to account for tooth wear (too worn specimens, such as the M^1 of IPS35027, where disregarded).

The RET results reported here for the Middle Miocene hominoids from the Vallès-Penedès Basin are based on higher resolution microCT-scans than those previously reported by Alba et al. (2010a). These new results are compared with those previously published by other extinct as well as extant hominoids (summarized in Alba et al., 2010a, their Table S2, and further complemented by Zanolli et al., 2010; see our Table S1). Differences in RET between the Middle Miocene hominoids from the Vallès-Penedès Basin were tested by means of analysis of variance (ANOVA) with SPSS v. 16.0 for Mac. A study of 3D relative enamel thickness of the Vallès-Penedès hominoids is currently underway, so that the 2D comparisons provided here might be further refined in the future when three-dimensional data become available.

Dental measurements

Dental measurements Measurements of mesiodistal length (MD), buccolingual breadth (BL)— separately at the mesial (BLm) and distal (BLd) lobes in molars— and buccal maximum height (H) were measured to the nearest 0.1 mm with a digital caliper and compared with measurements taken for other specimens from the Vallès-Penedès Basin by the authors of this paper. The breadth/length index (BLI, in %) was computed as BL (maximum)/MD * 100, whereas relative crown height (RCH, in %) was computed as H/MD * 100. Bivariate plots of BL versus MD were employed to visually assess dental size and occlusal proportions, whereas boxplots were used for comparing H and RCH.

Coefficient of variation To evaluate the significance of differences in dental measurements between *Anoiapithecus* and other Middle Miocene hominoids while taking into account the degree of intraspecific variability in extant taxa, we relied on M^1 and M^2 from mixed-sex samples of both chimpanzees and orangutans. Measurements were taken by DMA (American Museum of Natural History, New York, USA) and MPR (Muséum National d'Histoire Naturelle, Paris, France). The corrected coefficient of variation (CV, in %) was computed in these samples as CV = (SD/mean) * [1 + (1/4*N*)] * 100 (Sokal and Rohlf, 1995), where SD is the standard deviation and *N* the size of the sample. CV values derived from the extant samples were computed to those computed for the M^1 and M^2 of both *Anoiapithecus* and Middle Miocene hominoids from the Vallès-Penedès Basin as a whole.

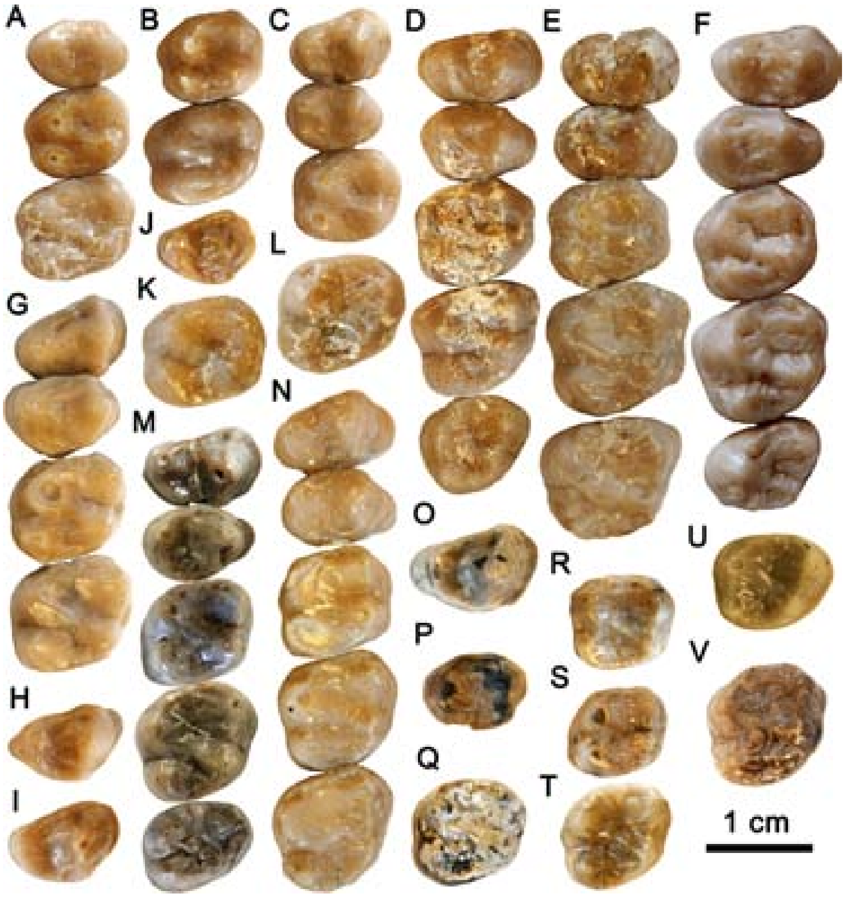

Figure 3. The new remains of *Anoiapithecus brevirostris* from ACM compared with selected most representative upper postcanine teeth of Vallès-Penedès hominoids, in occlusal view. A–B, Left P^4–M^2 (A) and right (reversed) M^1–M^2 (B) IPS35027 of *A. brevirostris* from ACM/C1-E*; C, left P^3–M^1 IPS41712 of *A. brevirostris* from ACM/C3-Aj; D, left P^3–M^2 and right (reversed) M^3 of *A. brevirostris* IPS43000 (holotype); E, left P^3–M^3 of *Dryopithecus fontani* IPS35026; F, right (reversed) P^3-M^3 of *Pierolapithecus catalaunicus* IPS21350 (holotype); G, left P^3–M^2 of *Hispanopithecus crusafonti* IPS1798 (holotype); H, left P^3 of *Hispanopithecus crusafonti* IPS1806; I, right (reversed) P^3 of *Hispanopithecus crusafonti* IPS1810; J, right (reversed) P^3 of *Hispanopithecus crusafonti* IPS1817; K, left M^1 of *H. crusafonti* IPS1818; L, left M^2 IPS1820 of *H. crusafonti*; M, composite left P^3–M^3 series of *H. laietanus* (IPS58334, IPS58336, IPS58338, IPS58339 and IPS58340); N, right (reversed) P^3–M^3 of *H. laietanus* IPS18000.5; O, right (reversed) P^3 of *H. laietanus* IPS1792; P, right (reversed) P^4 of *H. laietanus* IPS1787; Q, right (reversed) M^1 of *H. laietanus* IPS1844; R, left M^1 of *H. laietanus* IPS1781; S, left M^1 of *H. laietanus* IPS1788; T, left M^2 IPS1794 of *H. laietanus*; U, left M^2? of *H. laietanus* IPS1771 from Can Llobateres 1; V, right (reversed) M^2 of Dryopithecinae indet. MLGSB 48486.

Systematic paleontology[2]

Order Primates Linnaeus, 1758
Infraorder Catarrhini É. Geoffroy Saint-Hilaire, 1812
Superfamily Hominoidea Gray, 1825
Family Hominidae Gray, 1825
Subfamily Dryopithecinae Gregory and Hellman, 1939
Tribe Dryopithecini Gregory and Hellman, 1939
Genus *Anoiapithecus* Moyà-Solà et al., 2009a
A. brevirostris Moyà-Solà et al., 2009a
(Figs. 2, 3A–D, 4A–D, 7, S1A–B).

Holotype IPS43000, partial cranium with associated mandible from ACM/C3-Aj (see dental details in Figs. 3D, 4C–D, 7E–F, S1B).

Studied material IPS35027 (Figs. 2A–J, 3A–B, 4A–B, 7A–D, S1A), partial upper right and left maxillary fragments from ACM/C1-E*; IPS41712 (Figs. 2K–M, 3C; topotype), left partial maxillary fragment from ACM/C3-Aj.

Dental measurements (Table 1).

Preservation

IPS35027 The right maxillary fragment (Fig. 2A–E) preserves the partial roots of the canine and premolars, as well as the implanted M^1 and M^2. The right M^1 displays an intermediate degree of wear, with dentine exposure at the protocone, hypocone and protoconule, whereas the right M^2 displays a slighter degree of wear, with no dentine exposure. The left fragment (Fig. 2F–H) preserves a much more restricted portion of maxillary bone, including the lingual root of the P^3 as well as the implanted P^4 (whose buccal roots are missing) and M^1 (in which the tip of the distolingual root and most of the mesiolingual root are missing). Furthermore, the detached left M^2 is also preserved (Fig. 2F–J), including the whole crown and almost the complete mesiolingual and buccolingual roots, whereas the buccal one is broken close to

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[2] The taxonomy employed in this paper follows Alba (2012); see Begun (2009) and Begun et al. (2012) for an alternative interpretation regarding the validity of the genera *Anoiapithecus* and *Pierolapithecus*, which according to these authors might be junior synonyms of *Dryopithecus* (see Alba, 2012, for further details). Moreover, following Alba (2012; see also Casanovas-Vilar et al., 2011), *Rudapithecus* is considered a subgenus of *Hispanopithecus*, instead of a different genus as considered by other authors (Begun, 2009; Begun et al., 2012).

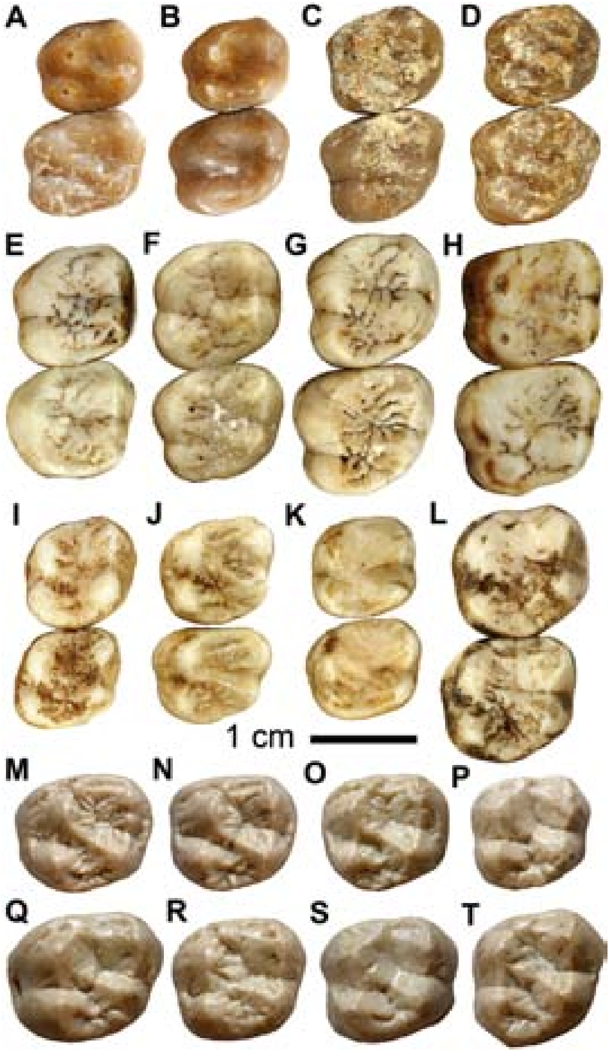

Figure 4. Variation in M^1 and M^2 occlusal proportions and talon development in *Anoiapithecus brevirostris* (A–D), compared with those displayed by selected extant and fossil hominoids, including orangutans (*Pongo pygmaeus*, E–H), chimpanzees (*Pan troglodytes*, I, J, L) and bonobos (*Pan paniscus*, K) housed at the American Museum of Natural History (AMNH) in New York (USA), as well as *Griphopithecus alpani* from Paşalar (M–T) on the basis of casts housed at the Institut Català de Paleontologia Miquel Crusafont. A–B, Left M^1–M^2 (A) and right (reversed) M^1–M^2 (B) IPS35027; C–D, left M^1–M^2 (C) and right (reversed) M^1–M^2 (D) of IPS43000; D, AMNH 239847, female left M^1–M^2; E, AMNH CA2511, female (?) left M^1–M^2; F, AMNH 18010, female left M^1–M^2; G, AMNH 28253, male right (reversed) M^1–M^2; H, AMNH 51378, female right (reversed) M^1–M^2; I, AMNH 5094 female right (reversed) M^1–M^2; J, AMNH 86857, female left M^1 and right M^2 (reversed); K, AMNH 89352, male right (reversed) M^1–M^2; L, C94, left M^1; M, C104, left M^1; N, C237, right (reversed) M^1; O, C107, right (reversed) M^1; P, C109, left M^2; Q, C307, left M^2; R, C233, right (reversed) M^2; S, C105, right (reversed) M^2.

its base. The left P^4 and M^2 show a moderate degree of wear with no dentine exposure, whereas the M^1 shows minimal dentine exposure at the protoconule and the tips of the protocone and hypocone (but less so than in its antimere).

IPS41712 This left maxillary fragment preserves the P^3–M^1 series (Fig. 2K–M) as well as the canine root (Fig. 2N–P). The P^3 crown is somewhat damaged, being broken into two fragments, which match perfectly except for minute enamel portions on the mesial and distal sides of the crown. The premolars display a moderate degree of wear with almost no dentine exposure, whereas the M^1 shows an intermediate degree of wear with some dentine exposure at the apices of the lingual cusps. The preserved portion of maxillary bone is abraded, especially on its outer side, so that the buccal roots of the cheek teeth are missing (P^3 and M^1) or somewhat damaged (P^4). The apical-most portion of the M^2 mesiolingual root is also preserved and attached to the bone. The breakage in this root is not fresh, suggesting that this tooth was not originally preserved. In contrast, the detached root of the left canine shows a fresh fracture, suggesting that the crown might have been present at the time of burial.

Description

Maxillary sinus The preserved molar portion of the right maxillary bone of IPS35027 shows that the maxillary sinus was quite restricted, since only a small sinus cell can be recognized over the M^2 roots. There is no evidence of the maxillary sinus spreading towards the anterior teeth (although this area is badly damaged), and in any case it can be securely ascertained that this sinus does not spread around the molar roots. There is neither any evidence of a zygomatic recess continuous with the maxillary sinus. The poor preservation of the maxillary bone in IPS41712 precludes providing further details on maxillary sinus extent based on this specimen.

Canines The preserved portion of the right canine root of IPS35027 (Fig. 2F–H) is 10.2 mm in height, and displays maximum preserved dimensions of 6.8 × 5.4 mm. In turn, the left canine root of IPS41712 (Fig. 2N–P) is 12.7 mm in height, with maximum preserved dimensions of 7.7 × 5.4 mm. Both specimens display a buccolingually compressed, suboval section, with a convex buccal profile and a biconvex lingual contour (due to the presence of a broad lingual sulcus). Although both roots are broken some millimeters above the cervix, their dimensions clearly suggest that the crown would not have been large compared with postcanine teeth, indicating that both specimens correspond to female individuals. This is further confirmed by the short length of the root, which in IPS35027 (still in situ) does not surpass the apical-most level of the molar roots.

Premolars The premolars (Figs. 2A–C,F–H,K–M) have three roots: a single and stouter lingual one, and two smaller and more slender buccal ones that become fused towards the crown base. The P^3 crown (only preserved in IPS41712; Fig. 2K–M) displays a suboval to subtriangular occlusal profile (being much broader than long), with convex contours except for the mesial side, which is straighter and obliquely oriented since the crown is much longer on the buccal than on the lingual side. The paracone is bucolingually-compressed, much higher than the protocone and very medially situated (resulting in a marked buccal flare). From the apex of the former cusp, a sharp crest of mesial direction descends towards the mesiobuccal corner of the crown. A similarly sharp but slightly shorter crest runs distalwards from this cusp. There is a narrow cingulum along the buccal crown wall at about one-third of crown height. A distinct style is present at the mesiobuccal corner of the crown, where the mesial crest and the cingulum merge. A less conspicuous style is present at the distobuccal corner of the crown. Two sinuous crests of transverse direction link the paracone apex with the protocone. The mesial crest delimits a very restricted mesial fovea, which is mainly eroded by wear on the mesial portion of the crown. The distal crest apparently divides the much more extensive fovea into two distinct portions, being partially interrupted by a mesiodistally-directed groove. The development of wrinkling in this fovea is somewhat obscured by wear.

The occlusal morphology and proportions of the P^4 IPS35027 (Fig. 2F–H) and IPS41712 (Fig. 2K–M) are entirely comparable.

Table 1
Dental measurements, provenance and age of the new upper cheek teeth of *Anoiapithecus brevirostris* reported in this paper (IPS35027 and IPS41712), compared with those of the holotype specimen of the same taxon (IPS43000).

Catalogue No.	Locality	Age	Tooth	MD	BLm	BLd	BLI	H	RCH
IPS35027	ACM/C1-E*	12.3–12.2 Ma	R M^1	8.6	10.4	9.8	120.9	4.6	53.0
IPS35027	ACM/C1-E*	12.3–12.2 Ma	R M^2	9.3	11.7	10.5	125.8	5.3	57.3
IPS35027	ACM/C1-E*	12.3–12.2 Ma	L P^4	6.4	10.0	–	156.3	–	–
IPS35027	ACM/C1-E*	12.3–12.2 Ma	L M^1	8.3	10.3	9.7	124.1	4.6	55.5
IPS35027	ACM/C1-E*	12.3–12.2 Ma	L M^2	9.5	11.6	10.5	122.1	5.2	54.7
IPS41712	ACM/C3-Aj	11.9 Ma	L P^3	6.4	9.4	–	146.9	–	–
IPS41712	ACM/C3-Aj	11.9 Ma	L P^4	6.3	8.9	–	141.3	–	–
IPS41712	ACM/C3-Aj	11.9 Ma	L M^1	8.5	9.9	9.4	116.5	4.7	55.3
IPS43000	ACM/C3-Aj	11.9 Ma	R P^4	7.3	>9.2	–	–	–	–
IPS43000	ACM/C3-Aj	11.9 Ma	R M^1	9.5	11.2	10.9	117.9	5.4	56.9
IPS43000	ACM/C3-Aj	11.9 Ma	R M^2	11.3	12.2	10.9	108.0	5.7	50.4
IPS43000	ACM/C3-Aj	11.9 Ma	R M^3	10.6	9.7	10.4	98.1	6.1	57.5
IPS43000	ACM/C3-Aj	11.9 Ma	L P^3	7.0	11.7	–	167.1	–	–
IPS43000	ACM/C3-Aj	11.9 Ma	L P^4	7.2	10.7	–	148.6	–	–
IPS43000	ACM/C3-Aj	11.9 Ma	L M^1	9.8	11.3	10.8	115.3	5.4	54.9
IPS43000	ACM/C3-Aj	11.9 Ma	L M^2	10.9	12.2	10.9	111.9	5.6	51.4

Abbreviations: BLI, breadth/length index (computed as BL (maximum)/MD * 100), in %; BLm, buccolingual breadth (maximum for premolars, of the mesial lobe for molars), in mm; BLd, buccolingual breadth of the distal lobe (only for molars), in mm; H, buccal crown height (only for molars), in mm; L, left; MD, mesiodistal length, in mm; R, right; RCH, relative crown height (computed as H/MD * 100), in %.

Unlike in the preceding premolar, the crown clearly displays a suboval occlusal contour, being broader than long, but somewhat narrower in absolute terms than that of the P^3. The P^4 further differs from the latter in the lesser cusp heteromorphy as well as in being somewhat longer on the lingual than on the buccal moieties of the crown. The P^4 thus displays two main cusps that are subequal in size, the paracone being somewhat more protruding, but also somewhat less extensive and more buccolingually compressed than the protocone. These cusps, situated towards the mesial portion of the crown, are linked by a transverse crest that runs from the protocone towards the mesial aspect of the paracone. This crest is partially interrupted by a sinuous longitudinal groove that runs from the restricted, slit-like mesial fovea (mostly situated on the buccal moiety of the crown) to the center of the much more extensive and subquadrangular distal fovea. Although partially eroded by wear, there is also a second, curved distal crest that connects the protocone with the postparacrista, thus further dividing the distal fovea into two portions. The distal portion is more restricted than the mesial one and, as far as it can be ascertained due to wear, it displays some enamel wrinkling and is distally enclosed by a well-developed marginal ridge. The buccal crown wall is more flaring and basally bulging than the lingual one (although less so than in the P^3), and the cervix does not extend very much onto the root. Unlike in the P^3, no cingula can be discerned, and the styles at the mesiobuccal and distobuccal corners of the crown are poorly developed. The junction between the distal transverse crest and the postparacrista results in a cuspule-like thickening of enamel just distal to the paracone, which can be better discerned in IPS41712, but can still be identified in IPS35027 despite wear.

Molars The molars are intermediate in enamel thickness (Fig. 7A and C and Table 2; see next section for further details) and display a subrectangular occlusal outline, being broader than long (particularly at the mesial lobe), with a convex buccal contour and a biconvex lingual one. The M^1 of both IPS35027 (Fig. 2A–D, F–H) and IPS41712 (Fig. 2K–M) display a similar degree of wear and entirely comparable occlusal proportions and morphology. The M^2, only preserved in IPS35027 (Figs. 2A–C, E–J, 3A–B, S1A), is larger and somewhat more distally tapering than the M^1, but otherwise shows the same occlusal morphology. There are four main cusps, the buccal ones being more mesially situated and more buccolingually compressed than the corresponding lingual ones. The cusps are not very peripherally situated, because the crown base is somewhat bulging on the buccal and, especially, the lingual sides. The protocone is the most extensive cusp, whereas the paracone and metacone are the highest cusps. On the M^1, the two latter cusps are similar in size, whereas in the M^2 the metacone is slightly smaller than the paracone. The hypocone is slightly smaller than the remaining cusps, but relatively larger and well-individualized from the trigon, being situated in a very lingual position relative to the protocone, close to the distolingual corner of the crown.

Table 2
Coefficients of variation for the various dental measurements employed in this paper for the M^1 and M^2 of *Anoiapithecus* (see individual measurements in Table 1) compared with Middle Miocene Vallès-Penedès (MMVP) hominoids as a whole (*Anoiapithecus*, *Pierolapithecus* and *Dryopithecus*) as well as extant chimpanzees and orangutans.

Length, breadth and occlusal proportions				
	N	M^1 MD	M^1 BL	M^1 BLI
Pan troglodytes	74	6.76	10.05	9.89
Pongo pygmaeus	30	8.25	7.50	6.07
Anoiapithecus brevirostris	5	7.82	5.99	3.15
MMVP hominoids	9	8.30	6.66	4.10
	N	M^2 MD	M^2 BL	M^2 BLI
Pan troglodytes	54	7.26	5.83	5.88
Pongo pygmaeus	22	7.13	9.21	8.30
Anoiapithecus brevirostris	4	10.35	2.85	7.62
MMVP hominoids	7	11.14	6.09	6.47
Crown height				
	N	M^1 H	M^1 RCH	
Pan troglodytes	7	5.15	9.56	
Pongo pygmaeus	9	11.65	10.18	
Anoiapithecus brevirostris	5	8.97	2.27	
MMVP hominoids	9	14.08	6.87	
	N	M^2 H	M^2 RCH	
Pan troglodytes	4	7.88	11.76	
Pongo pygmaeus	9	11.77	10.77	
Anoiapithecus brevirostris	2	4.64	6.08	
MMVP hominoids	7	16.22	7.94	

Abbreviations: BLI, breadth/length index, in %; BL, maximum buccolingual breadth, in mm; CV, corrected coefficient of variation; H, buccal crown height, in mm; MD, mesiodistal length, in mm; N, sample size; RCH, relative crown height, in %.

The short preparacrista and the longer, somewhat thicker and more obliquely-oriented preprotocrista join the distinct mesial marginal ridge. At the junction between the latter and the preprotocrista, close to crown midline, there is a relatively distinct protoconule, whose original development is difficult to completely ascertain due to wear. The hypoparacrista, originating from the mesiolingual apex of the paracone apex, is more or less transversely aligned towards to the protoconule, thereby delimiting a slit-like mesial fovea that is mostly situated on the buccal moiety of the crown. Despite wear, some development of enamel wrinkling can be still discerned within the trigon basin in the M^2. There is a marked transverse groove that runs through the ends of the postparacrista and premetacrista, from the lingual side of the crown towards the center of the trigon basin, where it bifurcates. There is a marked, thick and diagonally-oriented crista obliqua, constituted by a short hypometacrista and an equally well-developed but longer postprotocrista, separating the trigon basin from the somewhat smaller distal fovea. The short hypocrista runs towards the distal aspect of the protocone. Both cusps are separated at their bases by a marked transverse to distally-curving groove that runs from the lingual crown wall to the distal fovea. The latter is broader than long, being somewhat more extensive in the M^2 than in the M^1. It displays some development of secondary enamel folds and grooves (mostly obliterated by wear in the M^1), as well as a transverse crest that links the hypocone to the metacone apex (hypocone–metacone crista). This crest, which may be interrupted by the above-mentioned groove, is quite thick and divides the distal fovea into two portions. The distal one is very restricted (fissure-like), further being distally enclosed by the relatively well-developed marginal ridge, which progressively curves until merging with the short posthypocrista and postmetacrista. The crown walls display some faint and poorly-developed vertical enamel folds, particularly around the lingual side. There are no well-developed cingula, but merely poorly-developed remnants (slightly better developed in IPS41712 than in IPS35027). These cingular remnants consist of a short and narrow buccal style between the paracone and metacone (better developed in the M^1 than in the M^2), a vertical groove on the mesiobuccal corner of the crown, and in IPS41712 also poorly developed styles around the mesiolingual aspect of the protocone and between the protocone and hypocone.

Comparisons

Maxillary sinus

Extant hominoids display a large maxillary sinus, which is more developed in great apes than in hylobatids (Rae, 1999; Rae and Koppe, 2000). The presence of this sinus is probably primitive for catarrhines, as suggested by the similar condition displayed in this regard by both stem catarrhines (Rossie, 2005, 2008; Zalmout et al., 2010) as well as putative stem hominoids such as proconsulids and afropithecids (Pérez de los Ríos et al., 2012, and references therein). In contrast, the Middle Miocene dryopithecines from the Vallès-Penedès Basin more closely resemble the presumably derived condition of *Kenyapithecus* (Pickford, 1985), in which the maxillary sinus does not excavate the alveolar process and is also restricted anteriorly (Moyà-Solà et al., 2009a,b; Alba, 2012; Pérez de los Ríos et al., 2012).

As far as preservation enables the evaluation of this feature, no significant variation is found with regard to maxillary sinus development among Middle Miocene hominoids from the Vallès-Penedès Basin. In particular, the restricted maxillary sinus of IPS35027 (Fig. 2A–C), in which it does not reach the molar roots, resembles the condition of *Anoiapithecus* (Moyà-Solà et al., 2009a, their Fig. 5A), *Pierolapithecus* (Moyà-Solà et al., 2009a, their Fig. 5B; Pérez de los Ríos et al., 2012, their Figs. 1 and 2) and *Dryopithecus* (Moyà-Solà et al., 2009b). The phylogenetic significance of this feature should be interpreted very cautiously, given the small available samples for the Middle Miocene Vallès-Penedès hominoids, and the fact that the development of this sinus may vary within a single species (depending on ontogenetic stage, size and sex). This is best illustrated by *Sivapithecus*, in which the larger (male) specimens sometimes display a quite developed maxillary sinus invading the alveolar bone (Ward and Brown, 1986).

Variation in maxillary sinus development cannot be adequately evaluated with the small available samples. However, the fact that the new (female) specimen of *Anoiapithecus* displays a similar condition to the male Middle Miocene dryopithecine specimens further supports the view that these taxa differed in this regard from the Late Miocene *Hispanopithecus* (Pérez de los Ríos et al., 2012), with both *H.* (*H.*) *laietanus* and *H.* (*Rudapithecus*) *hungaricus* displaying a more extensive and anteriorly-projecting maxillary sinus (Moyà-Solà and Köhler, 1993, 1995; Kordos and Begun, 2001). IPS35027 further reinforces the view that *Anoiapithecus*, like *Dryopithecus* (Moyà-Solà et al., 2009a), differs from *Pierolapithecus* and extant great apes by lacking a zygomatic recess of the maxillary sinus (Pérez de los Ríos et al., 2012).

Occlusal morphology

The P^3 of IPS41712 (Fig. 3C) shows an occlusal morphology comparable with other Middle Miocene hominoids from the Vallès-Penedès Basin (Fig. 3D–F), but differs from the Late Miocene *Hispanopithecus* (Fig. 3G–J, M–O) by displaying a less triangular (more oval) occlusal crown profile as well as a lower crown in which the buccal wall does not extend rootwards. The P^4 morphology of both IPS35027 (Fig. 3A) and IPS41712 (Fig. 3C) is also comparable with other Middle Miocene hominoids from the Vallès-Penedès Basin (Fig. 3D–F). In *Hispanopithecus* spp. (Fig. 3G, M–N, P), the hypoparacrista is more mesially directed (it can even join the mesial marginal ridge), resulting in a more restricted mesial fovea (Alba et al., 2012a). Similarly, in this taxon (at least in *H. laietanus*; Fig. 3M–N, P) the curved distal crest running from the protocone to the distal aspect of the paracone is clearly disrupted by the longitudinal groove that runs along the trigon basin (Alba et al., 2012a). This crest is best developed in *Pierolapithecus* (Fig. 3F) and *Dryopithecus* (Fig. 3E), whereas in the newly reported specimens, the holotype of *A. brevirostris* (Fig. 3D), and maybe *H. crusafonti* (Fig. 3G), where it is difficult to ascertain due to wear, the distal transverse crest is only partly interrupted and more clearly recognizable than in *H. laietanus*.

The upper molars of both IPS35027 (Figs. 3A–B, S1A) and IPS41712 (Fig. 3C) are quite similar in morphology to other Miocene apes from the Vallès-Penedès Basin, including the slit-like mesial fovea restricted to the buccal moiety of the crown, the distinct protoconule, and the moderate development of cingula. The new specimens more closely resemble the molars of the Middle Miocene taxa from this basin (Figs. 3D–F, S1B–D), thus differing from *Hispanopithecus* (Fig. 3G, M–N, Q–U) and the isolated M^2 from Hostalets (Fig. 3V), by displaying less peripheral cusps and more bulging crown bases. The presence of a well-developed (usually continuous) secondary crest dividing the distal fovea in the M^2 of IPS35027 more closely resembles the condition of Middle Miocene taxa, since in *Hispanopithecus* spp. such a crest is thinner and usually interrupted by the longitudinal groove. On the other hand, the new specimens, like *Anoiapithecus* (Figs. 3D and S1B), *Dryopithecus* (Figs. 3E, S1C), *Hispanopithecus* (Fig. 3G, M–N, Q–V) and the molar from Hostalets (Fig. 3V), differ from *Pierolapithecus* (Figs. 3F, S1D) in the more moderate development of enamel wrinkling and the less inflated crest pattern (both regarding the main crests as well as the secondary ones and enamel folds). The very lingual position of the M^2 hypocone compared with the protocone in IPS35027 (Figs. 3A–B and S1A) is most comparable with the condition displayed by *Anoiapithecus* (Figs. 3D and S1B) and *H. crusafonti* (Fig. 3G and L), whereas in *Pierolapithecus* and *H. laietanus* these cusps are more longitudinally aligned. IPS35027 (Figs. 3A–B, S1A) only differs significantly from the holotype of *Anoiapithecus* (Figs. 3D, S1A), as well as *Dryopithecus* (Figs. 3E, S1C), *Pierolapithecus* (Figs. 3F and S1D) and *H. laietanus* (Fig. 3M–N, T–U), in displaying a less tapering M^2, due to the lesser development of the talon. As a result, the metacone does not display any accessory distal cuspule and the crown occlusal profile is squarer and more similar to that of the M^1. In these regards, the new specimen more closely resembles *H. crusafonti* (Fig. 3G and L). As for many other features, the currently available small samples hamper an adequate evaluation of the taxonomic significance of the restricted development of the talon in the M^2 of IPS35027. Given the considerable variation displayed in this regard by both extant apes (Fig. 4E–L) and extinct hominoids such as *Griphopithecus* (Fig. 4M–T), we consider it most likely that the above-mentioned differences in occlusal proportions merely reflect intraspecific variation.

Dental size and proportions The upper cheek teeth reported in this paper are smaller than previously known specimens of *Anoiapithecus*, *Pierolapithecus* and *Dryopithecus*, overlapping at most with the smaller (presumably female) specimens of *Hispanopithecus* (Fig. 5). Thus, only the P^4 (Fig. 5B) are somewhat smaller than those of *Hispanopithecus* spp. The P^3 (Fig. 5A) most closely resembles those of *H. crusafonti*, and the M^1 (Fig. 5C) and M^2 (Fig. 5D) resemble the smaller specimens of the two species of *Hispanopithecus*. For the P^4 (Fig. 5B) and M^1 (Fig. 5C), the teeth preserved in both IPS41712 and IPS35027, the new individuals fall very close to one another. Compared with the holotype of *A. brevirostris* (Table 1), the only difference worth mentioning is the proportions of the M^2 in IPS35027 (BLI 122–126%), which are relatively broader (BLI 108–112%) in IPS43000, in agreement with the above-mentioned more tapering profile of the latter.

Given the small samples and lack of female individuals for other Middle Miocene taxa, occlusal dental proportions are in itself of little use for making a taxonomic assignment. However, as further indicated by canine root size, the small size of the newly reported remains is consistent with an attribution to female individuals of previously-known taxa. With regard to crown height for the M^1 and M^2 (Fig. 6), the new specimens most closely approach the condition displayed by the holotype of *A. brevirostris* (see also Table 1) and specimens of *H. crusafonti*, thus differing from other Vallès-Penedès taxa (*Pierolapithecus*, *Dryopithecus* and *H. laietanus*), which display higher values both in absolute (Fig. 6A and B) and relative (Fig. 6C and D) terms.

The metrical variability displayed by the upper molars of *Anoiapithecus* is compared with that of chimpanzees and orangutans in Table 2. In most instances, the CV of *Anoiapithecus* does not surpass that of the extant species displaying a higher value (generally orangutans), except in the case of M^2 length. The latter might be simply attributable to a sampling effect, given that the CV values employed are corrected by sample size (so that small sample sizes tend to inflate CV values). For the remaining measurements, the degree of dental variation displayed by *Anoiapithecus* is generally consistent with a single, sexually-dimorphic species. The corresponding CVs for a sample of Middle Miocene Vallès-Penedès hominoids are generally slightly higher, but still within the range of a single species, except for buccal crown height in both the M^1 and M^2 (Table 2). These results suggest that at least another species

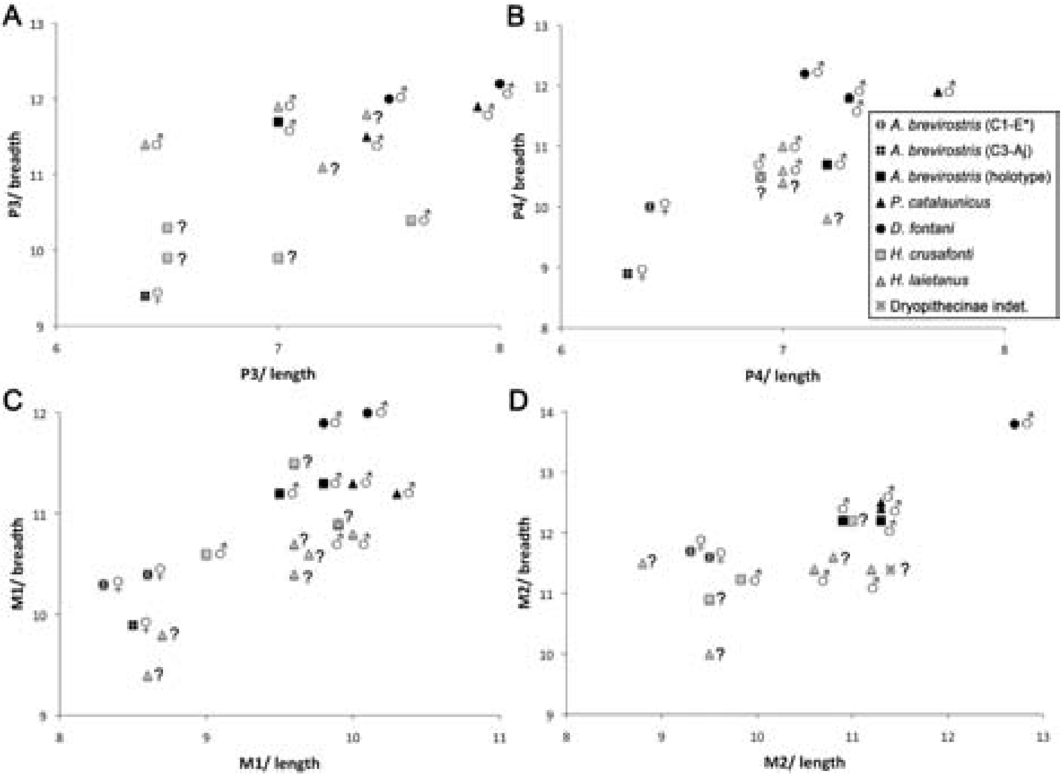

Figure 5. Bivariate plots of buccolingual breadth vs. maximum mesiodistal length of upper cheek teeth (in mm) in the Vallès-Penedès hominoids. A, P^3; B, P^4; C, M^1; D, M^2. Sex is depicted for each individual point when known: ♂, male; ♀, female; ?, unknown.

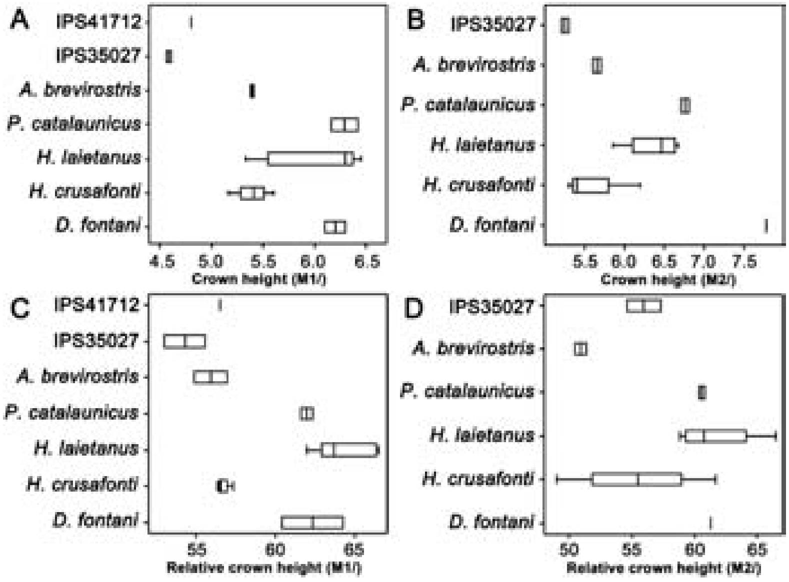

Figure 6. Boxplots depicting absolute (H) and relative (RCH) crown height in the upper molars (M^1 and M^2) of the Vallès-Penedès hominoids. A, H in M^1; B, H in M^2; C, RCH in M^1; D, RCH in M^2.

besides *A. brevirostris* is represented in the sample, differing from the latter much more markedly in crown height than in occlusal size and proportions.

Relative enamel thickness The results of RET for IPS35027 (Fig. 7A and C; Table 3) indicate the possession of intermediate enamel thickness (mean 16.7, range 16.2–17.3, $N = 2$ teeth), slightly thicker than in the holotype of *A. brevirostris* (mean 14.0, range 13.0–14.8, $N = 5$ teeth; Fig. 7E) and the analyzed (male) specimens of *Pierolapithecus* (Fig. 8A) and, especially, *Dryopithecus* (Fig. 8C; see also Tables 3 and 4). When comparing RET results for small samples, the confounding effects of sexual dimorphism and tooth position must be taken into account (e.g., Smith et al., 2005, 2012a). Among extant hominoids, 2D RET generally tends to increase from M1 to M3 (Smith et al., 2005), but this cannot be adequately evaluated in the above-mentioned Middle Miocene hominoids due to small samples sizes. In contrast, the minor differences in RET reported here between the holotype and the new specimen of *Anoiapithecus* might be simply accounted for by the fact that the former corresponds to a male and the latter to a female (based on canine size and shape). In orangutans, males tend to display larger enamel cap areas, enamel-dentine junction lengths, and dentine areas, typically resulting in lower RET values in males than in females across the whole dentition (Smith et al., 2012a).

When the RET results for new the individuals reported here are combined with those derived for the holotype, the values displayed by *Anoiapithecus* (range 13.0–17.3, $N = 7$ teeth, two individuals) do not exceed the maximum–minimum ranges displayed by extinct hominoid samples of similar size (Table S1) (*Griphopithecus* (Smith et al., 2003; after Martin, 1985), *Gigantopithecus* (Olejniczak et al., 2008c) and australopith species (Olejniczak et al., 2008b)— and is clearly surpassed by extinct (Olejniczak et al., 2008a) and extant (Smith et al., 2005, 2006; Olejniczak, 2006) taxa for which much larger samples are available. The differences between the two investigated individuals are therefore perfectly compatible with an attribution to a single species.

The combined results for the seven teeth of the two *Anoiapithecus* individuals indicate an intermediate enamel thickness (mean 14.8), which closely resembles the condition of *Pierolapithecus* (mean 14.9; Fig. 8A), but is somewhat higher than that of *Dryopithecus* (mean 12.7; Fig. 8C) (see Table 4 for descriptive statistics). Based on lower spatial resolution microCT data, Alba et al. (2010a) previously concluded that both *Anoiapithecus* and *Pierolapithecus* displayed a

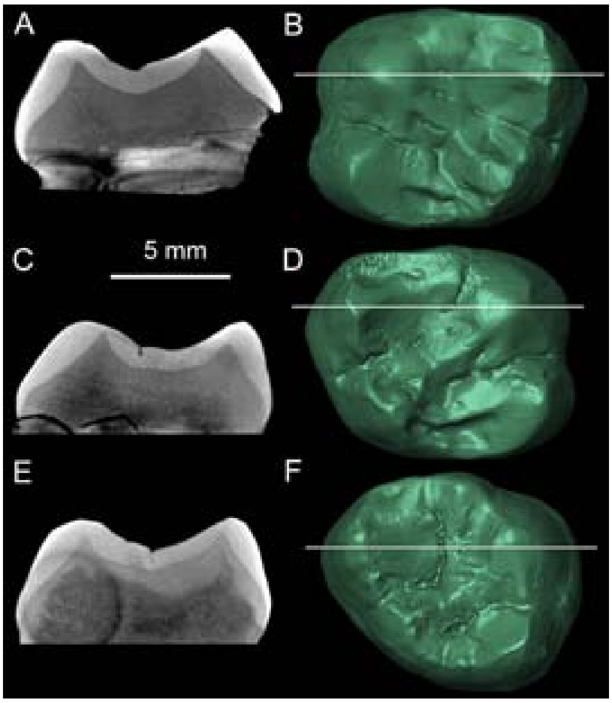

Figure 7. Radiographic coronal sections (A, C, E) and 3D virtual models indicating the plane corresponding to the coronal section (B, D, F) of *Anoiapithecus brevirostris*. A–B, Left M^2 of IPS35027; C–D, right M^2 of IPS35027; E–F, right M^3 of IPS43000 (holotype). Take into account that the sections employed pass through the apices of the mesial dentine horns, and hence not necessarily through the tips of the cusps. Note the common ring artifact in E, which nevertheless does not significantly affect the contrast between the enamel and dentine.

Table 3
Measured variables and computed results for enamel thickness in *Anoiapithecus brevirostris*, *Pierolapithecus catalaunicus* and *Dryopithecus fontani*.

Taxon	Catalogue No.	Tooth	*c*	*b*	*e*	AET	RET	TCA	RDP
Anoiapithecus brevirostris	IPS35027	R M^{2a}	15.06	29.25	17.24	0.87	16.16	44.31	66.00
Anoiapithecus brevirostris	IPS35027	L M^{2a}	12.93	23.76	15.33	0.84	17.31	36.69	64.75
Anoiapithecus brevirostris	IPS43000	R M^{1a}	13.37	28.28	18.04	0.74	13.94	56.00	50.49
Anoiapithecus brevirostris	IPS43000	R M^{2a}	16.69	39.02	18.84	0.89	14.18	55.71	70.04
Anoiapithecus brevirostris	IPS43000	R M^{3}	16.37	36.01	18.48	0.89	14.77	52.39	68.74
Anoiapithecus brevirostris	IPS43000	L M^{1a}	12.60	26.27	17.26	0.73	14.24	38.88	67.57
Anoiapithecus brevirostris	IPS43000	L M^{2}	14.37	36.07	18.45	0.78	12.97	50.44	71.51
Dryopithecus fontani	IPS35026	L M^{2a}	19.02	52.16	21.10	0.90	12.48	71.19	73.27
Dryopithecus fontani	IPS35026	L M^{3a}	19.62	51.55	21.10	0.93	12.95	71.17	72.43
Pierolapithecus catalaunicus	IPS21350	L M^{1a}	13.17	28.40	16.89	0.78	14.63	41.57	68.32
Pierolapithecus catalaunicus	IPS21350	R M^{1a}	12.64	27.04	17.38	0.73	13.99	39.68	68.14
Pierolapithecus catalaunicus	IPS21350	L M^{2}	17.66	39.11	19.40	0.91	14.56	56.78	68.89
Pierolapithecus catalaunicus	IPS21350	R M^{2}	16.70	38.47	18.71	0.89	14.39	55.17	69.72
Pierolapithecus catalaunicus	IPS21350	L M^{3a}	17.37	33.62	17.75	0.98	16.88	51.00	65.93

Abbreviations: AET, 2D average enamel thickness (mm), computed as c/e; b, dentine and pulp area (mm^2); c, enamel cap area (mm^2); e, length of the enamel–dentine junction (mm); L, left; R, right; RDP, relative dentine and pulp area, computed as $b/(b+c)$; RET, 2D relative enamel thickness (%), computed as $[(c/e)/(b)^{1/2}] \times 100$; TCA, total crown area (mm^2), computed as $b + c$.

[a] Corrected data by taking into account tooth wear (only when necessary).

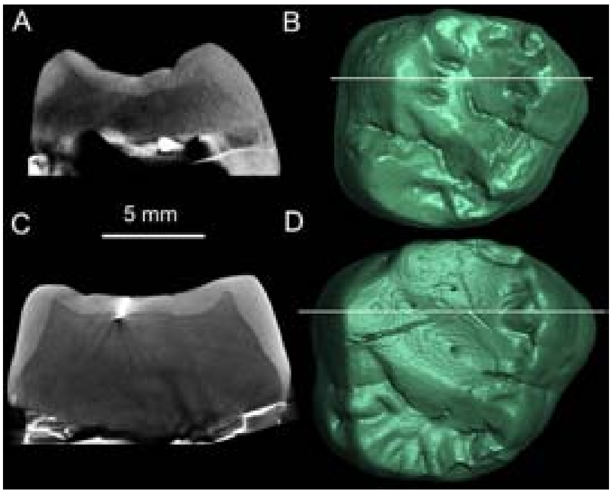

Figure 8. Radiographic coronal sections (A, C) and 3D virtual models indicating the plane corresponding to the coronal section (B, D) of other Middle Miocene Vallès-Penedès hominoids. A, Left M^2 of IPS21350 (*Pierolapithecus catalaunicus*, holotype); C, left M^3 of IPS35026 (*Dryopithecus fontani*).

thick-enameled condition (mean values of 18.6 and 19.5, respectively) that differed from the thin-enameled condition of *Dryopithecus* (mean value 10.6). The revised results reported here indicate that the amount of the differences between the taxa is lower than previously though. Thus, both *Anoiapithecus* and *Pierolapithecus* display an intermediate thick-enameled condition (most similar to orangutans among extant hominoids; Table S1), whereas *Dryopithecus* displays an intermediate thin condition (most similar to African apes; Table S1). In spite of the lower mean RET value of *Dryopithecus* (Fig. S1A), ANOVA comparisons indicate that the three Middle Miocene hominoids do not significantly differ ($F = 2.339$, $p = 0.142$). This is most likely attributable to the small available sample of *Dryopithecus* ($N = 2$ teeth), resulting in too large 95% confidence intervals for the mean in this taxon (Fig. S1B). Additional specimens of these taxa would be required to conclusively assert that such differences do not merely result from a sampling effect. However, based on available data, we provisionally consider that enamel thickness might be taxonomically relevant for distinguishing *Dryopithecus* from both *Anoiapithecus* and *Pierolapithecus*—the RET values of IPS35025 being more consistent with an attribution to *Anoiapithecus* than to *Dryopithecus*.

Table 4
Descriptive statistics for relative enamel thickness (RET) in the three Middle Miocene hominoids from the Vallès-Penedès Basin (see results for individual teeth in Table 2).

	N	Mean	SD	SE	95% CI		Min.	Max.
Anoiapithecus	7	14.80	1.47	0.55	13.44	16.15	12.97	17.32
Dryopithecus	2	12.72	0.33	0.24	9.73	15.70	12.48	12.95
Pierolapithecus	5	14.89	1.14	0.51	13.48	16.31	14.00	16.88

Abbreviations: CI, confidence interval; Max., maximum; Min., minimum; N, sample size; SD, standard deviation; SE, standard error.

Discussion and conclusions

Taxonomic attribution

On the basis of occlusal morphology, the hominoid upper dental remains reported in this paper (IPS35027 and IPS41712) show their greater similarities with the holotype of *A. brevirostris* (IPS43000), and are thus attributed to the same taxon. The specimens attributed to *Anoiapithecus* differ from *Pierolapithecus* in the less inflated crests, the less developed enamel wrinkling, the more lingually-situated hypocone, and the relatively lower-crowned molars. They differ from *Dryopithecus* in the relatively lower-crowned molars and the somewhat thicker dental enamel; from *Hispanopithecus* spp. in the more inflated crown bases, less peripheral cusps and more restricted maxillary sinus; and from *H. laietanus* also in the thicker crests, more restricted occlusal foveae, and relatively lower-crowned molars.

The only noteworthy difference between the newly-reported specimens and the holotype of *A. brevirostris* relates to dental size and the occlusal contour of the M^2. The smaller dental size of the new specimens (attributable to female individuals on the basis of canine root size) compared with the holotype of *A. brevirostris* (a male individual based on canine size and shape) is easily explained by sexual dimorphism. In turn, the less distally-tapering occlusal outline of the M^2 of IPS35027 is highly variable in both extant and extinct hominoids, and therefore attributable to intraspecific variation.

Although there are some differences in occlusal morphology between *Anoiapithecus* and the two Vallès-Penedès species of *Hispanopithecus*, it is worth mentioning that the morphology and proportions of the upper cheek teeth of *H. crusafonti* more closely resemble those of *Anoiapithecus* than those of *H. laietanus*. This 'intermediate' morphology of *H. crusafonti*, in accordance with its older age compared with *H. laietanus* (Casanovas-Vilar et al., 2011) might simply indicate a more plesiomorphic condition in the former. In any case, from a taxonomic viewpoint *H. crusafonti* can be clearly distinguished from *Anoiapithecus* on the basis of other dental details (e.g., male upper canine morphology; Begun, 1992; Moyà-Solà et al., 2009a), further being more similar to *H. laietanus* in other dental features, with some authors (Harrison, 1991; Ribot et al., 1996) having even questioned their distinct species status (see discussion in Alba et al., 2012a). The lack of cranial material for *H. crusafonti* precludes for the moment a more secure assessment of the phylogenetic implications of the above-mentioned similarities between *Anoipaithecus* and *H. crusafonti*. The assignment of the new remains to *A. brevirostris* is further reinforced by the fact that IPS41712 was found in the type locality of this taxon (same stratigraphic horizon as the holotype).

The FAD of hominoids in the Iberian Peninsula

Until about a decade ago, most of the Miocene hominoid remains from the Iberian Peninsula were known from Vallesian levels (Alba, 2012). Aragonian remains were much more scarce, including two lower molars and a molar germ fragment from Can Vila (Villalta Comella and Crusafont-Pairó, 1941, 1944; Golpe-Posse, 1982, 1993; Harrison, 1991), a female canine from Can Mata 1 (Crusafont-Pairó and Golpe-Posse, 1973; Golpe-Posse, 1982, 1993; Harrison, 1991), an isolated upper molar from Hostalets de Pierola (Made and Ribot, 1999), some postcranial remains from Castell de Barberà (Alba et al., 2011b; Almécija et al., 2012), and a tooth fragment from Sant Quirze (Trinxera del Ferrocarril) (Crusafont-Pairó, 1965; Harrison, 1991; Golpe-Posse, 1993).

Such a situation drastically changed in the last decade, due to the more complete finds made in the local stratigraphic series of ACM in els Hostalets de Pierola (Alba et al., 2006, 2011a; Moyà-Solà et al., 2009b; Casanovas-Vilar et al., 2011). On the basis of magnetostratigraphic correlation (Moyà-Solà et al., 2009b), most of the hominoid-bearing levels from ACM are correlated to subchron C5r.3r, with estimated ages between 11.9 and 11.8 Ma (Casanovas-Vilar et al., 2011; Alba, 2012; Alba et al., 2012b). The maxillary fragments from ACM/C1-E* reported here are however older, being correlated to C5An.2n, with an estimated age of 12.3–12.2 Ma (Casanovas-Vilar et al., 2011; Alba, 2012; Alba et al., 2012b).

Unfortunately, classical hominoid finds from Aragonian levels of the Vallès-Penedès Basin cannot be dated with accuracy, either because their exact stratigraphic provenance is unknown or because no magnetostratigraphic data are available from the sites. The age of Castell de Barberà is very uncertain, being usually correlated to the late Aragonian (Casanovas-Vilar et al., 2011), although it is most likely attributable to the earliest Vallesian (Alba and Moyà-Solà, 2012b, and references therein). San Quirze is more securely dated to the late MN7+8 (Casanovas-Vilar et al., 2011). However, the provenance of the tooth fragment labeled as coming from this site is very dubious. In particular, this specimen might actually come from Can Vila (Golpe-Posse, 1982), corresponding to an additional tooth fragment from this locality that was first mentioned by Crusafont-Pairó (1958) but never figured or described. The latter possibility is supported by the red patina and orange color of the enamel in this specimen (DMA and SMS, Personal observation), and in any case Sant Quirze would be somewhat younger than most ACM sites (Casanovas-Vilar et al., 2011).

With regard to the classical hominoid finds from the area of els Hostalets de Pierola, their exact stratigraphic provenance is unknown (Casanovas-Vilar et al., 2011). The upper molar from Hostalets was found in the 1920s by Màrius Guerín (Made and Ribot, 1999), who mostly surveyed the outcroups around Can Mata de la Garriga, especially the ravines from Font d'Ocata and Riera de Claret (Bataller Calatayud, 1938). These outcrops are latest Aragonian to early Vallesian in age (Moyà-Solà et al., 2009b), so that this specimen is most likely younger than all of the hominoid finds from ACM, and more similar in age to the canine from Can Mata 1. Given the lack of hipparionin remains, the latter locality is considered latest Aragonian in age, although lithostratigraphic correlation indicates that it is younger than all of the ACM localities (Moyà-Solà et al., 2009b; Casanovas-Vilar et al., 2011).

With regard to the Can Vila remains, it has been generally considered that their stratigraphic provenance was unknown (Moyà-Solà et al., 2004; Casanovas-Vilar et al., 2011; Alba, 2012). However, according to the recollection by Jordi Martinell, who visited the site in the 1970s together with Miquel Crusafont (Personal communication to DMA in 2011), the Can Vila remains would have been found within the Barranc de Can Vila (BCV), in somewhat lower stratigraphic levels than those corresponding to ACM/BCV1 (the type locality of *P. catalaunicus*). This allows us to discount an age older than 12.0 Ma for the Can Vila remains.

To summarize, with an estimated age of 12.3–12.2 Ma, IPS34027 from ACM/C1-E* represents the first appearance datum (FAD) of hominoids in the Iberian Peninsula. The hominoid FAD is at least 200 kyrs older than the earliest Iberian record of pliopithecids, which also corresponds to the ACM series (Alba et al., 2012b).

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Appendix A. Supplementary material

Supplementary material related to this article can be found at http://dx.doi.org/10.1016/j.jhevol.2013.07.003.

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Appendix A. Supplementary material

Table S1

Mean and range values of relative enamel thickness (RET) for selected extant and fossil hominoids.

Taxon	RET category[a]	N	RET Mean	Min.	Max.
Rangwapithecus gordoni[b]	Intermediate thick	1	14.90		
Proconsul major[b]	Intermediate thin	1	13.70		
Proconsul heseloni[b]	Intermediate thick	1	17.00		
Proconsul nyanzae[b]	Thick	1	22.40		
Proconsul africanus[b]	Thin	1	8.54		
Afropithecus turkanensis[b]	Thick	2	21.38	19.88	22.88
Griphopithecus sp.[b]	Thick	8	19.30	16.50	23.00
Samburupithecus kiptalami[b]	Thick	?	19.00		
Hylobates lar[b]	Thin	1	11.00		
Hylobates sp.[b]	Thin	1	11.09		
Hylobates muelleri[b]	Intermediate thick	11	15.27	10.37	21.83
Hylobates syndactylus[b]	Intermediate thin	17	12.58	9.02	15.59
Ouranopithecus macedoniensis[b]	Thick	1	25.53		
Ouranopithecus turkae[b]	Thick	1	27.30		
Hispanopithecus laietanus[b]	Intermediate thin	1	12.74		
Oreopithecus bambolii[c]	Intermediate thin	2	14.10		
Pierolapithecus catalaunicus[d]	Intermediate thick	5	14.89	14.00	16.88
Anoiapithecus brevirostris[d]	Intermediate thick	7	14.79	12.97	17.32
Dryopithecus fontani[d]	Intermediate thin	2	12.72	12.48	12.95
Pongo pygmaeus[b]	Intermediate thick	41	15.49	8.60	22.50
Sivapithecus sivalensis[b]	Thick	3	19.20	16.30	20.90
Sivapithecus parvada[b]	Thick	1	18.90		
Sivapithecus indicus[b]	Intermediate thick	1	16.50		
Lufengpithecus lufengensis[b]	Thick	?	24.20	24.10	24.60
Lufengpithecus hudiensis[b]	Intermediate thin	1	14.10		

Khoratpithecus piriyai[b]	Thick	1	17.60		
Khoratpithecus chiangmuanensis[b]	Thick	2	17.52	17.23	17.8
Gigantopithecus blacki[b]	Thick	7	21.77	18.99	25.10
Gorilla gorilla[b]	Intermediate thin	15	11.68	9.02	15.22
Pan troglodytes[b]	Intermediate thin	40	13.23	8.50	16.6
Pan paniscus[b]	Intermediate thin	1	13.60		
Paranthropus robustus[b]	Thick	9	28.38	22.49	35.68
Australopithecus africanus[b]	Thick	9	22.79	15.69	31.32
Homo sapiens[b]	Thick	257	20.06	11.76	31.84
Homo neanderthalensis[b]	Intermediate thick	42	16.44	13.77	20.85

Abbreviations: RET, Relative enamel thickness; N = sample size; Min. = minimum; Max. = maximum.

[a] Categories based on Martin (1985) on the basis of mean RET values: thin (<11.31); intermediate thin (11.31–14.64); intermediate thick (14.65–17.49); and thick (>17.49).

[b] Data compiled in Alba et al. (2010b, Table S2) from various references.

[c] Zanolli et al. (2010).

[d] Data from this study (Table 3).

Table S2

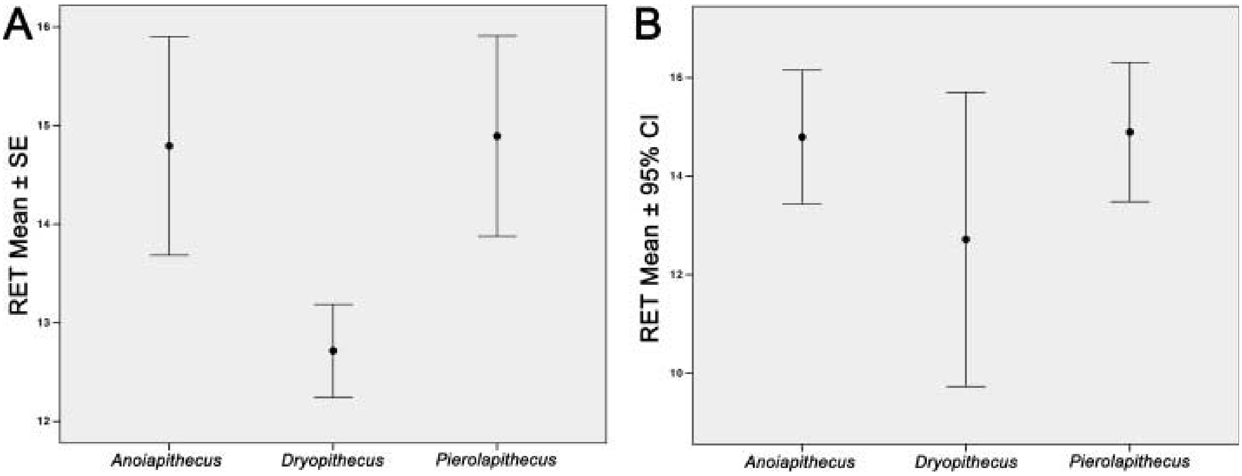
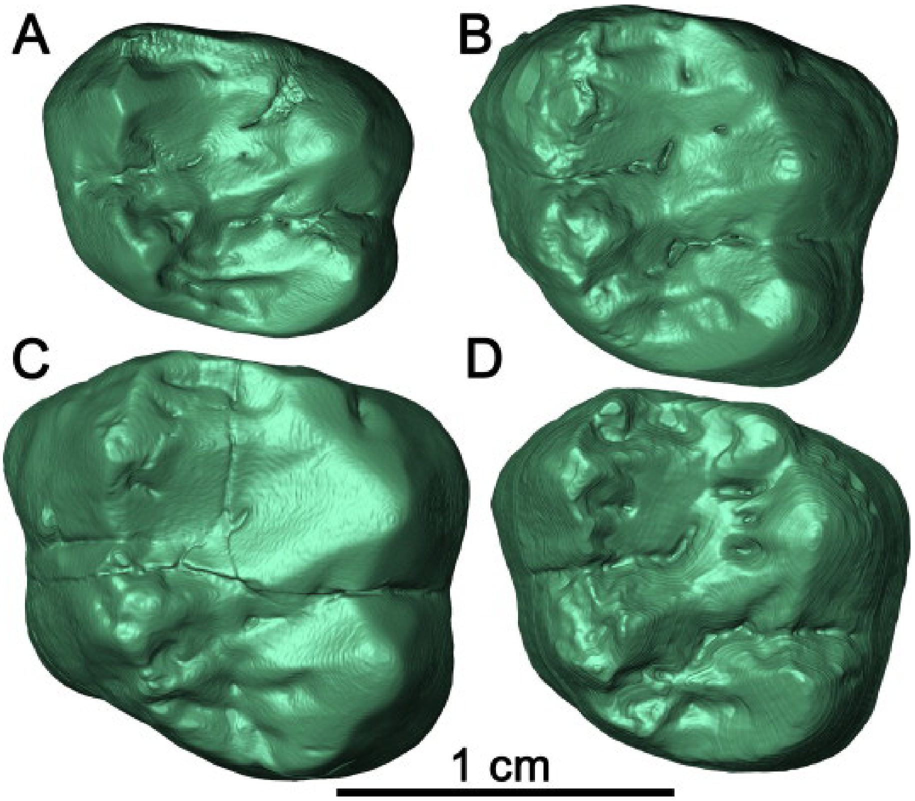


Figure S1



Chapter 4

The nasal and paranasal architecture of the Middle Miocene ape *Pierolapithecus catalaunicus* (Primates: Hominidae): Phylogenetic implications

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The nasal and paranasal architecture of the Middle Miocene ape *Pierolapithecus catalaunicus* (primates: Hominidae): Phylogenetic implications

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ABSTRACT

The internal (nasal and paranasal) cranial anatomy of the Middle Miocene (11.9 Ma [millions of years ago]) great ape *Pierolapithecus catalaunicus* (Hominidae: Dryopithecini) is described on the basis of computed-tomography scans of the holotype specimen (IPS21350), with particular emphasis on its phylogenetic implications. *Pierolapithecus* displays the following characters: an anteriorly-restricted maxillary sinus that posteriorly spreads towards the ethmoidal area (thus resembling the pongine condition), although being situated well above the molar roots (as in kenyapithecins, other dryopithecins and pongines); lack of frontal sinus (a synapomorphy of derived pongines, independently acquired by both cercopithecoids and hylobatids); posteriorly-situated turbinals (as in *Pongo*); anteriorly-projecting nasolacrimal canal (as in *Pongo*); and probably stepped nasal floor with non-overlapping premaxillary–maxillary contact (as in dryopithecines and stem hominoids, although it cannot be conclusively shown due to bone damage). Overall, *Pierolapithecus* displays a mosaic of primitive hominid and derived pongine features that are inconsistent with this taxon being a hominine (as previously suggested). Two alternative phylogenetic interpretations are possible: *Pierolapithecus* may be a stem member of the Hominidae as previously suggested in its original description, or alternatively this taxon may be a stem member of the Ponginae s.l. (with the European dryopithecines being the sister taxon to the Asian pongines).

Introduction

The fossil ape *Pierolapithecus catalaunicus* is known on the basis of the holotype specimen (IPS21350), which includes a partial cranium and skeleton (Moyà-Solà et al., 2004) from the Middle Miocene site of Barranc de Can Vila 1 (ACM/BCV1, Vallès-Penedès Basin, Catalonia, Spain) (Casanovas-Vilar et al., 2008), with an estimated age of 11.9 Ma (millions of years ago) (Moyà-Solà et al., 2009b; Casanovas-Vilar et al., 2011; Alba, 2012). On the basis of cranial and postcranial anatomy, Moyà-Solà et al. (2004) originally considered this taxon to be a stem hominid (see also Moyà-Solà et al., 2005, 2009a, b), although other authors have considered it a stem hominine (Begun and Ward, 2005; Begun, 2009). Most recently, this taxon was included together with *Anoiapithecus*, *Dryopithecus* and several Late Miocene hominoids from Europe into the subfamily Dryopithecinae (Casanovas-Vilar et al., 2011; Alba, 2012).

Besides the information provided in the original description of *Pierolapithecus* (Moyà-Solà et al., 2004) and some additional details discussed in later publications dealing with other Middle Miocene hominoid specimens from the same basin (Moyà-Solà et al., 2009a, b; Pérez de los Ríos et al., 2010; Alba, 2012), the cranial morphology of *Pierolapithecus* remains to be described in detail. The paranasal sinuses and other nasal structures deserve particular attention from a phylogenetic viewpoint (Ward and Kimbel, 1983; Brown and Ward, 1988; Rae and Koppe, 2004; Rossie, 2008; Pérez de los Ríos et al., 2010), potentially being able to refine previous inferences on the most likely phylogenetic relationships of this taxon. Here we describe the internal cranial anatomy of the *Pierolapithecus* splanchnocranium, including the configuration of the paranasal sinuses (ethmoidal, sphenoidal, maxillary and frontal) as well as the morphology of other nasal structures, with the aid of non-invasive computed-tomography techniques. The morphology displayed by *Pierolapithecus* is compared with that of other fossil and extant hominoids, and the phylogenetic implications of the newly-reported data are further discussed.

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Material and methods

Fossil sample

The holotype (IPS21350) of *P. catalaunicus* is housed at the Institut Català de Paleontologia Miquel Crusafont (Catalonia, Spain) and is composed of a partial skeleton that includes the splanchnocranium and most of the upper dentition of a single adult individual (on the basis of the fully erupted C^1 and M^3).

Computed tomography

Computed-tomography (CT) was employed to investigate the internal cranial anatomy of *Pierolapithecus* with non-invasive techniques. IPS21350 was scanned using high-resolution CT (Yxlon Compact 225) at Burgos University (Spain). The line of the X-ray beams was guided perpendicular to the coronal plane of the specimen, oriented in the alveolar plane. CT scanning was performed at 210 kV and 2.20 mA, obtaining up to 440 slices with an inter-slice distance of 0.2 mm and an output of 1024 × 1024 pixels per slice and a resolution of 0.123 mm/pixel. The final CT image of the specimen is composed by the integration of 720 projections. Cross-sectional images processed from the slices were obtained by using the CT scan software MIMICS (Materialise, Belgium), which is required to minimize deficiencies on the image due to differences in density, momentary lack of X-ray beam and other artifacts (Koppe et al., 1999b). Final images were processed with Photoshop CS4 11.0.2. CT scans of extant adult male great ape specimens (*Gorilla*, *Pan* and *Pongo*) were taken from the digital platform Digital Morphology of the University of Texas at Austin (http://digimorph.org/) for comparison and illustrative purposes. Observations on such specimens were supported by extensive data reported in the literature (Cave and Haines, 1940; Cave, 1961; Brown and Ward, 1988; Schwartz, 1990; Koppe and Ohkawa, 1999; Rae and Koppe, 2000; Rossie, 2005, 2008). The CT images obtained in this work enable us to adequately discriminate the matrix from the bone thanks to their differential densities and well-defined structural boundaries, thus allowing us to identify and describe the cranial internal anatomy of *Pierolapithecus*. Transitions between fossil and matrix are sometimes hard to define, but preservation of some structures can differ between the two sides of the cranium, so that when all of the CT slices are taken into account simultaneously, they enable a complete and accurate interpretation of the specimen. Although several internal structures have suffered some damage due to taphonomic processes, such as the turbinals, most of them can still be adequately described.

Description

Preservation

The splanchnocranium of *Pierolapithecus* is generally well preserved, except for some missing portions and distortion. Externally, the cranium shows slight deformation of the sagittal plane towards the right side, mainly affecting the frontal bone, which is also broken at the right upper orbital rim. Furthermore, the two zygomatics are partially broken at the frontozygomatic suture and close to maxillozygomatic suture, being somewhat folded posteriorly. The anterior part of the right and left maxillae, and their external contact with the premaxilla, are lacking, and the premaxilla also lacks its posterior-most portion and its contact with the hard palate. The two palatines and sphenoids are only partially preserved and crushed against the orbital walls.

The configuration of the internal architecture of the nasal and paranasal cavities, although affected by deformation to some degree, can be unambiguously assessed in most instances. The nasal cavity walls are partially crushed, mainly on the left side at the level of M^2, but better preserved on the right side, showing the original morphology of the maxillary sinus and the nasoalveolar canal, which have a continuous development except for very small missing portions. At the interorbital area, the slight deformation externally affecting the contact between the frontal and the nasals does not affect the internal pneumatizations, which are well delimited. At the frontal area, however, several cracks in the bone are infilled with heavy minerals that are perceived as very dense structures in the CT scans. Their interpretation is discussed in greater length below. The left palatine bone displays a low position at the level of M^1, originating a step that is not further observed at the level of the remaining teeth, so it has not influenced the description of the relationship between the hard palate and the premaxilla. The position of the turbinals has been affected by burial processes, being mainly accumulated in the central part of the nasal cavity due to the entry of sediment. Furthermore, the nasal septum is well preserved from the middle M^2 until the posterior portion of the palate, and some of the turbinals are displaced from their original position (being mainly accumulated in the middle of the cavity over the M^3), whereas the more anteriorly-positioned turbinals have been slightly displaced to the right and the nasal septum to the left. This suggests that deformation has mainly affected the anterior part of the nasal cavity but not the paranasal areas, as indicated by the fact that their bony walls are mostly continuous and well preserved.

Paranasal sinuses

The maxillary sinus is the largest cavity identified, although in *Pierolapithecus* it is remarkably reduced in comparison with extant great apes, even more so than in *Pongo*, where the maxillary sinus can spread around the molar roots, a condition not observed in *Pierolapithecus*. In particular, the maxilla is pneumatized all along the area of the molars, occupying a restricted area below the medial side of the orbit. In parasagittal view, the maxillary sinus only extends anteriorly to the M^1 level, although it further extends towards the zygomatic arch (constituting a zygomatic recess) and below the orbits (Fig. 1a). The lower margin of the maxillary sinus is situated well above the molar roots, thus being more restricted than in extant great apes. In some genera, the extension of the maxillary sinus is variable, such as it is the case of *Sivapithecus* (Ward and Brown, 1986; Rae, 1999). Moreover, no palatal recess is present (Fig. 2a). Unambiguously determining the posterior limit of the maxillary sinus is precluded by poor preservation at this area, so that it cannot be conclusively asserted whether a sphenoidal sinus or merely a continuation of the maxillary sinus is present. Moreover, the pneumatization observed at the interorbital/ethmoidal region appears to be linked to the maxillary sinus, due to the absence of recognisable bone boundaries separating these cavities (Fig. 3a). Two distinct cavities, situated below the orbits, can be recognized. The left cavity further extends upwards along the inferior orbital rim, thus spreading towards the nasals until orbital mid height. However, since this cavity does not reach the glabella and it is not separated from the maxillary sinus, the former is most likely interpreted as a frontal recess of the maxillary sinus instead of as an ethmoidal sinus. Finally, the frontal area is characterized by the lack of a distinct frontal sinus, since only a slight porosity (Fig. 3a) can be discerned at the frontal squama, interorbital and glabellar region.

The interpretation of the *Pierolapithecus* condition regarding the frontal sinus is hindered by the presence of very dense internal structures (Fig. 5a) that, if interpreted as bone, would indicate the presence of bony struts (and accompanying epithelia) demarcating

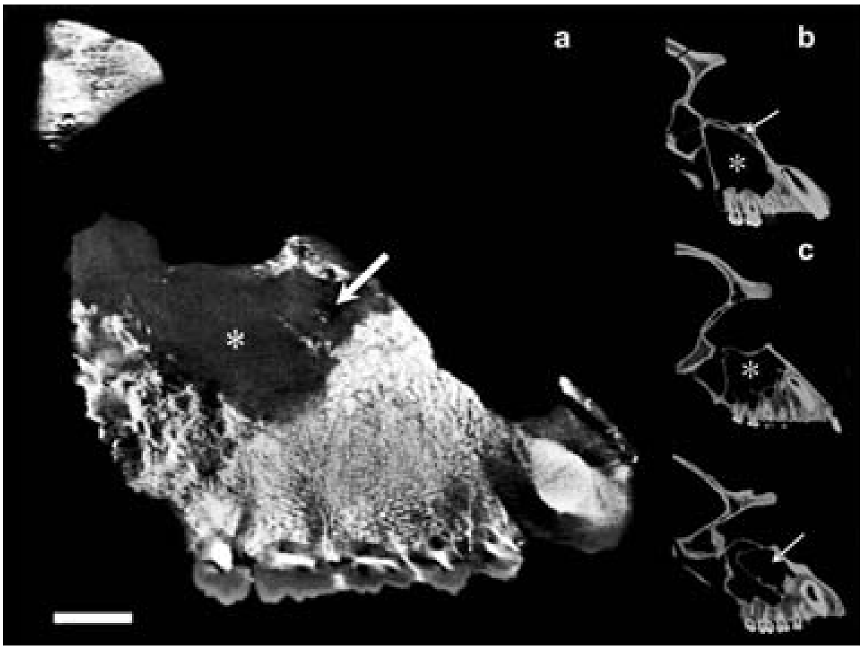

Figure 1. Parasagittal CT scans at the level of the right C^1 in *Pierolapithecus* (a), *Pongo* (b), *Pan* (c) and *Gorilla* (d). The images show the relationship between the maxillary sinus (MS, asterisks) and the nasolacrimal canal (NLC) or bulla (NLB) (white arrow), as well as the extension of the maxillary sinus. In *Pierolapithecus*, the MS only extends anteriorly to the M^1 level, like in *Pongo*, whereas in *Pan* and *Gorilla* the MS is very developed and reaches the molar roots. Moreover, in *Pierolapithecus* the NLD reaches anteriorly the M^1 under the nasals, whereas in *Pongo* the NLC is situated under the nasals (adopting their orientation), and unlike *Pan* and *Gorilla*, although the latter further differs by displaying a larger NLB instead of NLC. CT images of the extant hominoids modified from the originals courtesy of Dr. Kappelman and DigiMorph.org. Scale bar in *Pierolapithecus* equals 10 mm. Extant hominoids not to scale. For additional details regarding these structures, see Supplementary Video 1.

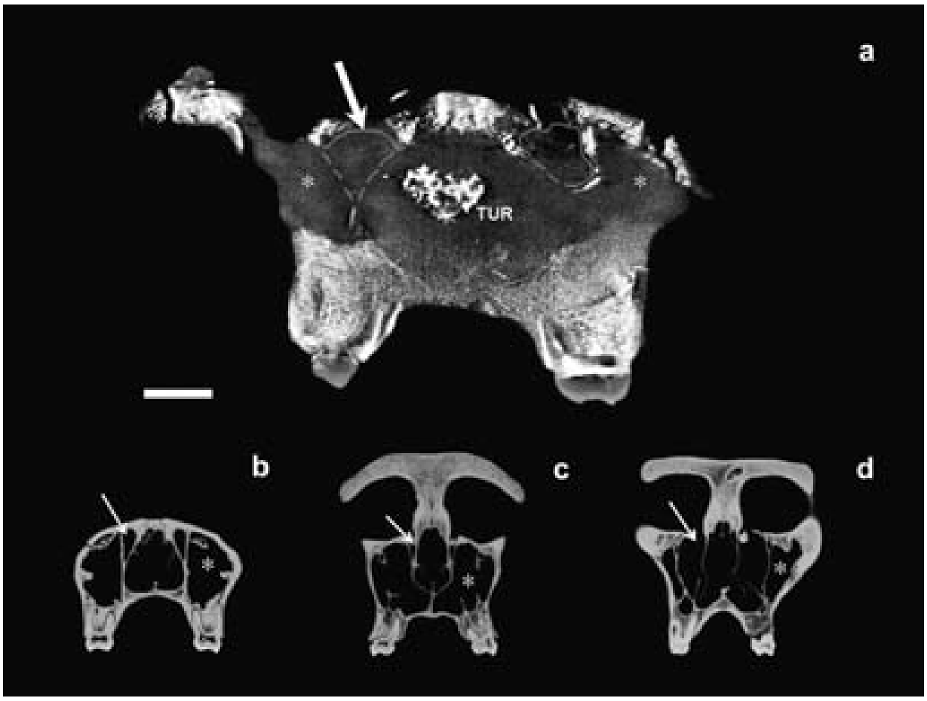

Figure 2. Coronal CT scan in *Pierolapithecus* (a), *Pongo* (b) and *Gorilla* (d), at the level of the M^2, and in *Pan* (c) and at the level of the M^1, showing the nasolacrimal canal (NLC, white arrow and continuous-discontinuous grey line), the maxillary sinus (MS, asterisks) and the turbinals. The configuration of the MS and the NLC in *Pierolapithecus* and *Pongo* display a very similar pattern, different from that of *Pan* (completely vertical over M^1) and *Gorilla* (large and rounded shape, and vertically-situated). In *Pan*, the MS has a palatal recess that is not observed in either in *Gorilla*, *Pongo* or *Pierolapithecus*. The turbinals of *Pierolapithecus* reach their greater development over the M^2. CT images of the extant hominoids modified from the originals courtesy of Dr. Kappelman and DigiMorph.org. Scale bar in *Pierolapithecus* equals 10 mm. Extant hominoids not to scale. For additional details regarding these structures, see Supplementary Video 2.

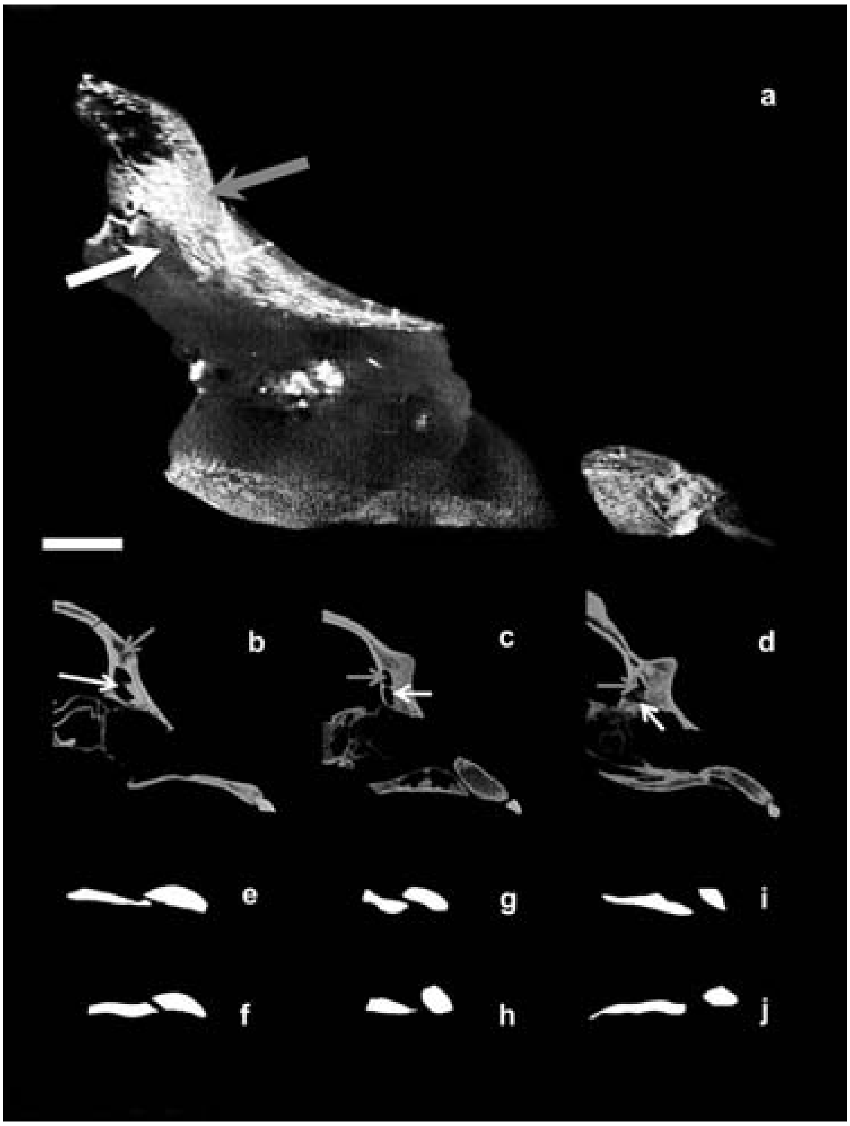

Figure 3. Parasagittal CT scan at the level of the right I^1 in *Pierolapithecus* (a) compared with *Pongo* (b), *Pan* (c) and *Gorilla* (d), and schemes of the subnasal morphology of *Sivapithecus indicus* (e), *Ankarapithecus meteai* (f), *Nacholapithecus kerioi* (g), *Hispanopithecus hungaricus* (h), *Rangwapithecus gordoni* (i) and *Morotopithecus bishopi* (j); (e–i) are after Nakatsukasa and Kunimatsu (2009). Observe the ethmoidal pneumatization (probably a recess of the maxillary sinus) (white arrow) and the lack of frontal sinus (grey arrow) in *Pierolapithecus*. Although the subnasal morphology cannot be unambiguously ascertained in *Pierolapithecus* due to damage, it was probably most similar to that of other dryopithecines (h). CT images of the extant hominoids modified from the originals courtesy of Dr. Kappelman and DigiMorph.org. Scale bar in *Pierolapithecus* equals 10 mm. Extant hominoids not to scale.

some sort of cavity. The shape of the space demarcated by these bony partitions is similar to a chimpanzee frontal sinus (Fig. 5d), thus raising the possibility that *Pierolapithecus* could have a frontal sinus filled with sediment or minerals. Such interpretation, however, is contradicted by the fact that the putative chambers are completely filled by a structure that in our opinion cannot be interpreted as sediment, but which is more consistent with trabecular bone (Fig. 5a). Moreover, an external examination of the supraorbital area (Fig. 5b) shows that these dense internal structures revealed by the CT scans do in fact correspond to bone cracks infilled by sediment, which given the CT signal, must display a high concentration of metal ions. Such preservation is common in other vertebrate crania from Abocador de Can Mata, as revealed for example by the very opaque, unequivocal cracks displayed by the CT scans of a barbourofelid cranium (Robles et al., in press). Given that the above-mentioned ‘bony struts’ are merely a preservational artefact, we conclude that the internal configuration of the frontal region in *Pierolapithecus* is essentially comparable with that of extant orangutans (Fig. 5c), where this area is occupied by cancellous bone that becomes denser towards the interorbital region.

Other nasal structures

Besides paranasal cavities, several nasal structures can be recognized in the *Pierolapithecus* cranium. Within the nasal cavity, the nasal septum can be distinguished in axial sections posteriorly to the M^2, being slightly deformed to the left on its anterior part, and reaching its greatest development after the M^3. The turbinals

Figure 4. 3D reconstruction on the basis of the CT scan of *Pierolapithecus catalaunicus* showing a parasagittal section at the level of I^1 (black plane). The frontal area lacks the frontal sinus and just a slight porosity is observed. For further images regarding the paranasal sinuses and other nasal structures, see Supplementary Videos 1 and 2.

can be also discerned, running from the nasal cavity walls to the ethmoidal region, extending along the level of the whole molar series and being more strongly accumulated over the M^2. The terminology employed in this manuscript follows Rossie (2005) instead of Moore (1981). Due to their fragility, the ectoturbinals and maxilloturbinals are damaged to a large extent, being accumulated in the central part of the nasal cavity. Thus, although in some areas the turbinals are almost in situ, it is not possible to discern the ectoturbinals from the maxilloturbinals or atrioturbinals (Fig. 2a). Regarding the positional relationship between the premaxilla and the hard palate, it is difficult to evaluate due to a bone fracture in the area of the incisive fenestra. The premaxilla is short and high, and it tends to project posteriorly, although due to bone damage it is not possible to ascertain whether it overlapped the maxilla to some degree (Fig. 3a). Finally, the nasolacrimal canals are well preserved, being situated between the maxillary sinus and the nasal cavity. Anteriorly they reach the level of M^1 (Fig. 2a), whereas posteriorly they extend, although progressively reducing, until the lacrimal fossa. In parasagittal section, it can be seen that these canals are inclined in relation to the sagittal plane, displaying approximately the same orientation as the nasals (Fig. 1a).

Comparison with other taxa

The maxillary sinus

The presence of a maxillary sinus is a primitive eutherian feature that has been repeatedly modified in several primate groups, being even lost in cercopithecoids and some ceboids (Koppe et al., 1999b; Rossie, 2006). This sinus is mostly housed within the maxillary bone, although in some taxa it further spreads out thought the palate, the zygomatic and even the interorbital pillar (Rae and Koppe, 2000). Previous studies have noted two increases in maxillary pneumatization during primate evolution: after the cercopithecoid–hominoid split, and also at the base of the hominid clade (Koppe et al., 1999a). However, the stem catarrhine *Aegyptopithecus* already displayed a large and invasive maxillary

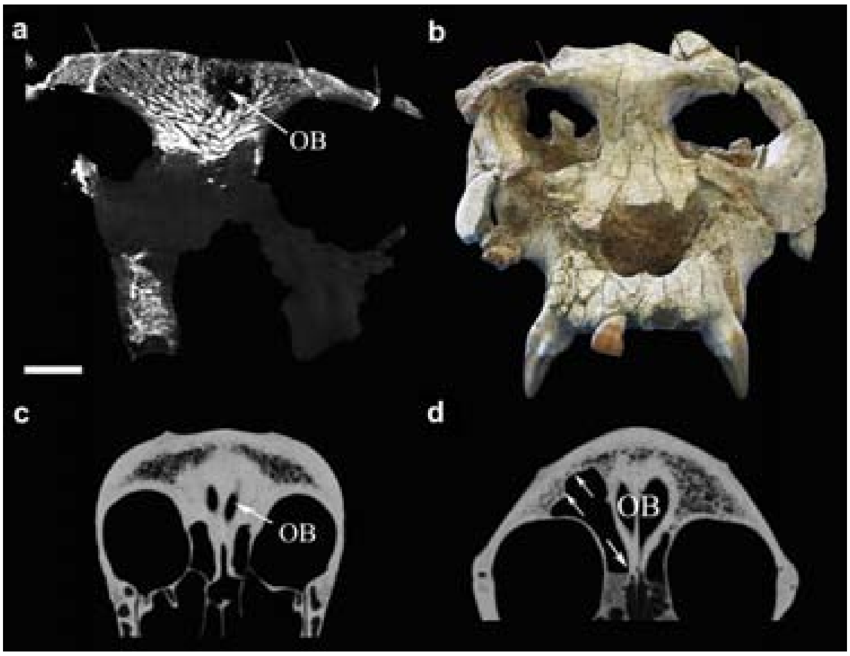

Figure 5. Internal and external anatomy of *Pierolapithecus* (a–b), compared with the internal anatomy of *Pongo* (c) and *Pan* (d). CT scans correspond to a coronal slice running through the frontal region. Note that *Pierolapithecus* displays internal dense structures (a, black arrows) that resemble the bony walls demarcating the frontal sinus of chimpanzees (d, white arrows). However, the external morphology of this specimen reveals that such structures correspond in fact to bone cracks filled with sediment with metal ions (a, b, grey arrows), as it is frequent in specimens from Abocador de Can Mata. OB denotes the situation of the olfactory bulbs. CT images of the extant hominoids modified from the originals courtesy of Dr. Kappelman and DigiMorph.org. Scale bar in *Pierolapithecus* equals 10 mm.

sinus (Rossie, 2005), and other analyses have shown that there is no relation between maxillary sinus volume and hominoid evolution (Rae and Koppe, 2000), further being potentially influenced by external environmental conditions in some taxa (Rae et al., 2003; Rae and Koppe, 2004; Koppe et al., 2005).

The lack of maxillary sinus in *Victoriapithecus* and most extant cercopithecoids suggests that this feature is a synapomorphy of this group (Rae et al., 2002; Rae and Koppe, 2004; Rossie, 2005), which is further confirmed by the presence of this sinus in the stem catarrhines *Saadanius* (Zalmout et al., 2010) and *Aegyptopithecus* (Rossie, 2005, 2008). As such, the presence of a large maxillary sinus in hominoids, where it is the largest paranasal cavity, must be considered a catarrhine symplesiomorphy, although being more developed in great apes than in hylobatids (Rae, 1999; Rae and Koppe, 2000). Amongst stem hominoids (sensu Moyà-Solà et al., 2009a; Casanovas-Vilar et al., 2011), proconsulids (including *Turkanapithecus*) display an invasive maxillary sinus, which anteriorly reaches the level of the premolars and laterally extends into the zygomatic root (Andrews, 1978; Leakey et al., 1988; Bilsborough and Rae, 2007). Afropithecids similarly display primitively an extensive maxillary sinus, as shown by *Afropithecus* and *Morotopithecus* (Leakey and Walker, 1997; Young and MacLatchy, 2004) as well as *Equatorius* (Pickford, 1985; Ward et al., 1999), although the more derived *Kenyapithecus* displays a more restricted maxillary sinus situated well above the molar roots (Pickford, 1985; Ward et al., 1999; Moyà-Solà et al., 2009b). A similar condition is displayed by *Pierolapithecus*, where the maxillary sinus does not excavate the alveolar process and is further restricted anteriorly. *Pierolapithecus* therefore resembles both derived afropithecids and other Middle Miocene dryopithecines (*Anoiapithecus* and *Dryopithecus*; Moyà-Solà et al., 2009a, b). Among other features, this has been interpreted as supporting a phylogenetic link between derived afropithecids and the Middle Miocene putative stem hominids included in the Dryopithecinae (Moyà-Solà et al., 2009a). *Pierolapithecus*, on the contrary, differs in this respect from the Late Miocene *Hispanopithecus* (or *Rudapithecus*) from Spain and Hungary[1] (Moyà-Solà and Köhler, 1993, 1995; Kordos and Begun, 2001), which display a more extensive and anteriorly-projecting maxillary sinus.

Rae and Koppe (2000) showed that, contrary to previous accounts (e.g., Rae, 1999, and references therein), the several genera of crown hominids do not differ regarding maxillary sinus volume, although depending on the taxa it can occupy different positions or invade different regions. In *Pan*, the maxillary sinus extends anteriorly until the canine root and posteriorly until slightly behind the M^3, further reaching the molar roots (Fig. 1c), whereas in *Gorilla* it is less extended anteriorly (without reaching the premolars) (Cave, 1961) (Fig. 1d). *Pan* further displays a strongly-developed palatal recess at the root of the sinus, between the hard palate and the nasal cavity, and a zygomatic recess is observed, whereas in *Gorilla* the maxillary sinus further spreads through the alveolar recess, and it is markedly developed below the inferior orbital rims (Fig. 2c, d) (Moore, 1981; Koppe and Ohkawa, 1999). *Pongo* differs from African apes by displaying a more anteriorly-restricted maxillary sinus that merely reaches the M^1, although posteriorly it invades the ethmoidal area by developing a frontal recess (Moore, 1981; Koppe and Ohkawa, 1999), further displaying a zygomatic recess but no palate recess (Fig. 1b). The development of a frontal recess of the maxillary sinus is considered a synapomorphy of the Ponginae (Rae, 1999; Kappelman et al., 2003), being displayed by the putative fossil pongines *Sivapithecus* (Ward and Pilbeam, 1983), *Lufengpithecus* (Schwartz, 1990, 1997), and *Ankarapithecus* (Begun and Güleç, 1998). The condition displayed by the maxillary sinus of *Pierolapithecus* (Fig. 1a) resembles the condition displayed by pongines regarding the well-developed posterior invasion into the ethmoidal region and the lack of palate recess, although these features might merely reflect the primitive condition for crown hominoids (with African apes being derived in these regards). Similarly, the moderate anterior extension and very restricted expansion above the molar roots of the maxillary sinus more closely resemble the morphology of pongines than that of hominines. In particular, the *Pierolapithecus* condition somewhat resembles that of orangutans and some *Sivapithecus* specimens, although it should be taken into account that the extent of the maxillary sinus is variable in the latter taxon, with larger (male) specimens sometimes displaying considerably invasive maxillary sinuses into the alveolar bone (Ward and Brown, 1986). In this regard, it is interesting to note that the *Pierolapithecus* face, corresponding to a male individual, most closely resembles the female rather than the male *Sivapithecus* condition. In any case, the *Pierolapithecus* condition may be merely interpreted as a primitive feature inherited from derived afropithecids, since it most closely resembles the maxillary sinus extent of *Kenyapithecus*.

The frontal sinus

The frontal sinus among extant hominoids originates as an expansion of the ethmoidal sinus towards the frontal squama, orbital rims and the glabellar region (Paulli, 1900; Wegner, 1936; Cave and Haines, 1940), although such an origin cannot be usually verified in fossil specimens, which is the reason why we merely refer to frontal instead of ethmofrontal sinus. Although the development of the frontal sinus can be variable amongst extant human populations (Fatu et al., 2006), the lack of a frontal sinus in several hominoid and primate subgroups constitutes a feature of phylogenetic significance (Koppe and Ohkawa, 1999).

Amongst hominoids, the presence of a frontal sinus appears to be synapomorphic, given that this feature is absent in the stem catarrhines *Saadanius* (Zalmout et al., 2010) and *Aegyptopithecus* (Rossie, 2008). Incidentally, it should be noted that the latter taxon was initially depicted as displaying a frontal sinus (Rossie et al., 2002; Rossie, 2005), leading to the conclusion that this was the primitive catarrhine condition, having been independently lost in cercopithecoids, hylobatids and pongines (Rossie et al., 2002; Rae and Koppe, 2004; Rossie, 2005). Later reanalyses, however, showed that *Aegyptopithecus* has only an ethmoid but not a frontal sinus (Simons et al., 2007; Rossie, 2008). On the contrary, both proconsulids and afropithecids display a moderately-developed frontal sinus (Rossie, 2008), which probably represents the primitive condition for the group (Moyà-Solà and Köhler, 1995; Pickford et al., 1997). From the latter, both the more extensive frontal sinus of extant hominines (where it penetrates into the supraorbital torus and glabella) and the absent frontal sinus of *Pongo* and closely-related extinct taxa would have evolved (Moyà-Solà and Köhler, 1995), although such interpretation is not straightforward, given pervasive homoplasy and uncertain phylogenetic relationships for extinct hominoids (see Alba, 2012). The condition for the presence/absence of a frontal sinus has been mapped in a cladogram (Fig. 6) depicting the most likely phylogenetic relationships for a selected sample of extant and fossil catarrhines (but see the Discussion for further alternatives).

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[1] Some cranial and postcranial differences between *Hispanopithecus laietanus* and the Rudabánya sample might justify a distinction at the genus level, i.e. *Rudapithecus hungaricus* for the latter (Begun et al., 2012; contra Moyà-Solà et al., 2009a,b). However, pending a more comprehensive review of this issue, here we tentatively favour Alba's (in press; see also Alba et al., 2012) taxonomic opinion, according to which these taxa would be only distinguished at the subgenus level, i.e. *Hispanopithecus (Hispanopithecus) laietanus* and *Hispanopithecus (Rudapithecus) hungaricus*, respectively.

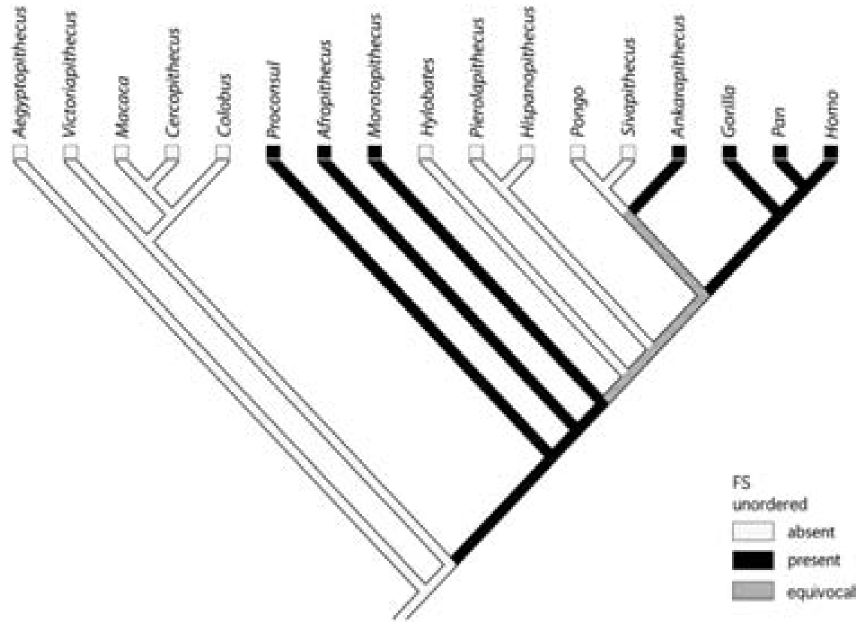

Figure 6. Presence/absence of frontal sinus mapped on a cladogram of selected extant and extinct catarrhine taxa, based on the 'Begun' and 'Horovitz' trees (modified from Rossie, 2008), as well as on the authors' views on hominoid evolution.

Given that a frontal sinus is lacking in cercopithecoids, as well as hylobatids and orangutans, the possession of an ethmofrontal sinus has been sometimes considered a hominine synapomorphy (Rae and Koppe, 2004). As explained above, however, this interpretation seems unlikely when fossil hominoids are taken into account, with the ethmofrontal sinus being primitive for all hominids at the very least (Rossie, 2008). In fact, the presence of a small frontal sinus in the Late Miocene dryopithecine *Hispanopithecus* has long been interpreted as a possible primitive retention (Begun, 1992; Moyà-Solà and Köhler, 1993, 1995; Pickford et al., 1997; Kordos and Begun, 2001), although its restricted condition around nasion, without penetrating into the orbital rim, glabella or frontal squama (Moyà-Solà and Köhler, 1993, 1995; Pickford et al., 1997), may be alternatively interpreted as a derived feature towards the *Pongo* condition (Fig. 3b) (Köhler et al., 2001; Rossie et al., 2002; Pérez de los Ríos et al., 2010). The interpretation that *Hispanopithecus* from Spain and *Hispanopithecus* (or *Rudapithecus* [Begun, 2009]) from Hungary displays a frontal sinus extending around nasion (Kordos and Begun, 2001; Begun, 2009), used in support of a purported hominine status of this taxon, might merely result from an incorrect identification of the ethmoidal recess as part of the frontal sinus (Fig. 3c, d) (Pérez de los Ríos et al., 2010). The presence of an invasive frontal sinus that spreads through the supraorbital region and the glabella in the primitive pongine *Ankarapithecus* (Kappelman et al., 2003) supports the interpretation of this feature as a crown-hominid symplesiomorphy, further indicating that the lack of this sinus is only a synapomorphy of a clade comprising *Pongo* and closely-allied fossil taxa such as *Sivapithecus* (Rossie, 2008; Begun, 2009) as well as *Lufengpithecus* (Brown and Ward, 1988; Schwartz, 1990), but not of pongines as a whole. In this light, the lack of a true frontal sinus in *Pierolapithecus*, which merely shows a slight porosity under the glabella (Fig. 4), most closely resembles the derived condition of both hylobatids and pongines (Figs. 3a and 4). However, an unambiguous interpretation of this feature in *Pierolapithecus* as a pongine synapomorphy is precluded by the retention of a frontal sinus in the primitive pongine *Ankarapithecus*, so that the *Pierolapithecus* condition might be alternatively interpreted as homoplastic. The latter interpretation is further reinforced by the fact that the similarly-aged dryopithecine *Anoiapithecus* displays a primitive configuration, with a well-developed frontal sinus that invades the glabella and part of the frontal squama (Moyà-Solà et al., 2009a).

The turbinals

The turbinals are bone structures supporting epithelial invaginations from the nasal mucous membrane involved in respiratory, olfactory and thermoregulatory functions (Koppe et al., 1999a). Extant hominoids display a reduction in the turbinals, further lacking the ectoturbinals (Lund, 1988). This is confirmed by the great turbinal development in the stem catarrhine *Aegyptopithecus*, whereas only the atrioturbinals are preserved in *Proconsul* (Rossie, 2005). Although the potential of turbinals for providing phylogenetic informative features has been previously noted (Hershkovitz, 1977), this potential has been seriously hampered among extinct taxa by the fragility of these structures, generally due to a poor preservation. In extant African apes, the main development of the turbinals is attained at about the level of distal M^1, whereas in *Pongo* it is attained more posteriorly over the M^3 (Fig. 2b). As far as it can be ascertained, in *Pierolapithecus* the main accumulation of the turbinals is observed at the level of distal M^2 (Fig. 2a). Moreover, in *Pan* the turbinals are situated higher within the nasal cavity (due to the larger extension of the maxillary sinus over the palate) (Fig. 2c), whereas in *Gorilla* they are reduced (so that their spatial configuration cannot be directly compared with *Pierolapithecus*) (Fig. 2d). However, it should be taken into account that although the CT scan images show the position of the turbinals in *Pierolapithecus*, the bone attachments have not been preserved, so that a more accurate description is not possible. Moreover, detailed comparisons with other taxa are further precluded by the fact that only few comparative data on turbinal development are available for fossil hominoids. As such, the configuration of these bones in

Pierolapithecus described above currently remains of little phylogenetic significance.

The nasolacrimal canal

Amongst primates, the vertical orientation and posterior position of the nasolacrimal canal is considered a haplorhine synapomorphy related to the reduction of the vomeronasal complex (Rossie and Smith, 2007). Extant African great apes display this condition, although in *Gorilla* there is an enlarged nasolacrimal cavity (also termed nasolacrimal bulla) that spreads between the maxillary sinus and the ethmoidal air cell (Fig. 1d) (Wood Jones, 1938; Moore, 1981). Such enlarged nasolacrimal bulla might be easily misinterpreted as part of the maxillary sinus, although their boundaries are well marked by bone structures. In *Pan*, the nasolacrimal canal is completely vertical, being situated over the M^1, and further displaying a reduced lateral expansion (Fig. 1c). *Pongo*, on the contrary, displays a slightly different condition, the nasolacrimal canal being anteriorly-projected from the lacrimal foramen (over the M^3) under the nasal bone, thus reaching the level of the M^1 (Fig. 1b). This condition might be related to the pronounced lower-facial prognathism of this taxon. In *Pierolapithecus*, the nasolacrimal canal projects anteriorly under the nasals from the level of the M^3 until the area above the M^1, most closely resembling the orangutan condition (Fig. 1a). On the basis of available data for extant primates, the condition shared by *Pierolapithecus* and *Pongo* may be interpreted as a derived feature, although additional data for other fossil hominoids (particularly derived afropithecids) would be required in order to rule out that it could not be symplesiomorphic for crown hominids.

Nasoalveolar morphology

The primitive hominoid nasoalveolar morphology, present in both proconsulids and most afropithecids, is characterized by a short premaxilla with a nearly horizontal clivus, an unstepped nasal floor and a wide incisive fossa lacking an incisive fenestra (Fig. 3i, j) (Ward and Pilbeam, 1983). As far as it can be ascertained, *Nacholapithecus* is the only afropithecid displaying a somewhat derived intermediate condition, as shown by its more elongated and procumbent alveolar process that partially overlaps the hard palate (Fig. 3g) (Nakatsukasa and Kunimatsu, 2009). Extant African apes and orangutans possess each a different derived condition (Ward and Pilbeam, 1983; McCollum et al., 1993; Moyà-Solà and Köhler, 1995). Thus, African apes display a long premaxilla that moderately overlaps the hard palate, the latter being deflected beneath the nasospinale, thereby defining a well-defined incisive canal and a stepped nasal floor (Fig. 3c, d). Orangutans, on the contrary, display a long and procumbent premaxilla that intersects in a shallow angle with the alveolar plane, thereby defining a narrower and longer incisive canal and further lacking a stepped nasal floor (Fig. 3b). The condition displayed by *Hispanopithecus* most closely resembles the primitive condition of stem hominoids, by retaining a larger incisive fossa than extant great apes and further lacking overlap between the premaxilla and the hard palate (Fig. 3h) (Ward and Pilbeam, 1983; Moyà-Solà and Köhler, 1995). On the contrary, both *Ankarapithecus* and *Sivapithecus* display a *Pongo*-like condition that further reinforces the status of the latter as members of the Ponginae (Fig. 3e, f) (Ward and Pilbeam, 1983; Begun and Güleç, 1998). On the basis of currently available remains, the nasoalveolar morphology of *Pierolapithecus* cannot be unambiguously evaluated due to bone damage on this area, other than asserting that the alveolar process is short and thick (Fig. 3a). Hence, the premaxilla might have not overlapped the hard palate, thus resembling other dryopithecines, but this cannot be concluded with certainty.

Conclusions

Internal anatomy

On the basis of non-invasive CT techniques, the internal (paranasal and nasal) anatomy of the fossil great ape *P. catalaunicus* is described in the holotype specimen, further being compared with extant and other fossil hominoids. The maxillary sinus of *Pierolapithecus* is anteriorly-restricted and apparently spreads posteriorly towards the ethmoidal area as in *Pongo* and the extinct pongine *Sivapithecus*, whereas its very moderate inferior development (being situated well above the molars roots) most closely resembles the condition of *Kenyapithecus*, other Middle Miocene dryopithecines and pongines (*Sivapithecus* and, to a lesser extent, *Pongo*), thus contrasting with the Late Miocene *Hispanopithecus* (which shows a more extensive maxillary sinus). *Pierolapithecus* further resembles several pongines (*Lufengpithecus*, *Sivapithecus* and *Pongo*) in the lack of a true frontal sinus (Fig. 6), although an unambiguous interpretation of this feature as a pongine synapomorphy is precluded by the presence of a well-developed frontal sinus in the pongine *Ankarapithecus*. The posteriorly-situated turbinals and anteriorly-projecting nasolacrimal canal in *Pierolapithecus* further resemble the condition of extant orangutans, although the lack of information for a wide array of fossil hominoids currently precludes a confident assessment of these features as pongine synapomorphies. Moreover, the nasoalveolar morphology of *Pierolapithecus* cannot be adequately assessed due to bone damage, although on the basis of the preserved morphology, a primitive configuration including a stepped nasal floor with no overlap between the maxilla and premaxilla, as in other dryopithecines (*Dryopithecus* and *Hispanopithecus*), seems more likely than the derived condition shared by orangutans and fossil pongines (where the nasal floor is unstepped and there is a large premaxillary-maxillary overlap).

Phylogenetic and systematic implications

On the basis of several postcranial features, an orthograde body plan has been inferred for *Pierolapithecus* (Moyà-Solà et al., 2004; Susanna et al., 2010), leading to the conclusion that orthogrady might be homologous between crown hominoids (Moyà-Solà et al., 2004), even though the lack of suspensory adaptations in this taxon (Almécija et al., 2009; Alba et al., 2010a) suggests that the latter might be homoplastic at least between hylobatids and hominids (Moyà-Solà et al., 2004, 2005; Almécija et al., 2009; Alba et al., 2010a). Besides orthogrady, on the basis of the possession of several derived features of the great ape and human clade (e.g., high zygomatic root; nasals, orbits and frontal processes of the maxillae on the same plane; and broad nasal aperture, broadest at the base), *Pierolapithecus* was originally interpreted as a member of the stem lineage of the Hominidae closely reflecting the morphology of the last common ancestor of crown hominids (Moyà-Solà et al., 2004, 2005, 2009a, b). This interpretation has been however disputed by Begun and co-authors, who have argued that *Pierolapithecus* (and even *Anoiapithecus*) are likely to be junior subjective synonyms of *Dryopithecus* (Begun, 2007, 2009, 2010; Begun et al., 2008) and that they may be alternatively interpreted as stem hominines (Begun and Ward, 2005; Begun, 2007, 2009, 2010). The purported synonymy among *Pierolapithecus*, *Dryopithecus* and *Anoiapithecus* seems difficult to reconcile with the differences in facial morphology between these genera (Moyà-Solà et al., 2009a, b), as well as with the differences in relative enamel thickness between *Dryopithecus* and the two remaining Middle Miocene dryopithecines (Moyà-Solà et al., 2009a; Alba et al., 2010b). The differences in frontal sinus development between *Pierolapithecus* and *Anoiapithecus* further confirm that more than a single genus is represented by these Middle Miocene nominal taxa. Moreover, differences between the three above-mentioned dryopithecine genera with regard to the restricted development of the maxillary sinus (as in derived afropithecids), compared with the much more extensive development in the Late Miocene *Hispanopithecus*, supports the previous allocation of these genera into two distinct tribes (Dryopithecini and Hispanopithecini) within the Dryopithecinae (Casanovas-Vilar et al., 2011). The diversity of Middle to Late Miocene Spanish hominoids is clearly at odds with the previous definition of the Dryopithecina (Begun, 2009) (equivalent to our Dryopithecini + Hispanopithecini; Casanovas-Vilar et al., 2011; Alba, 2012), which would supposedly display a large maxillary sinus (false for the three Middle Miocene genera), a well-developed frontal sinus (false for *Pierolapithecus*, as shown in this paper) and thin-enamelled molars (false for both *Pierolapithecus* and *Anoiapithecus*; Alba et al., 2010b).

It is however uncertain whether the Dryopithecini, as conceived here (i.e., incuding *Pierolapithecus*, *Anoiapithecus* and *Dryopithecus*), represent a clade or a paraphyletic assemblage, and several phylogenetic and paleobiogeographic interpretations of its morphologic diversity are possible on the basis of currently available evidence (Casanovas-Vilar et al., 2011; Alba, 2012). The retention of kenyapithecin-features in both *Pierolapithecus* and *Anoiapithecus*, including the restricted development of the maxillary sinus, the robust gnathic morphology and the possession of thick enamel, has been previously interpreted as indicating a close phylogenetic link between Eurasian derived afropithecids and undoubted Middle Miocene European hominids included into the Dryopithecini (Moyà-Solà et al., 2009a; Alba et al., 2010b; Casanovas-Vilar et al., 2011; Alba, 2012). Following the interpretation of these taxa (*Pierolapithecus*, *Anoiapithecus* and *Dryopithecus*) as stem hominids (Moyà-Solà et al., 2004, 2009a, b), a Eurasian origin of the great ape and human clade (Hominidae) followed by a back to Africa dispersal of hominines seems rather likely (Moyà-Solà et al., 2009a; Alba et al., 2010b), as previously argued by several authors (Begun et al., 1997; Stewart and Disotell, 1998; Begun, 2007, 2009, 2010). However, as recently noted, available evidence is also compatible with an alternative interpretation that all European Dryopithecinae (including both Middle and Late Miocene forms) are more closely related to the monotypic Asian Ponginae (Pongini) than to the African Homininae, with Ponginae s.l. and Homininae having independently evolved respectively in Eurasia and Africa from similar ancestors during the Middle Miocene (Casanovas-Vilar et al., 2011; Alba, 2012). The mosaic of primitive and derived cranial features displayed by *Pierolapithecus*, even when information from paranasal and nasal anatomy is taken into account, cannot resolve this issue, especially when contradictory evidence is provided by other contemporary (and purportedly closely-related) taxa such as *Anoiapithecus*. To sum up, available evidence permits to securely discount an attribution of *Pierolapithecus* to the Homininae, as evidenced by the restricted maxillary sinus and the lack of a true frontal sinus in the former. Rather, similarities regarding some paranasal and nasal structures (anteriorly-restricted maxillary sinus that might have extended backwards towards the ethmoid, lack of frontal sinus, posteriorly-situated turbinals, and anteriorly-projecting nasolacrimal canal) would support the contention that *Pierolapithecus* (and presumably other dryopithecines) are the sister taxon of Asian pongines within a broadly-defined Ponginae s.l. If this hypothesis were confirmed by later studies including all available craniodental and postcranial features, the Dryopithecinae as conceived here (Casanovas-Vilar et al., 2011; Alba, 2012) might be best considered merely as a tribe (Dryopithecini) within the Ponginae. We refrain from formally adopting such view, however, since several of the above-mentioned features can be alternatively interpreted as being primitive retentions from derived afropithecids, homoplasies or characters of doubtful interpretation.

Supplementary video related to this article can be found at http://dx.doi.org/10.1016/j.jhevol.2012.05.012

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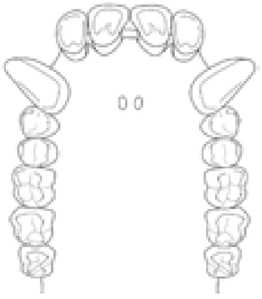

Chapter 5

Taxonomic attribution of the La Grive hominoid teeth

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Taxonomic Attribution of the La Grive Hominoid Teeth

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KEY WORDS Middle Miocene; Dryopithecinae; taxonomy; *Dryopithecus*; *Pierolapithecus*; *Anoiapithecus*

ABSTRACT The two hominoid teeth—a central upper incisor (NMB G.a.9.) and an upper molar (FSL 213981)—from the Middle Miocene site of La Grive-Saint-Alban (France) have been traditionally attributed to *Dryopithecus fontani* (Hominidae: Dryopithecinae). However, during the last decade discoveries in the Vallès-Penedès Basin (Spain) have shown that several hominoid genera were present in Western Europe during the late Middle Miocene. As a result, the attribution of the dryopithecine teeth from La Grive is not as straightforward as previously thought. In fact, similarities with the upper incisor of *Pierolapithecus* have led to suggestions that either the latter taxon is present at La Grive, or that it is a junior synonym of *Dryopithecus*. Here, we re-describe the La Grive teeth and critically revise their taxonomic assignment based on metrical and morphological comparisons with other Middle to Late Miocene hominoids from Europe and Turkey, with particular emphasis on those from the Vallès-Penedès Basin. Our results suggest that the I^1 differs in several respects from those of *Pierolapithecus* and *Hispanopithecus*, so that an attribution to either *Dryopithecus* or *Anoiapithecus* (for which this tooth is unknown) seems more likely. The molar, in turn, most likely corresponds to the M^1 of a female individual. Compared to other Middle Miocene taxa, its occlusal morphology enables its distinction from *Pierolapithecus*, whereas relative crown height agrees well with *Dryopithecus*. Therefore, based on available evidence, we support the traditional attribution of the La Grive hominoid to *D. fontani*. Am J Phys Anthropol 151:558–565, 2013. © 2013 Wiley Periodicals, Inc.

Two upper teeth (a molar and a central incisor) from the Middle Miocene of La Grive-Saint-Alban (Isère, France) have been traditionally attributed to the dryopithecine hominid *Dryopithecus fontani* (Depéret, 1911; Andrews et al., 1996; Begun, 2002; Mein and Ginsburg, 2002; Moyà-Solà et al., 2009b; Casanovas-Vilar et al., 2011; Begun et al., 2012). The upper molar was first described as an M^3 by Depéret (1911), whereas the I^1 was discovered much later among the collections of the Naturhistorisches Museum Basel (Mein, 1986), being figured and briefly described by Andrews et al. (1996). The exact fissure filling of provenance for these teeth is unknown (Mein and Ginsburg, 2002), although the gray patina of the molar suggests that it comes from either fissure L3 or L5 (Mein, 1986), with an estimated age of 11.8–11.2 Ma (Casanovas-Vilar et al., 2011), whereas the red patina and year of collection of the incisor suggests that it comes from La Grive M, with a somewhat older age of about 12.5–11.9 Ma (Casanovas-Vilar et al., 2011).

Until the recent discovery of a partial face of *D. fontani* from Abocador de Can Mata (ACM; 11.9 Ma) in Spain (Moyà-Solà et al., 2009b), the dentognathic remains of this taxon—other than those from La Grive—were restricted to mandibular remains from St. Gaudens in France and St. Stefan in Austria (Begun, 2002), with an age of 12.5–11.2 Ma (Casanovas-Vilar et al., 2011). Accordingly, the La Grive upper teeth were merely assigned to *D. fontani* on the basis of age similarities and the assumption that this was the only late Middle Miocene genus recorded in Europe (e.g., Begun, 2002). However, the recent discovery of craniodental remains of several Middle Miocene dryopithecine genera at ACM (*Pierolapithecus*, *Anoiapithecus*, and *Dryopithecus*; Moyà-Solà et al., 2004, 2009a,b) evidenced a previously unsuspected diversity of hominoids in Western Europe by this time (Casanovas-Vilar et al., 2011; Pickford, 2012; Alba, 2012; Alba and Moyà-Solà, 2012). Even though some researchers remain skeptical of such generic diversity (Begun, 2009; Begun et al., 2012), it clearly indicates that an attribution of the La Grive material to *D. fontani* is not straightforward, as shown by

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[1] See Alba (2012) for the taxonomy employed in this paper.

Additional Supporting Information may be found in the online version of this article.

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their recent attribution to *Pierolapithecus* by Pickford (2012). Here, we re-describe the two available teeth from La Grive and, on the basis of comparisons with other Middle to Late Miocene hominoids, re-evaluate the taxonomic affinities of the hominoid material from this locality (see Pérez de los Ríos et al., 2012b for a preliminary report in abstract form).

MATERIALS AND METHODS

The right I^1 from La Grive (NMB G.a.9.; Fig. 1A–E; Andrews et al., 1996; Begun, 2002) is housed at the Naturhistorisches Museum Basel (Switzerland), whereas the left upper molar (FSL 213981; Fig. 1F–J; Depéret, 1911) is housed at the Université Claude Bernard Lyon 1 (France). Dental measurements of labiolingual/buccolingual breadth (BL), mesiodistal length (MD) and labial/buccal maximum height (H) were taken with a digital caliper to the nearest 0.1 mm. Based on these variables, two indices were computed in order to assess occlusal proportions (breadth/length index, computed as BLI = BL/MD × 100) and relative crown height (RCH = H/MD × 100). Occlusal dental dimensions were depicted by means of bivariate plots of BL vs. MD, whereas RCH was compared using boxplots.

Besides the La Grive teeth, dental measurements for the same tooth positions were also taken in the hominoid sample from the Vallès-Penedès Basin housed at the Institut Català de Paleontologia Miquel Crusafont (ICP; Barcelona, Spain), including *Pierolapithecus catalaunicus* from ACM/BCV1 (Moyà-Solà et al., 2004; Pérez de los Ríos et al., 2012a), *D. fontani* from ACM/C3-Ae (Moyà-Solà et al., 2009b), *Anoiapithecus brevirostris* from ACM/C3-Aj (Moyà-Solà et al., 2009a), *Hispanopithecus crusafonti* from Can Poncic 1 (Begun, 1992; Golpe Posse, 1993), and *Hispanopithecus laietanus* from Can Llobateres 1 and 2 (Begun et al., 1990; Golpe Posse, 1993; Moyà-Solà and Köhler, 1995; Ribot et al., 1996; Alba et al., 2012).

Measurements were also taken from the original specimens of kenyapithecines housed at the Nairobi National Museum (National Museums of Kenya, Nairobi), including *Nacholapithecus kerioi* (Ishida et al., 2004), *Equatorius africanus* (Pickford, 1985; Kelley et al., 2002), and *Kenyapithecus wickeri* (Pickford, 1985), as well as from *Hispanopithecus hungaricus* (Kordos and Begun, 1997, 2001) housed at the Magyar Állami Földtani Intézet (Hungarian Geological Institute) and at the Magyar Természettudományi Múzeum (Hungarian Natural History Museum) in Budapest (Hungary). Finally, additional measurements were taken from the literature regarding the Neuhausen incisor SMNS 47444 (Pickford, 2012), or kindly provided by Jay Kelley regarding occlusal measurements of *Griphopithecus alpani* and *Kenyapithecus kizili* from Paşalar (Kelley et al., 2008). Crown height measurements for the latter taxa were measured from casts housed at the ICP.

DESCRIPTIONS

The La Grive incisor

NMB G.a.9 (Fig. 1A–E) is a right I^1 preserving the crown but lacking the mesiolabial portion of the root. Measurements: MD = 8.6 mm; BL = 7.1 mm; BLI = 82.6%; H = 11.3 mm; RCH = 131.4%.

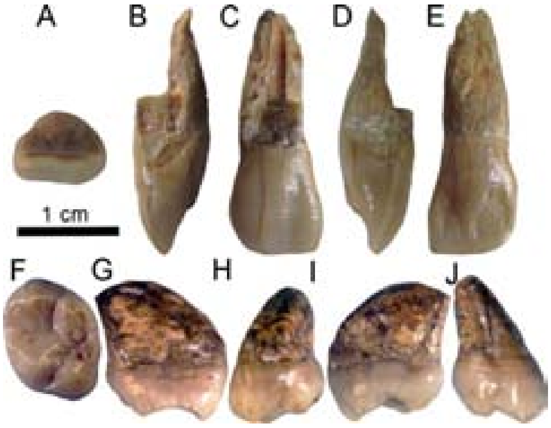

Fig. 1. Hominoid teeth from La Grive. **A–E**: Right I^1 (NMB G.a.9) in occlusal (A), mesial (B), labial (C), distal (D) and lingual (E) views. **F–J**: Left upper molar (FSL 213981) in occlusal (F), mesial (G), buccal (H), distal (I) and lingual (J) views. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

The labial and apical portions of the root are missing (exposing the pulp canal), although in lingual view it can be seen that it tilts slightly mesialward. The cemento-enamel junction is V-shaped on the mesial and distal sides, being more pronounced on the former. The crown is spatulate, high compared to occlusal dimensions, and waisted at the cervix. It is somewhat worn apically, with some dentine exposure along the apical margin, and it further displays an apical contact facet against its antimere on the mesial side. The lingual side displays a relatively restricted (about one-third of crown height) concave incisal portion, as well as a very extensive and protruding basal swelling (bulge) with no distinct lingual cingulum. The bulge is apically continued by a broad and triangular lingual tubercle that tapers apically until reaching about two-thirds of crown height. This tubercle, flanked by relatively marked grooves, is apically prolonged by a narrower and fainter enamel protrusion that does not reach the apical margin but partially separates the mesial and distal foveae. These foveae are subequal in size (the distal one being slightly larger than the mesial one), further being delimited by marked and relatively thick mesial and distal ridges along the crown margins. In lingual view, the crown is slightly asymmetrical (tilted to mesial), with the distal ridge being more markedly convex than the mesial one, thus progressively curving toward the mesial margin (instead of shaping a right angle). In occlusal view, the crown displays a subtriangular contour, being much longer on the labial than on the lingual portion, and further displaying a marked concavity along its mesiolabial portion.

The La Grive upper molar

The left upper molar FSL 213981 (Fig. 1F–J) is most likely attributable to an M^1 (see below for further discussion in this regard). It preserves the whole crown (with a moderate degree of wear, mainly at the trigon basin, with no dentine exposure at the main cusps), but only minor portions of the roots. Measurements: MD = 8.8 mm; BL = 10.8 mm; BLI = 122.7%; H = 5.4 mm; RCH = 61.4%.

Although the specimen seems to display a single fused root, at close inspection it can be ascertained that multiple, partial roots are preserved, with the space between

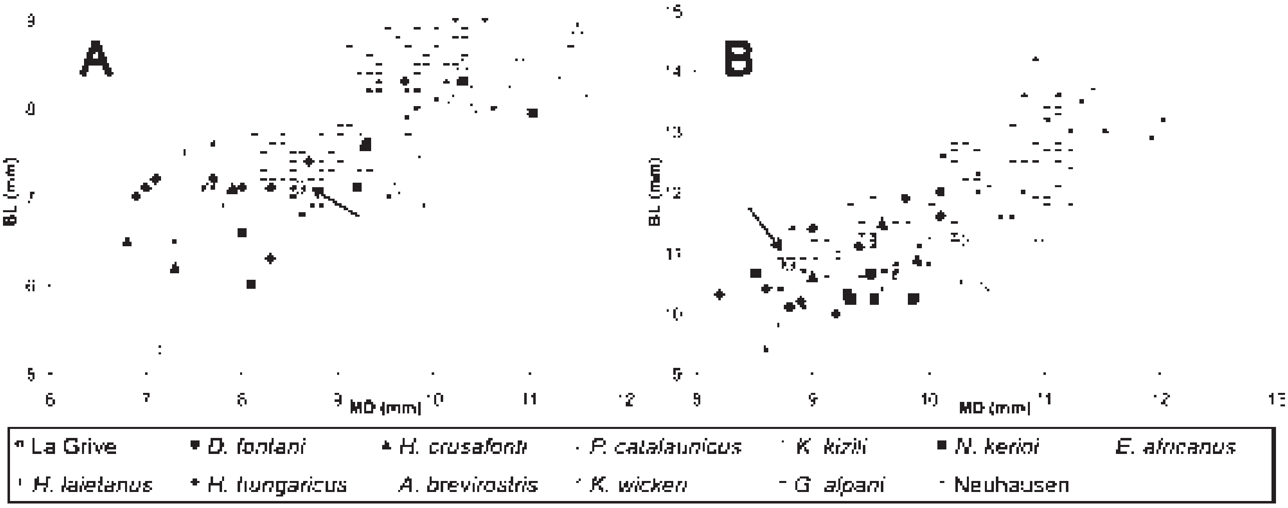

Fig. 2. Dental proportions of the La Grive teeth compared to selected Middle to Late Miocene hominoids from Europe and Africa. Bivariate plots of BL vs. MD in I^1 (**A**) and M^1 (**B**). The La Grive specimens are indicated by black arrows.

them filled by another material—either sediment or plaster. In particular, the external portion of the single lingual root (which shows a median groove slightly tilted distalwards) is the most completely preserved one, including most of its cervical and distal portions, but only a minor portion of its mesial portion. The mesiobuccal root is even more incompletely preserved (only its basal-most portion remains), whereas the distobuccal root is completely broken away.

The crown displays a subrectangular occlusal profile (being somewhat broader than long). There are four main cusps, the buccal ones being more buccolingually compressed and more mesially positioned than the corresponding lingual cusps. The protocone is the largest cusp, whereas the paracone is the most protruding one. The metacone is distinct but smaller than the paracone, whereas the hypocone is well-individualized and intermediate in size between the mesial cusps and the metacone, being situated more lingually than the protocone. The preparacrista gently curves until merging with the mesial marginal ridge, whereas the preprotocrista is longer, straighter, and more obliquely oriented. At the mesial end of the preprotocrista there is a distinct protoconule that is partly worn away. Trigon crests and secondary enamel folds and grooves are also somewhat worn, although it can still be discerned that a mesially-positioned hypoparacrista (directed toward the protoconule or the mesial marginal ridge) originally delimited a very restricted and fissure-like mesial fovea. Only the transverse groove running from the buccal side toward the center of the trigon basin, thus transecting the contact between the ends of the postparacrista and the shorter premetacrista, is not partly obscured by wear. There is a well-developed and continuous crista obliqua linking the apices of the protocone and metacone, although the postprotocrista is longer and more obliquely oriented than the hypometacrista, which is more transversely aligned. The prehypocrista is very short and directed toward the distal aspect of the protocone, although the hypocone, situated on the distolingual corner of the crown, is separated from the trigon by a marked oblique groove that runs from the distal fovea to a poorly-developed cingular remnant on the lingual side of the crown. The distal fovea, smaller than the trigon basin, is broader than long and relatively restricted, being distally enclosed by a marked distal marginal ridge. This distal fovea lacks a continuous transverse secondary crest linking the hypocone and the metacone, but shows instead a considerable development of enamel wrinkling (mainly secondary crests and folds that radiate from the crista obliqua as well as the bases of the surrounding cusp bases). The cingular remnants, situated at about mid-crown length on both the lingual and buccal sides of the crown, are very poorly developed.

MORPHOLOGIC COMPARISONS

The La Grive incisor

Metrical comparisons. Comparisons of dental size and occlusal proportions of the La Grive incisor with other taxa have been reported in Figure 2A and Supporting Information Table S1. Compared to other dryopithecines, the occlusal dimensions of the La Grive specimen closely resemble the largest specimens of *H. crusafonti*, which nevertheless display, like the one from Neuhausen and those of *H. laietanus* and *H. hungaricus*, a slightly higher BLI (although overlapping with the latter taxon). The La Grive incisor is only slightly smaller than that of *Pierolapithecus*, further displaying a very similar breadth/length index. The La Grive incisor further displays a relatively thicker crown than kenyapithecine species on average, except as compared to *Griphopithecus*, with which it largely overlaps. The considerable variation shown by the large sample of the latter taxon, contrasting with the small samples available for most dryopithecines, make such comparisons of occlusal proportions of little utility. This contrasts with the pattern displayed by RCH (Fig. 3A), in which more consistent differences can be found. Thus, the La Grive specimen most closely resembles the intermediate condition displayed by *H. hungaricus*, *H. laietanus* and, to a lesser extent, *Equatorius*. The remaining kenyapithecines and *Pierolapithecus* display in contrast a relatively lower-crowned incisor, whereas the Neuhausen specimen and those of *H. crusafonti* are clearly higher-crowned. No comparisons with either *Dryopithecus* or

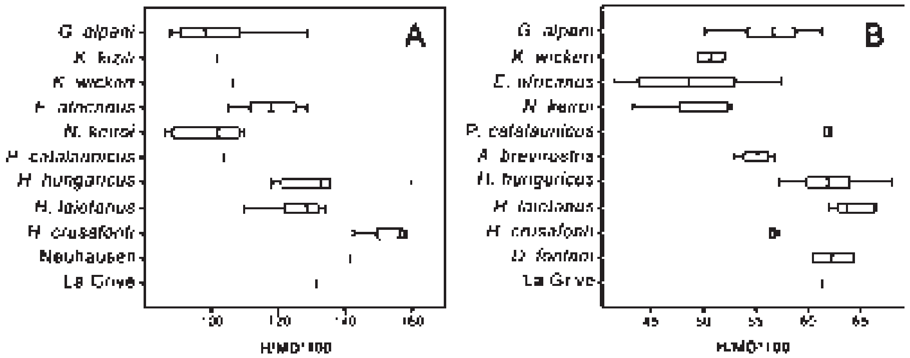

Fig. 3. Boxplots of RCH (computed as H/MD × 100) in I^1 (**A**) and M^1 (**B**) of the La Grive teeth compared to selected Middle to Late Miocene hominoids.

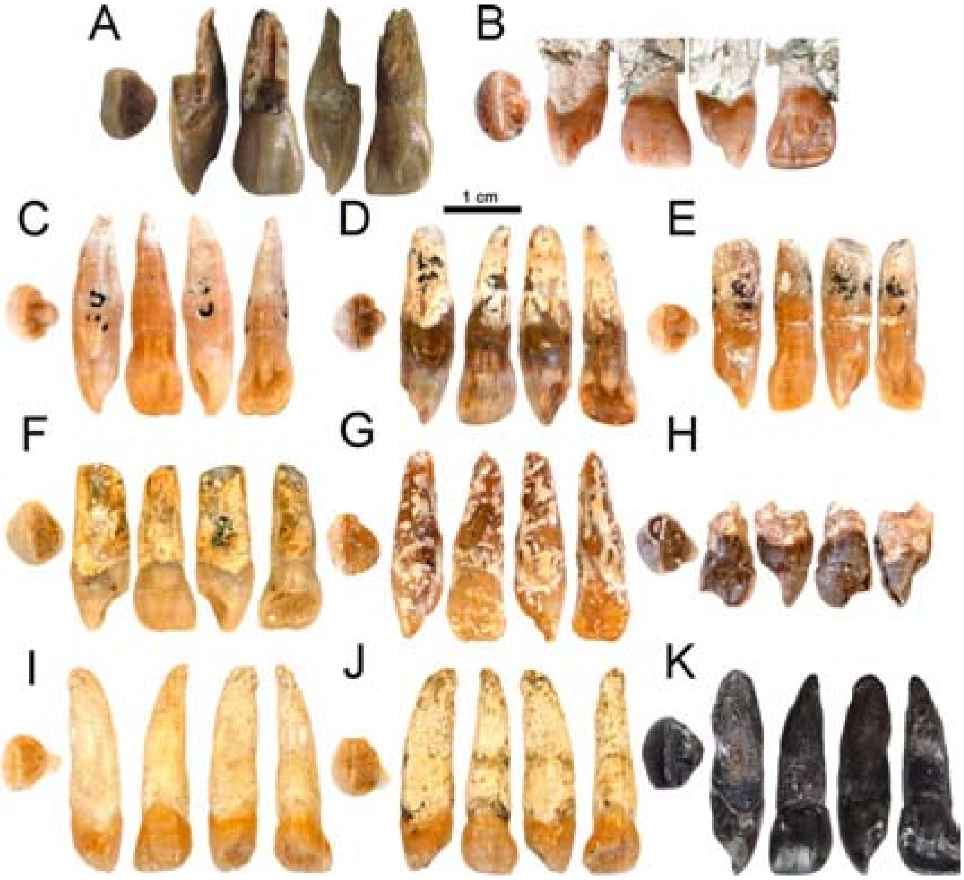

Fig. 4. Upper central incisor from La Grive, compared to those of Middle to Late Miocene hominoids from the Vallès-Penedès Basin and Rudabánya. **A**: Right I^1 NMB G.a.9. from La Grive; **B**: Right I^1 IPS 21350 (holotype) of *Pierolapithecus catalaunicus* from ACM/BCV1; **C–E**: Right I^1 IPS 1807 (C), left I^1 IPS 1809 (D) and left I^1 IPS 1808 (E) of *Hispanopithecus crusafonti* from Can Poncic; **F–J**: Right I^1 IPS 1770 (F), right I^1 IPS 1778 (G), right I^1 IPS 61398 (H), left I^1 IPS 18000.9 (I) and right I^1 IPS 18000.10 (J) of *Hispanopithecus laietanus* from Can Llobateres 1 and 2; **K**: Left I^1 RUD 142 of *Hispanopithecus hungaricus* from Rudabánya. All incisors depicted (from left to right) in occlusal, mesial, labial, distal and lingual views. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Anoiapithecus are possible in these regards since no I^1 is available for these taxa.

Occlusal morphology comparisons. The La Grive incisor is compared to Middle and Late Miocene dryopithecines in Figure 4. The upper central incisor of *Nacholapithecus* has a relatively spatulate crown with a broad lingual tubercle (Ishida et al., 2004; Kunimatsu et al., 2004). *Equatorius* similarly displays a triangular-shaped lingual tubercle, which is surrounded by distinct fovea, partially disrupted by abundant crenulations, and distinct from the weak lingual cingulum (Pickford, 1985; Kelley et al., 2002). The incisors of *Kenyapithecus wickeri* and *Kenyapithecus kizili*, in contrast, display very inflated marginal ridges and a diffuse shelf-like tubercle with abundant crenulations and no distinct foveae (Pickford, 1985; Alpagut et al., 1990; Martin and Andrews, 1993; Kelley et al., 2002, 2008). The incisor of *Griphopithecus alpani* more closely resembles *Equatorius* than *Kenyapithecus*, but it also differs from the former because the basal bulge is apically continued by a relatively narrow, but protruding and distinct, lingual pillar that tapers apically (Alpagut et al., 1990; Martin and Andrews, 1993; Kelley et al., 2002, 2008).

The single I^1 available for *Pierolapithecus* (Fig. 4B) displays a weak lingual cingulum between the marked basal swelling and a broad and triangular tubercle that is prolonged until about two-thirds of crown height, being partially disrupted by crenulations and surrounded by distinct foveae (Pérez de los Ríos et al., 2012a). This morphology resembles that of *Griphopithecus*, in which the expression of the cingulum and the lingual crenulations are variable, although the latter displays a somewhat narrower pillar instead of broad lingual tubercle (Kelley et al., 2008). *Hispanopithecus* species display two different morphologies, since a distinct but narrow pillar is present in *H. crusafonti* (Fig. 4C–E), whereas it is generally absent or poorly developed in *H. laietanus* (Fig. 4F–J) and variably expressed in *H. hungaricus* (Fig. 4K) (Begun, 1992; Andrews et al., 1996; Pilbrow, 2006). In *H. crusafonti*, however, the pillar is narrower and flanked by more marked clefts than in Middle Miocene taxa, thus more strongly contrasting with the *H. laietanus* condition, characterized by a shelf-like basal bulge with vertical crenulations but no well-developed pillar, as well as by a lower crown. There is disagreement on whether such differences are taxonomically relevant (Andrews et al., 1996; Begun, 2002) or might be merely attributable to intraspecific variability (Ribot et al., 1996; Pilbrow, 2006). A dryopithecine incisor from Neuhausen (Pickford, 2012) resembles *H. crusafonti* in crown height, but displays a less spatulate and a non-waisted morphology, as well as a wider, triangular pillar.

Compared to the above-mentioned taxa, the incisor from La Grive differs from all kenyapithecines except *Griphopithecus* in the lack of a distinct lingual cingulum and in the presence of a distinct lingual tubercle—absent in *Kenyapithecus*, and more restricted and non-apically projecting in *Equatorius* and *Nacholapithecus*. The broad and triangular morphology of the tubercle in the La Grive specimen, together with the presence of distinct mesial and distal foveae, most closely resembles the lingual morphology of *Griphopithecus* and, especially, *Pierolapithecus*, the Neuhausen specimen and some specimens of *H. hungaricus*, being readily distinguished from the two *Hispanopithecus* morphotypes found in the Vallès-Penedès Basin. The La Grive incisor can be readily distinguished from the Neuhausen specimen by its less barrel-like crown, and from *Pierolapithecus* and *H. hungaricus* by several lingual features, such as the less crenulated, broader, and more extensive tubercle (variably developed in *H. hungaricus*), as well as the subtriangular occlusal outline with a markedly concave mesiolabial portion (especially compared to *Pierolapithecus*, which displays a uniformly elliptical occlusal profile).

The La Grive upper molar

Metrical comparisons. The dimensions of the La Grive upper molar are compared to those of M^1 of other hominoid taxa in Figure 2. With regard to occlusal dimensions (Fig. 2B), the La Grive specimen is relatively small, being most similar to the smaller (presumably female) specimens of *Hispanopithecus*, *Griphopithecus*, and other kenyapithecines, and smaller than the known (male) specimens of the Vallès-Penedès Middle Miocene hominoids. Such differences would stand out more if the La Grive specimen was attributed to an M^2 or M^3. We therefore favor the attribution of the La Grive molar to a female specimen. Given the small available samples for other Middle Miocene dryopithecines, its occlusal proportions are of little use for making a taxonomic assessment. However, when RCH is taken into account (Fig. 3B), the La Grive specimen more closely resembles the condition of *Dryopithecus*, *Pierolapithecus*, *H. hungaricus* and, to a lesser extent, *H. laietanus*—the latter displaying the relatively highest molar crown on average. In contrast, both *H. crusafonti* and *Anoiapithecus* display a relatively lower molar crown, largely overlapping with *Griphopithecus*—which despite its broad range of variation displays, like the former taxa, an intermediate condition between other kenyapithecines and the remaining dryopithecines.

Occlusal morphology comparisons. Depéret (1911) first described the La Grive specimen as an M^3, but Begun (2002) considered that it might be interpreted either as an M^2 or as an M^3. Most recently, Begun (2009) and Pérez de los Ríos et al. (2012b) identified it as an M^3, whereas Moyà-Solà et al. (2009b) identified it as an M^2. There are some features that would support the identification of the La Grive molar as an M^3: the lack of a distal contact facet, the somewhat smaller size of the metacone compared to the paracone, the less obliquely oriented hypometacrista compared to the postprotocrista, and the disruption by enamel wrinkling of the secondary transverse crest dividing the distal fovea. However, the lack of a distal contact facet does not necessarily imply that this tooth is a last molar (especially given its moderate degree of wear), and other occlusal features suggest that an attribution to an M^1 is more likely. In particular, the talon is markedly reduced compared to the trigon, and the La Grive molar lacks the marked distal tapering that is characteristic of M^3 (and even the more or less tapering profile that is frequently displayed also by M^2). Moreover, the metacone of the La Grive specimen is not as markedly reduced as in dryopithecine M^3, and the hypocone is more well-developed and better-individualized than usual in M^3. In fact, its very lingual position is most consistent with this tooth being attributed to an M^1, especially when it is taken into account that its dimensions fit well with the female M^1 of other dryopithecine taxa. The lack of a distal contact facet can be easily accounted by the moderate degree of wear displayed by this tooth, which is mostly restricted to the mesial fovea—suggesting that the specimen belongs to a juvenile individual in which the M_2 was not yet into occlusion.

Given that our interpretation contradicts all previous tooth position attributions for this specimen, the La Grive specimen is compared to the M^1, M^2, and M^3 of Middle and Late Miocene dryopithecines in Figure 5. The restricted cingular development of the La Grive specimen enables its distinction from the upper molars of *Griphopithecus*, which display a more developed cingular remnant on the buccal side, and a more

Fig. 5. Upper molar from La Grive, compared to M^2 and M^3 of other Middle to Late Miocene hominoids from the Vallès-Penedès Basin and Rudabánya, in occlusal view. **A**: Left M^1 FSL 213981 from La Grive; **B**: Left M^1-M^3 IPS 35026 of *Dryopithecus fontani* from ACM/C3-Ae; **C**: Left M^1-M^2 and right (reversed) M^3 IPS 43000 (holotype) of *Anoiapithecus brevirostris* from ACM/C3-Aj; **D**: Right (reversed) M^1-M^3 IPS 21350 (holotype) of *Pierolapithecus catalaunicus* from ACM/BCV1; **E**: Right (reversed) M^1-M^3 IPS 18000.5 of *Hispanopithecus laietanus* from Can Llobateres 2; **F:** Left M^1-M^3 IPS 58338, IPS 58339 and IPS 58340 of *Hispanopithecus laietanus* from Can Llobateres 1; **G–J:** Right M^1 IPS 1844 (reversed) (G), left M^1 IPS 1798 (H), left M^2 IPS 1794 (I), left M^2? IPS 1777 (J) and left M^3 IPS 1772 of *H. laietanus* from Can Llobateres 1; **K–O:** Left M^1 IPS 1818 (K), left M^1–M^2 IPS 1798 (holotype; L), left M^2 IPS 1820 (M), right (reversed) M^3 IPS 1812 (N) and right (reversed) M^3 IPS 1814 (O) of *Hispanopithecus crusafonti* from Can Poncic; **P–V**: Left M^1 RUD 45 (P), right (reversed) M^1 RUD 12 (Q), right (reversed) M^2 RUD 141 (R), left M^2 RUD 44 (S), left M^3 RUD 85 (T), and right (reversed; U) and left (V) M^1-M^3 RUD 200 of *Hispanopithecus hungaricus* from Rudabánya. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

conspicuous (albeit usually incomplete) lingual cingulum (particularly around the mesiolingual aspect of the protocone). Compared to Middle to Late Miocene dryopithecines, the La Grive specimen can be most readily distinguished from *Pierolapithecus* (Fig. 5D)—which displays thicker and more inflated crests, secondary enamel folds and cusp bases—as well as from both *H. laietanus* (Fig. 5E–J) and *H. hungaricus* (Fig. 5P–V)—which display clearly less inflated crown bases, more peripheralized cusps, and finer crests. The La Grive molar can be further distinguished from *Pierolapithecus* by the relatively larger and more lingually positioned hypocone. In all these regards, the La Grive molar more closely resembles *Anoiapithecus* (Fig. 5C), *Dryopithecus* (Fig. 5B), and *H. crusafonti* (Fig. 5K–O).

DISCUSSION

In dental size, proportions, and lingual morphology, the La Grive incisor does not fit any of the previously-known Vallès-Penedès hominoids. Its occlusal proportions enable its distinction from the labiolingually thicker specimens of *Hispanopithecus* (most clearly in the case of *H. laietanus*), but fit well with the single known I^1 of *Pierolapithecus*. The RCH of the La Grive specimen, however, not only enables distinguishing these specimens from the higher-crowned *H. crusafonti* and the Neuhausen hominoid, but also from the much lower-crowned specimen of *Pierolapithecus*—as already noted by Moyà-Solà et al. (2009b). In lingual morphology, the La Grive incisor most closely resembles those of *Griphopithecus* and *Pierolapithecus*. In particular, given the presence of a pronounced basal bulge with a broad and triangular tubercle and distinct foveae, the La Grive incisor resembles that of *Pierolapithecus*, as previously noted by other authors (Begun, 2007, 2009; Begun et al., 2012; Pickford, 2012). On this basis, Begun (2009) suggested that *Pierolapithecus* might be a junior subjective synonym of *Dryopithecus*, whereas Pickford (2012) alternatively interpreted that *Pierolapithecus* was recorded at La Grive. However, such a lingual morphology does not necessarily imply that both specimens belong to the same taxon, since the presence of a lingual tubercle or pillar, variously expressed in all extant great apes (Pilbrow, 2006), is probably primitive for this group (Andrews et al., 1996), being already present in *Griphopithecus* (Kelley et al., 2008).

Moreover, besides RCH, there are several differences in lingual morphology between the La Grive specimen and that of *Pierolapithecus*. Thus, the La Grive incisor differs from that of *Pierolapithecus* in the broader and more massive tubercle, which is not separated from the basal bulge by a weak lingual cingulum; the more restricted foveae, separated from each other above the tubercle by a faint apical prolongation of the latter; the lesser-developed lingual crenulations; and the subtriangular instead of elliptical occlusal profile (with a conspicuous mesiolabial concavity, instead of being markedly and uniformly convex). The morphology of upper incisors is very variable within extant and extinct hominoid taxa (Kelley et al., 1995, 2008; Ribot et al., 1996; Pilbrow, 2006), so that their taxonomic implications for small fossil samples should be taken with great care (Pilbrow, 2006). Hence, the small available samples do not enable to entirely discount the possibility that the above-mentioned differences might finally prove to be intraspecific. However, currently available evidence strongly suggests that the taxon recorded by the La Grive incisor is not *Pierolapithecus* (contra Pickford, 2012), being alternatively attributable to either *D. fontani* or *A. brevirostris*, for which no I^1 is otherwise available (Moyà-Solà et al., 2009a,b).

With regard to the upper molar, dental size and occlusal morphology suggest that the La Grive specimen corresponds to the M^1 of a female dryopithecine species. Several details of the occlusal morphology (the thinner crest pattern with less inflated cusp bases, and the larger and more peripheral hypocone) lead us to conclude that an attribution to *Pierolapithecus* is not justified. An attribution to *H. laietanus* and *H. hungaricus* can be further discounted on the basis of the thicker crests, more peripheralized cusps and less inflated crown bases displayed by the La Grive molar. The latter thus more closely resembles the occlusal morphology of *Dryopithecus*, *Anoiapithecus*, and *H. crusafonti*. Compared to these the La Grive specimen displays a relatively higher crown than both *Anoiapithecus* and *H. crusafonti*, thus resembling the proportions found in *Dryopithecus* (as well as *Pierolapithecus* and the remaining *Hispanopithecus* species). By taking all the above-mentioned comparisons into account, we concur with Depéret's (1911) original attribution of the La Grive specimen to *D. fontani*.

CONCLUSIONS

Given the hominoid paleodiversity recorded at ACM, it is uncertain whether the two teeth from La Grive—which probably come from different fissure fillings—correspond to a single taxon, although this remains the most parsimonious hypothesis. The upper central incisor from La Grive shows several differences compared to *Pierolapithecus*, thus contradicting the opinions of other authors based on this specimen, according to which *Pierolapithecus* would be recorded at La Grive (Pickford, 2012) or might even be a synonym of *Dryopithecus* (Begun et al., 2008; Begun, 2009). Despite the high variability displayed by extant great apes in lingual incisor features, the small available samples do not enable completely discounting such possibility, which is however contradicted by differences in crown height between both taxa. Given the lack of upper central incisors for both *Anoiapithecus* and *Dryopithecus*, an attribution of the La Grive incisor to these taxa seems more likely. This is further supported by the occlusal morphology of the La Grive upper molar (here identified as a female M^1), which enables its distinction from *Pierolapithecus*. The occlusal morphology of the La Grive might be compatible with that of *Anoiapithecus*, *H. crusafonti*, and *Dryopithecus*, but RCH only supports an attribution to the latter taxon. Taking all this evidence into account, we therefore support the traditional attribution of the La Grive hominoid remains to *Dryopithecus fontani*, while stressing that an alternative attribution to *Pierolapithecus* is most unlikely and unsupported by available evidence.

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CHAPTER 6

Discussion

Dryopithecines constitute an extinct subfamily of apes (Hominoidea: Hominidae: Dryopithecinae) that is recorded in the Middle and Late Miocene of Western Eurasia. The Vallès-Penedès Basin is particularly rich in dryopithecine remains, but until a decade ago, most of the available remains from this basin came from Late Miocene (Vallesian) sites (such as Can Llobateres, Can Poncic and Castell de Barberà), whereas the Middle Miocene Aragonian ones were comparatively very scarce and little informative (Alba 2012a). These Aragonian dryopithecine remains, coming from the classical sites of the area of els Hostalets de Pierola (Villalta Comella and Crusafont Pairó 1941, 1944; Crusafont-Pairó and Golpe-Posse 1973; Golpe-Posse 1982, 1993; Harrison 1991; van der Made and Ribot 1999) and maybe Trinxera del Ferrocarril in Sant Quirze (Crusafont Pairó 1965; Golpe-Posse 1982, 1993; Harrison 1991), merely included isolated teeth or very fragmentary dentognathic remains. In contrast, during the last decade the paleontological works associated to the construction of a landfill (Abocador de Can Mata, ACM; Alba et al. 2006, 2011a;) in els Hostalets de Pierola have provided a new wealth of more complete cranial and postcranial dryopithecine remains (Moyà-Solà et al. 2004, 2009a,b; Alba 2012a). In this dissertation, craniodental remains of both Middle and Late Miocene dryopithecines from the Vallès-Penedès Basin and nearby areas are described and compared with other hominoids, both extant and extinct. The main implications for the biochronology, taxonomy and phylogeny of the Vallès-Penedès dryopithecines are discussed below.

Biochronology

Casanovas-Vilar et al. (2011a) provided an updated review on the chronology of Western Eurasian hominoids, which incorporated the results of the litho-, bio- and magnetostratigraphic works performed at ACM during the last decade (Alba et al. 2006; Moyà-Solà et al. 2009b). According to Casanovas-Vilar et al. (2011a; see also Alba 2012a; Alba et al. 2012c), most of the hominoid remains from ACM would be correlated to subchron C5r.3r, with an estimated age (depending on the site) between 11.9 and 11.8 Ma. Following the new chron age boundaries published by Hilgen et al. (2012), the estimated age range for most of the ACM hominoid remains must be updated to 12.0 and 11.9 Ma (David M. Alba, pers. com.). In Chapter 3, the oldest hominoid remains from the Vallès-Penedès Basin (and, hence, the whole Iberian Peninsula) are described, consisting of a maxillary fragment (IPS 34027) from locality ACM/C1-E*, which is attributed to *Anoiapithecus brevirostris*. As noted in Chapter 3, most of the classical Aragonian hominoid-bearing localities from the ACM cannot be accurately dated, although available evidence conclusively indicates that all of them (including the classical localities from els Hostalets de Pierola) are younger than ACM/C1-E*. Based on lithostratigraphic and magnetostratigraphic data, the latter locality (representing the first appearance datum of hominoids in the Iberian Peninsula) is correlated to subchron C5An.2n, with an interpolated age of 12.3-12.2 Ma (Casanovas-Vilar et al. 2011a; see Chapter 3), which following the recent recalibration of chron boundaries (Hilgen et al. 2012) would currently correspond to 12.4-12.3 Ma (David M. Alba, pers. comm.). The last appearance datum (LAD) of dryopithecines in the Iberian Peninsula is the record of *H. laietanus* at La Tarumba 1, which is correlated to subchron C4Ar.2r (9.647-9.426 Ma), with an interpolated age of 9.6 Ma based on the data by Hilgen et al. (2012; Casanovas-Vilar, pers. comm.). However, this datum is not the LAD of dryopithecines in Europe, as *Ouranopithecus* and *Oreopithecus* survived well into the Turolian, until ca. 7.4-6.7 Ma (Güleç et al. 2007; Rook et al. 2011).

During the Miocene, another group of primates are recorded in Europe, the pliopithecids, which are customarily considered stem catarrhines (e.g., Begun 2002b; Harrison 2013). They are recorded from the Middle to the Late Miocene of Europe (Begun 2002b), although in the Vallès-Penedès Basin they are recorded exclusively from the Late Aragonian (MN7+8; ca 12.1-11.7 Ma) to the Late Vallesian (MN10; ca. 9.0 Ma; Alba et al. 2010, 2012c; age estimates updated after Hilgen et al., 2012; David M. Alba, pers. comm.), with the oldest record in this basin corresponding to an upper molar from locality ACM/C3-B2 (Alba et al. 2012c). The FAD of pliopithecoids in the Vallès-Penedès Basin is therefore slightly younger than that of hominoids, although the scarcity of primate remains along the ACM series does not allow one to conclude that this difference of merely 0.2-0.3 million years is but a preservational artifact.

Interestingly, the oldest hominoid record from the Vallès-Penedès (12.4-12.3 Ma) is only slightly younger than the FAD of hominoids in Asia, where *Sivapithecus* is already recorded by ca. 13.0-12.5 Ma (Kappelman et al. 1991; Kunimatsu et al. 2004). The coexistence of members of the great-ape-and-human clade at both sides of Eurasia roughly by the same time (pongines in Asia, and dryopithecines in the Iberian Peninsula) suggests that the divergence of these groups took place somewhat earlier (Alba 2012a). Both groups might have originated from the kenyapithecines recorded earlier in Eurasia, since these taxa apparently display some hominid derived features. The oldest hominoid find from Eurasia is a partial molar of cf. *Griphopithecus* from Engelswiess, with and estimated age of more than 16 Ma (Heizmann and Begun 2001; Casanovas-Vilar et al. 2011a), although the preserved morphology does not enable to establish a clear link with later kenyapithecines from Turkey (Casanovas-Vilar et al. 2011a; Alba 2012a). The oldest possible age of ca. 16 Ma for these remains, currently attributed to *Griphopithecus* and *Kenyapithecus* (Kelley et al. 2008), has been favored by some authors (Begun 2002a; Begun et al. 2003), according to which kenyapithecines might have subsequently dispersed back into Africa. However, biostratigraphic evidence rather suggests alternative magnetostratigraphic correlations for these kenyapithecine-bearing Turkish localities, indicating an age closer to ca. 14 Ma (Casanovas-Vilar et al. 2011a). Based on the available record, kenyapithecines are likely ancestors for later Eurasian hominoids (Moyà-Solà et al. 2009a; Alba 2012a), suggesting that dryopithecines and pongines (and maybe hominines) would have probably diverged between 14 and 12.5 Ma. Hopefully, additional finds from this time span in Eurasia and Africa will further clarify the controversial phylogenetic relationships among these taxa (see below).

Taxonomy

Until a decade ago, all the Vallès-Penedès hominoids were included into a single genus, *Dryopithecus* (e.g., Begun 1992; Moyà-Solà and Köhler 1993, 1995; Köhler et al. 2001a,b; Begun 2002a, 2007). However, the discoveries of Aragonian hominoid remains that have taken place in the Vallès-Penedès during the last decade have revealed a previously unsuspected diversity of dryopithecines in this region, with as much as four genera and five species being recognized (Alba 2012a). This high dryopithecine diversity for such a small geographic area has been accepted by some authors (e.g., Pickford 2012), but has been questioned by others (e.g., Begun 2009). Thus, there is agreement (Moyà-Solà et al. 2009a; Begun 2009; Alba 2012a) that the Late Miocene species from the Vallès-Penedès Basin must be included into a different genus (*Hispanopithecus*) than the Middle Miocene ones. However, disagreements persist regarding several taxonomical aspects: (a) whether *Pierolapithecus* and *Anoiapithecus* are distinct genera or merely junior synonyms of *Dryopithecus*; (b) whether *Pierolapithecus*, if distinct, is recorded outside the Vallès-Pendès Basin; and (c) whether *Hispanopithecus* must be restricted to the Vallès-Penedès material (or even *Hispanopithecus laietanus* only), or whether the hominoid remains from Rudabánya (Hungary) must be also included within this genus.

Synonymy with *Dryopithecus*. Regarding the purported synonymy of *Pierolapithecus* and *Anoiapithecus* with *Dryopithecus* (Begun et al. 2008; Begun 2009, 2010, 2013), the evidence provided in this dissertation regarding dental occlusal morphology and proportions (Chapter 5), relative enamel thickness (Chapter 3), paranasal sinuses (Chapter 4), and external cranial morphology (Chapter 2) strongly supports the view that *Pierolapithecus* and *Anoiapithecus* are distinct from one another, and that neither of them may be considered a synonym of *Dryopithecus*. To a large extent, the purported synomymy between the three Middle Miocene genera from the Vallès-Penedès is based on the contention that the cranium of *Pierolapithecus* is considerably distorted. Although some distortion is evident, as discussed in Chapters 2 and 4, such a distortion is clearly insufficient to explain the differences in cranial morphology between the ACM remains of the three genera, especially if it is taken into account that differences cannot be attributed to sexual dimorphism and/or ontogenetic differences (since the holotypes of both *P. catalaunicus* and *A. brevirostris*, like the most complete specimen of *D. fontani*, are adult males). Differences in external cranial morphology (Chapter 2) are further reinforced by minor differences in dental morphology and proportions (Chapters 3 and 5), relative enamel thickness (Chapter 3), and internal cranial morphology (Chapter 4). Thus, as mainly discussed in Chapter 2, *Anoiapithecus* differs from *Pierolapithecus* and *Dryopithecus* in the extremely ortognathous face, the narrower anterior palate, the shorter nasoalveolar clivus and the more downwardly-inclined zygomatic. Moreover, *Pierolapithecus* shows a non-domed muzzle, a shorter face superoinferiorly, a shorter nasoalveolar clivus, a more prognathous lower face, a thicker zygomatic crest and a more posteriorly located glabella than both *Anoiapithecus* and *Dryopithecus*. These cranial differences are reinforced by dental features (Chapter 3), with *Anoiapithecus* showing less inflated crests, less development of enamel wrinkling, a more lingually-located hypocone and lower-crowned molars than *Pierolapithecus*, whereas *Dryopithecus* displays relative higher crown molars than the other two genera. Moreover, *Dryopithecus* apparently displays thinner enamel than both *Anoiapithecus* and *Pierolapithecus* (Chapter 3), although larger samples would be required to reach more confindent conclusions in this regard. In any case, the differences in dental morphology between these taxa are relatively minor and would justify at most the distinction of different species within a single genus. The latter option, however, is contradicted by differences in both internal and external morphology. In particular, the lack of frontal sinus in *Pierolapithecus* (contrasting with the well-developed frontal sinus of *Anoiapithecus*) and the striking differences in facial prognathism most strongly support the distinction of these genera. Other differences further support the distinction between these two genera and *Dryopithecus*, although, unfortunately, the presence/absence of frontal sinus cannot be currently ascertained in *D. fontani*, due to incomplete preservation.

The identity of the La Grive hominoid. With regard to the possibility that *Pierolapithecus* might be recorded outside the Vallès-Penedès Basin, Begun (2007) and Pickford (2012) suggested that the material from the French locality of La Grive, traditionally attributed to *Dryopithecus fontani* (Andrews et al. 1996), might belong in fact to *P. catalaunicus*. Pickford's (2012) suggestion was mainly on purported similarities in central upper incisor morphology. In Chapter 5, the similarities in incisor proportions and lingual morphology between the holotype of *P. catalaunicus* and the La Grive specimen are analyzed. It is shown that the La Grive incisor, although more clearly distinct from those of Late Miocene *Hispanopithecus* spp., is higher-crowned than that of *P. catalaunicus*, as previously noted by Moyà-Solà et al. (2009b). Moreover, the morphology of the La Grive specimen does not fit well with that of *P. catalaunicus* (including differences in the central pillar, the lower degree of crenulations, the more restricted foveae, and the different occlusal profile). In fact, the similarities previously noted between the La Grive specimen and *Pierolapithecus* by several authors (Begun 2007, 2009; Pickford 2012) further recall the features displayed by the kenyapithecine *Griphopithecus* (Kelley et al. 2008), suggesting that they are merely primitive retentions (as already suggested by Andrews et al. 1996 regarding the La Grive specimen). Differences between the La Grive specimen and the holotype of *P. catalaunicus* must be interpreted with great care, given the scarcity of the available material and the considerable variation in lingual incisor morphology displayed by extant hominoids (Kelley et al. 1995, 2008; Ribot et al. 1996; Pilbrow 2006). However, available evidence argues against an assignment of the La Grive incisor to *Pierolapithecus*, and is compatible with the traditional attribution to *Dryopithecus*, although the lack of upper incisors of *Anoiapithecus* and *Dryopithecus* precludes conclusively discounting an alternative attribution to the former. An attribution to the hominoid taxon from La Grive to *D. fontani* is further reinforced by the morphology of the upper molar originally described by Depéret (1911). The analysis of the dental proportions of this specimen reported in Chapter 5 suggests that this specimen probably corresponds to an upper first molar (instead of a second or third molar, as interpreted by previous authors; Begun 2009; Moyà-Solà et al. 2009b), which is most likely attributable to *D. fontani* rather than *P. catalaunicus* or *A. brevirostris*, based on differences in occlusal morphology and relative crown height.

The genus *Hispanopithecus.* Based on differences between the Late Miocene remains from Can Llobateres 2 and the Middle Miocene maxilla from ACM/C3-Ae, Moyà-Solà et al. (2009b) resurrected the genus *Hispanopithecus* for its nominotypical species (*H. laietanus*) and *H. crusafonti* (formerly attributed to *Dryopithecus*; e.g., Begun, 1992) from the Vallès-Penedès, as well as for *H. hungaricus* (formerly *Rudapithecus hungaricus*, considered a junior synonym of *Dryopithecus brancoi*; Begun and Kordos 1993, 1997; Begun 2002a, 2007) from Hungary. By the same time, Begun (2009) resurrected the genus *Rudapithecus* for the Hungarian material. Therefore, there is currently consensus that the Late Miocene forms are distinct at the genus rank from the Middle Miocene ones, although disagreement persists as to whether the Rudabánya material can be subsumed to *Hispanopithecus* (e.g., Casanovas-Vilar et al. 2011a), with *Rudapithecus* being merely recognized as a subgenus of the former (Alba 2012a; Alba et al. 2013), or whether the Hungarian material belongs to a different genus, *Rudapithecus* (e.g., Begun 2009, 2010, 2013; Begun et al. 2012). The analysis of the craniodental morphology of these taxa (Chapter 2) indicates that *Hispanopithecus* (*H.*) *laietanus* and *H.* (*Rudapithecus*) *hungaricus* share multiple features that distinguish them both from Middle Miocene dryopithecines (cranium with broad interorbital pillar, thick supraorbital rim, presence of a frontal notch, high zygomatic root, deep glenoid fossa, low frontozygomatic suture, and reduced midfacial prognathism, as well as a mandible with parallel tooth rows, posteriorly shallowing corpora, short and almost vertical symphysis, and strongly-developed transverse tori), thereby supporting their distinction at the genus and even tribe rank (Hispanopithecini) of these taxa from Middle Miocene dryopithecines (Dryopithecini). On the other hand, both species display several cranial differences (less laterally-oriented zygomatic, flatter glabella, more superiorly situated orbits, lower angle beween the frontal squama and the interorbital plane, more numerous zygomaticofacial foramina, broader palate, thinner zygomaticoalveolar crest, more posteriorly located nasal aperture and zygomatic root, broader extramolar sulcus and oval instead of triangular symphyseal cross-section in *H. laietanus*), which support their distinction at a supraspecific level, although reflecting these differences at the genus or subgenus rank seems rather arbitrary at the moment.

The content of genus *Hispanopithecus* is further controversial regarding a second species from the Vallès-Penedès, based on the material from Can Poncic and further including the mandible from Teuleria del Firal (Begun 1992; Alba 2012a). This species was originally described within the genus *Dryopithecus* by Begun (1992) and subsequently reassigned to *Hispanopithecus* by Moyà-Solà et al. (2009b). Given that, over the years, several authors have favored the synonymy of this species with *H. laietanus* (formerly *Dryopithecus laietanus*), reassigning it to *Hispanopithecus* seemed the most reasonable option when Moyà-Solà et al. (2009b) resurrected this genus. A reanalysis of the dental morphology of these taxa, including additional material of *H. laietanus* (Alba et al. 2012b), supported the view that *H. crusafonti* is distinct at the species level from *H. laietanus*. However, as explained in Chapter 2, it should be taken into account that the attribution of these two species to the same genus is entirely based on dental similarities, given the lack of cranial material (other than the mandible from Teuleria del Firal) for *H. crusafonti*. Moreover, in Chapter 3 (see also Moyà-Solà et al. 2009a) it is shown that the dental morphology of *H. crusafonti* is more primitive in several regards than that of *H. laietanus*, being more similar to that of Middle Miocene dryopithecines (especially *Anoiapithecus*). Therefore, until more complete remains of *H. crusafonti* are recovered, the attribution of the latter species to genus *Hispanopithecus* must be considered tentative.

Phylogeny

A cladistic analysis of the Vallès-Penedès dryopithecines if not formally performed in this work. However, the description of their internal and the external cranial morphology, and its comparison, within a phylogenetic framework, with both extant and other extinct hominoids, enables the evaluation of the various competing phylogenetic hypotheses that have been put forward for these taxa by previous authors. There is currently a consensus that dryopithecines are members of the great-ape-and-human clade, being thus customarily included within the Hominidae (Begun 2009, 2010, 2013; Moyà-Solà et al. 2009a,b; Casanovas-Vilar et al. 2011a; Alba 2012a; Alba et al. 2013). This is justified by the possession in dryopithecines of various extant hominid synapomorphies (Harrison 1986; Rae 1999), such as the flat nasals, the high and robust mandible or the lack of contact between the premaxillary suture and the nasals. However, the specific phylogenetic relationships among dryopithecine genera, as well as regarding other hominoids, remain very controversial, as discussed in Chapters 2 and 5. Thus, some or all the Vallès-Penedès dryopithecines have been alternatively considered stem hominids (Moyà-Solà et al. 2004, 2009a,b; Alba and Moyà-Solà 2009; Alba 2012a), stem pongines (Moyà-Solà and Köhler 1993, 1994, 1995; Cameron 1997; Köhler et al. 2001a; Alba 2012a; Pérez de los Ríos et al. 2012), or stem hominines (Begun 1994, 2002a, 2007, 2009, 2010; Begun and Kordos 1997; Kordos and Begun 2001, 2002; Begun and Ward 2005; Begun et al. 2012). The pros and cons of these contrasting hypotheses are discussed in further detail below.

Dryopithecines as crown hominids. Before the description of the cranial remains from ACM, most of the relevant information on the phylogenetic relationships of Vallès-Penedès hominoids was based on the cranial and postcranial morphology of *Hispanopithecus laietanus* (formerly *Dryopithecus*) from Can Llobateres 2 (Moyà-Solà and Köhler 1993, 1995, 1996; Begun 1994). Several authors argued that this taxon must be interpreted as a stem pongine (Schwartz 1990, 1997; Moyà-Solà and Köhler 1993, 1995; Agustí et al. 1996; Cameron 1997; Köhler et al. 2001a), based on the interpretation of several cranial features (most notably relating to zygomatic and supraorbital morphology, as well as the development of the frontal sinus). However, as discussed in Chapter 2, the interpretation of these features is not unambiguous, with some characters being of doubtful phylogenetic significance (the presence of multiple zygomaticofacial foramina, which is highly polymorphic; Eckhardt 1994) or not being uniformly present in all dryopithecines (e.g., the zygomatic morphology, which is different in *H. hungaricus*). It is currently uncertain whether the condition displayed in the latter regard by some the Vallès-Penedès dryopithecines reflects the primitive condition for crown hominids, being subsequently modified in hominines, or whether the similarities between pongines and some dryopithecines are merely homoplastic. Be that as it may, as shown in Chapter 2, all of the Vallès-Penedès dryopithecines lack the pongine synapomorphies shared by *Pongo* and *Sivapithecus*, including the concave facial profile, the ovoid and high orbits, the narrow interorbital pillar and the smooth subnasal floor with the premaxilla overlapping the hard palate and defining a long and thin incisive canal (Pilbeam 1982, 1986; Kelley and Pilbeam 1986; Benefit and McCrossin 1995; Ward 1997). Even *Ankarapithecus*, with a less derived cranial morphology more similar to that of dryopithecines, already displays the subnasal morphology characteristic of *Pongo* and *Sivapithecus* (Begun and Guleç 1998; Andrews and Alpagut 2001; Kappelman et al. 2003), thereby suggesting that the Vallès-Penedès dryopithecines (both dryopithecins and hispanopithecins) occupy a more basal phylogenetic position among hominoids.

Following the description of the Can Llobateres 2 material as well as that from Rudabánya, *Hispanopithecus* was alternatively interpreted as a stem hominine (Begun 1994; Begun and Kordos 1997; Kordos and Begun 2001, 2002; Begun 2002a). This phylogenetic hypothesis, favored by Begun and coauthors and further extended to ouranopithecines (Begun 1994, 2002a; Begun and Kordos 1997; Kordos and Begun 2001, 2002), has been more recently expanded to include the Middle Miocene dryopithecine remains described during the last decade from the Vallès-Penedès (Begun and Ward 2005; Begun et al. 2006, 2008, 2012; Begun 2007, 2009, 2010, 2013). The contention that the Vallès-Penedès dryopithecines are most parsimoniously interpreted as stem hominines is based on the controversial interpretation of several key features related to the supraorbital morphology (purported presence of an incipient supraorbital torus with post-toral sulcus) and subnasal morphology (supposed moderate overlap between the premaxilla and the hard palate) of these taxa, together with other features (such as the purported presence of a frontal sinus of ethmoidal origin, the more klinorhynchous cranium or the broad temporal fossa). However, as discussed in Chapter 2, the supraorbital and subnasal morphology displayed by the Vallès-Penedès dryopithecines differs from the derived hominine condition, and most closely resembles that displayed by more primitive, stem hominoids from the Early Miocene of Africa (as already noted by Moyà-Solà and Köhler 1995, regarding *Hispanopithecus*). Similarly, the polarity of other features (such as the degree of klinorhynchy vs. airorhynchy) is ambiguous at best, and the scarcity of complete crania among the Miocene record of hominoids precludes deciphering the ancestral condition for the last common ancestor of crown hominids. Finally, the dryopithecine finds from the last decade have shown that the evolution of particular features, such as the configuration of the frontal sinus, is much more complex than previously thought, with several dryopithecine taxa displaying a different condition in this regard.

According to Begun (2009), dryopithecines as a whole (including the Vallès-Penedès taxa, as well as *Ouranopithecus*) would be characterized by the presence of a large maxillary sinus, a well-developed frontal sinus, and thin enamel. However, it is clear that when Begun (2009) proposed such a diagnosis of the group, this author had basically *Hispanopithecus* in mind. Subsequently, the analysis of the Middle Miocene dryopithecins has shown that these features do not hold for some of the taxa (Chapters 3 and 5). Thus, the interpretation of the frontal sinus of *Hispanopithecus* as a true frontal sinus of ethmoidal origin, as previously noted by Moyà-Solà and Köhler (1993, 1995), is controversial, being alternatively interpretable as a frontal recess of the maxillary sinus. In any case, whereas *Anoiapithecus* displays a well-developed and much more extensive frontal sinus (Moyà-Solà et al. 2009a), it is shown in Chapter 5 that *Pierolapithecus* lacks a frontal pneumatization altogether. Similarly, *Pierolapithecus*, like *Anoiapithecus* and *Dryopithecus*, displays an anteriorly restricted maxillary sinus that does not reach the molar roots (Chapters 3 and 5; see also Moyà-Solà et al. 2009a,b), thus more closely resembling the primitive condition displayed by kenyapithecines (Pickford 1985; S.C. Ward et al. 1999), rather than the more extensive and anteriorly projecting maxillary sinus of hispanopithecins (Moyà-Solà and Köhler 1993, 1995; Kordos and Begun 2001). It is similarly shown in Chapters 3 and

5 that not all dryopithecines display thin-enameled molars, since *Anoiapithecus* and, especially, *Pierolapithecus* are characterized by thicker enamel.

Whereas enamel thickness is of little phylogenetic significance (given its highly adaptive value), the presence/absence of a frontal sinus has played a prominent place in the debates on hominoid phylogeny, with the possession of a well-developed frontal sinus being interpreted as the primitive hominoid condition, and the lack of sinus a pongine synapomorphy shared by *Pongo* and *Sivapithecus* (Moyà-Solà and Köhler 1995; Pickford et al. 1997; Rossie 2008; Begun 2009). In this sense, the lack of a frontal sinus in *Pierolapithecus*, together with other similarities in internal cranial morphology with pongines (Ward and Pilbeam 1983; Begun and Guleç 1998; Rae 1999), including the presence of frontal recess of the maxillary sinus invading the ethmoidal area, the lack of palate recess of the maxillary sinus, the position of the turbinals over the second molars, and the anteriorly projecting nasolacrimal canal (Chapter 3), might indicate a closer phylogenetic link of this taxon with pongines. However, the lack of evidence of some of these features (position of the turbinals and projection of the nasolacrimal canal) for other extinct hominoids, together with the fact that frontal sinuses have been repeatedly lost in catarrhine evolution (Rossie 2008), do not enable to confidently conclude that the above-mentioned features strongly support a pongine status for *Pierolapithecus*. Indeed, the fact that the stem pongine *Ankarapithecus* displays a well-developed frontal sinus (Kappelman et al. 2003), like some contemporary dryopithecines (*Anoiapithecus*; Moyà-Solà et al. 2009a), rather suggests that the condition of *Pierolapithecus* in this regard might be merely interpreted as homoplastic (i.e., not indicating a close phylogenetic link with pongines). This is further reinforced by the apparent nasoalveolar morphology of *Pierolapithecus* (Chapter 4). Although the exact configuration of the premaxilla relative to the maxilla is difficult to conclusively ascertain due to damage, preserved evidence suggests that the premaxilla is short and thick, and that it does not overlap the hard palate, as in other dryopithecines (Ward and Pilbeam 1983; Moyà-Solà and Köhler 1995; Moyà-Solà et al. 2009a,b), but unlike the condition displayed by either pongines (including the extinct *Ankarapithecus* and *Sivapithecus*) or African apes (Ward and Pilbeam 1983; McCollum et al. 1993).

Dryopithecines as stem hominids. Although the Vallès-Penedès dryopithecines display a number of primitive cranial features in common with kenyapithecines, the former display additional crown-hominid synapomorphies (Chapter 2), indicating a closer relationship with both pongines and hominines. However, as explained above, dryopithecines lack clear pongine or hominine synapomorphies, thereby favoring their interpretation as stem hominids preceding the pongine-hominine split, as already suggested by previous authors (Andrews 1992; Benefit and McCrossin 1995, 1997; Begun 2002a, 2007, 2009, 2010, 2013; Moyà-Solà et al. 2004, 2005, 2009a,b; Alba and Moyà-Solà 2009; Alba 2012a,b). The same can be argued of lufengpithecins, traditionally considered pongines by most authors (Leakey et al. 1988; Schwartz 1990, 1997; de Bonis and Koufos 1993; Moyà-Solà and Köhler 1993, 1995; Pickford et al. 1997; Andrews and Alpagut 2001), although it has been more recently recognized that at least *Lufengpithecus* lacks clear pongine synapomorphies (Kelley and Gao 2012; Ji et al. 2013). This fact, coupled with the quite dryopithecine-like cranial morphology of *Lufengpithecus*, leaves open the possibility that this taxon might be a dryopithecine after all, although pending a formal cladistic analysis this has not been reflected in the systematic scheme adopted in this dissertation.

Overall, the evidence presented in Chapters 2 and 4 of this dissertation enables to confidently reject the hypothesis that dryopithecines can be interpreted as stem hominines, and rather favors their interpretation as stem hominids. As already noted by Alba (2012a) and in Chapter 4, the possibility remains that dryopithecines might be the sister taxon of Asian pongines, with both subfamilies being more closely related to one another than with hominines. However, no synapomorphies of this putative dryopithecine+pongine clade have been identified to date (Chapter 2), thereby favoring the alternative interpretation that dryopithecines are stem hominids. Unfortunately, as noted in Chapter 2, there are no clear dryopithecine synapomorphies supporting that this taxon constitutes a clade (i.e., a strictly monophyletic group) instead of a paraphyletic (or even polyphyletic) assemblage. Based on the currently available evidence, the possibility remains that dryopithecines are successive members of the hominid stem lineage, or even that some of them are more closely related to crown hominids.

CHAPTER 7

Conclusions

The craniodental remains of Miocene hominoids from the Vallès-Penedès Basin (including not only previously-published material, but also some unpublished remains) are described and compared to other hominoids (both extant and extinct), with significant implications for the biochronology, taxonomy and phylogeny of the Dryopithecinae. They are summarized below.

1. The first appearance datum (FAD) of hominoids in the Iberian Peninsula is recorded in the local stratigraphic series of Abocador de Can Mata (ACM; els Hostalets de Pierola, Vallès-Penedès Basin), and corresponds to two maxillary fragments of *Anoiapithecus brevirostris* from locality ACM/C1-E*, which is correlated with subchron C5An.2n, with an estimated age of 12.4-12.3 Ma

2. The comparison of both internal and external craniodental morphology among the hominoid sample of the Vallès-Penedès Basin, including dental occlusal morphology, relative enamel thickness, external cranial features and paranasal sinuses, indicates the existence of significant differences that support the recognition of five species and four distinct genera: the Middle Miocene *Pierolapithecus catalaunicus*, *Anoiapithecus brevirostris* and *Dryopithecus fontani*, as well as the Late Miocene *Hispanopithecus laietanus* and *Hispanopithecus crusafonti*. Regarding the latter, an attribution to genus *Hispanopithecus* is favored by dental similarities with *H. laietanus*, although the lack of cranial material and the retention of a more primitive dental morphology (most similar to that of *A. brevirostris*), makes such an attribution rater tentative. The comparison of the Vallès-Penedès hominoids with the material from Rudabánya indicates for the latter closer taxonomic affinities with *Hispanopithecus*, but recognizing it as a distinct genus (*Rudapithecus*) or merely subgenus of *Hispanopithecus* remains somewhat arbitrary.

3. A comparison of the two hominoid teeth (an upper molar and an upper central incisor) from the Middle Miocene site of La Grive (France) with the dental remains of the Vallès-Penedès dryopithecines supports the traditional attribution of the former to *D. fontani*. Dental morphology and proportions suggests that the upper molar corresponds to a first molar of a female individual (in-

stead of a second or third molar, as traditionally considered) of *D. fontani*. Similarly, the lingual morphology of the La Grive incisor shows several differences compared with that of the holotype specimen of *P. catalaunicus*, thus contradicting previous suggestions that *Pierolapithecus* would be recorded at La Grive. Overall, available evidence supports the traditional attribution of the La Grive hominoid to *D. fontani*, although the scarcity of the available material from this locality, together with the lack of upper central incisors of both *Anoiapithecus* and *Dryopithecus* from other localities, preclude a more conclusive taxonomic assessment.

4. The description of both the internal and external cranial morphology of the Vallès-Penedès dryopithecines, and their comparison with both extant and other extinct hominoids, enables discussing the phylogenetic status of the former. The dryopithecine cranial morphology is characterized by a mosaic of primitive hominoid features (shared with kenyapithecines) and more derived features (shared with crown hominids), thus being confidently interpreted as members of the great-ape-and-human clade (Hominidae) more derived by kenyapithecines.

5. Although the Vallès-Penedès dryopithecines have been interpreted as either pongines or hominines by several authors, it is shown that the former taxa lack both the clear pongine synapomorphies shared by *Pongo* and *Sivapithecus* (and, to a lesser extent, *Ankarapithecus*) as well as the hominine synapomorphies displayed by extant African apes. This fact supports the view that dryopithecines are best interpreted as stem hominids preceding the pongine-hominine split. On the other hand, the differences displayed among the Vallès-Penedès dryopithecines for several key features (such as the configuration of the frontal sinus) and the lack of derived features exclusively shared by dryopithecines (with the exclusion of other hominoids) indicate that, as currently conceived, dryopithecines must not necessarily constitute a monophyletic clade, but might alternatively configure a paraphyletic assemblage of stem hominids, or even a polyphyletic assemblage including both stem and crown hominids.

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Vivir es encontrase en el mundo

Si existo yo que pienso, existe el mundo que pienso

José Ortega y Gasset