

A unique Middle Miocene European hominoid and the origins of the great ape and human clade

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The great ape and human clade (Primates: Hominidae) currently includes orangutans, gorillas, chimpanzees, bonobos, and humans. When, where, and from which taxon hominids evolved are among the most exciting questions yet to be resolved. Within the Afroplithecidae, the Kenyapithecinae (Kenyapithecini + Equatorini) have been proposed as the sister taxon of hominids, but thus far the fragmentary and scarce Middle Miocene fossil record has hampered testing this hypothesis. Here we describe a male partial face with mandible of a previously undescribed fossil hominid, *Anoiapithecus brevirostris* gen. et sp. nov., from the Middle Miocene (11.9 Ma) of Spain, which enables testing this hypothesis. Morphological and geometric morphometrics analyses of this material show a unique facial pattern for hominoids. This taxon combines autapomorphic features—such as a strongly reduced facial prognathism—with kenyapithecine (more specifically, kenyapithecini) and hominid synapomorphies. This combination supports a sister-group relationship between kenyapithecins (*Griphopithecus* + *Kenyapithecus*) and hominids. The presence of both groups in Eurasia during the Middle Miocene and the retention in kenyapithecins of a primitive hominoid postcranial body plan support a Eurasian origin of the Hominidae. Alternatively, the two extant hominid clades (Homininae and Ponginae) might have independently evolved in Africa and Eurasia from an ancestral, Middle Miocene stock, so that the supposed crown-hominid synapomorphies might be homoplastic.

Anoiapithecus gen. nov. | evolution | Hominidae | Hominoidea | Paleoprimatology

There is a general consensus on the relevance of Middle Miocene hominoids for understanding hominid origins (1, 2). However, the question of the initial great-ape/human radiation still remains elusive. In this paper we describe a previously undescribed Middle Miocene thick-enameled hominid [see supporting information (SI) Text and Table S1, regarding the systematic framework used in this paper], which displays a unique and unusual combination of facial characteristics with significant phylogenetic implications. *Anoiapithecus brevirostris* gen. et sp. nov. shows the basic great-ape synapomorphies and some generalized afropithecine and several kenyapithecine-derived features, coupled with a striking reduction of the face. This combination is unknown from any fossil or extant great ape, which has important implications for reconstructing the initial evolutionary history of the great ape and human clade.

Stratigraphic Setting. The description of this taxon is based on a hominoid partial face with mandible (IPS43000) discovered at locality Abocador de Can Mata (ACM)/C3-Aj, in the area of Els Hostalets de Pierola (Vallès-Penedès Basin, Catalonia, Spain). This region is characterized by thick Middle to Late Miocene stratigraphic sequences. The construction of a rubbish dump (ACM) near the country house of Can Mata (Fig. S1) prompted a paleontological intervention to control the removal of Miocene

sediments by the diggers and bulldozers. After 6 years of fieldwork, 150 fossiliferous localities have been sampled from the 300-m-thick local stratigraphic series of ACM, which spans an interval of 1 million years (≈ 12.5 – 11.3 Ma, Late Aragonian, Middle Miocene). To date, 38,000 macrovertebrate remains and thousands of small mammal teeth have been recovered from the above mentioned localities, some of which have yielded primate remains (3–5). These localities can be accurately dated because of detailed litho-, bio-, and magnetostratigraphic control (4). An age close to 11.9 Ma can be estimated for ACM/C3-Aj, from which IPS43000 was excavated.

Description. The face of IPS43000 (Fig. 1) lacks the nasals and the right maxilla, some parts of the orbits, and parts of both zygomatics. The palate is nearly complete, lacking only the left C¹ and M³, as well as the incisors; part of the frontal also is preserved. The mandible preserves the symphysis and a large portion of the 2 corpora, but lacks the 2 rami; the left I₁ and C₁–M₂ series and the right C₁–M₁ series are preserved. Complete eruption of the M³ indicates that IPS43000 belongs to an adult individual, because the slight displacement of this tooth from the alveolar plane merely results from bone distortion at the level of M²–M³.

Systematic Paleontology. Systematic paleontology is as follows: Order Primates Linnaeus, 1758; suborder Anthroipoidea Mivart, 1864; infraorder Catarrhini Geoffroy, 1812; superfamily Hominoidea Gray, 1825; family Hominidae Gray, 1825; subfamily incertae sedis; tribe Dryopithecini Gregory and Hellman, 1939; *Anoiapithecus* gen. nov. type species *A. brevirostris* gen. et sp. nov. Etymology is from Anoi (the region where the site is situated) and the Greek *pithekos* (ape). Generic diagnosis is as for the type species, *A. brevirostris* gen. et sp. nov. Holotype is IPS43000, a partial face with mandible of an adult male individual, housed at the Institut Català de Paleontologia (Fig. 1; see Table 1 for dental measurements). Type locality is ACM/C3-Aj (Abocador de Can Mata, Cell 3, locality Aj), in the municipal term of Els Hostalets de Pierola (Catalonia, Spain). Age is subchron C5r.3r (Middle Miocene, ≈ 11.9 Ma), on the basis of the local ACM magnetostratigraphic series (4), corresponding to the local biozone *Megacricetodon ibericus* + *Democricetodon larteti* (MN 7 Mammal Neogene biozone), on the basis of biostratigraphic data (3, 4). Etymology is from the Latin *brevis* (short) and *rostrum* (snout).

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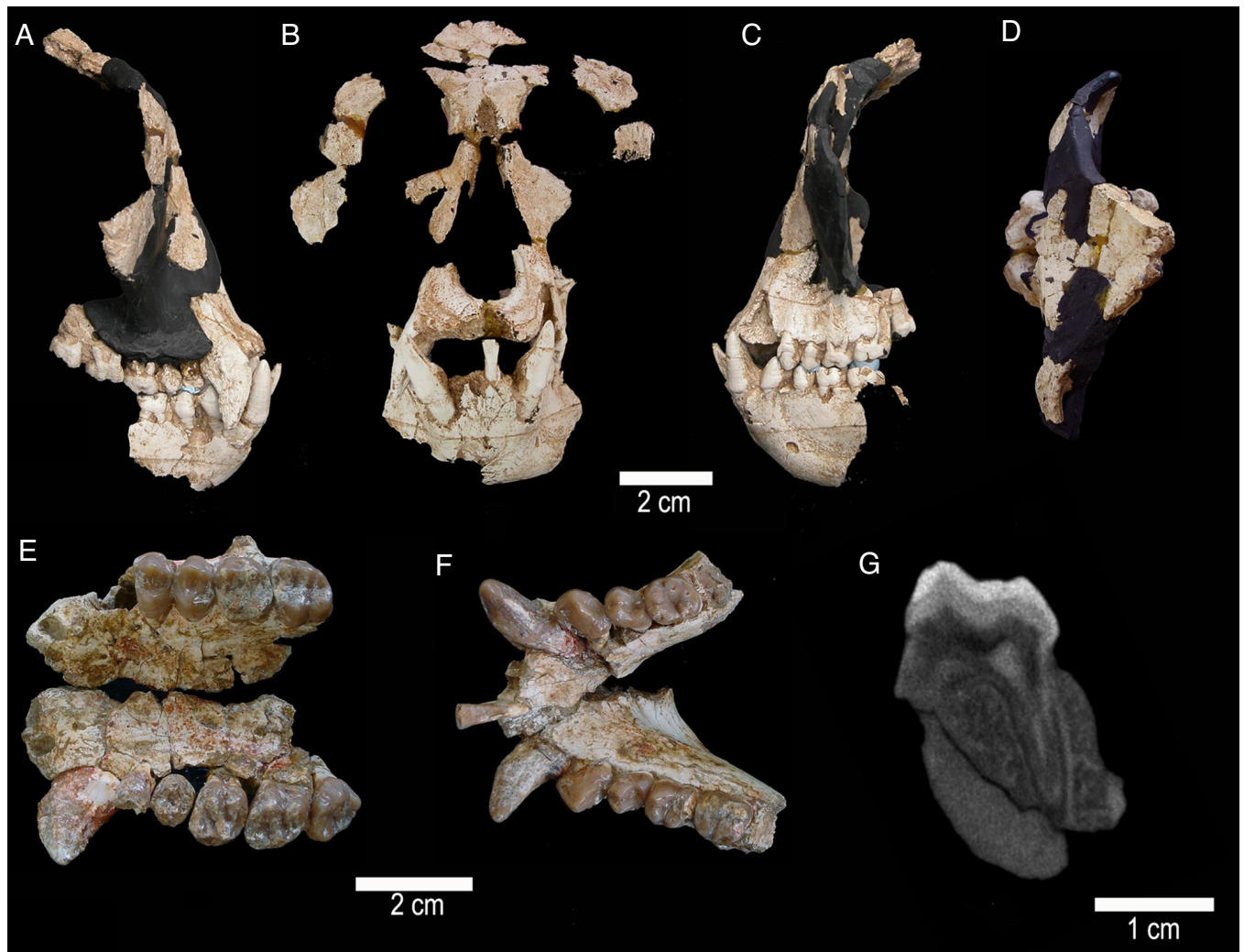


Fig. 1. Cranium and mandible of *Anoiapithecus brevisrostris* (IPS43000, holotype). (A) Right lateral view. (B) Frontal view. (C) Left lateral view. (D) Superior view. (E) Palatal view. (F) Occlusal view of the mandible. (G) CT scan of the right M², showing enamel thickness. All photographs were taken with the tooth row oriented horizontally. For safety reasons, the cranial reconstruction (A–D) is based on casts of the original specimens.

Specific Diagnosis. The face is characterized by reduced nasal and alveolar prognathism with a very short premaxilla. The anterior border of the orbit is situated over the P³–P⁴ limit, the glabella is over the P⁴, and the anteriormost nasomaxillary contact is over

Table 1. Dental measurements (in millimeters) of *Anoiapithecus brevisrostris* gen. et sp. nov. from ACM/C3-Aj

	Upper teeth		Lower teeth	
	MD	BL	MD	BL
L I1	—	—	4.8	6.7
R C1	14.2	9.6	12.9	8.5
L C1	—	—	13.2	9.2
R P3	—	—	12.7	7.3
L P3	7.0	11.7	12.3	7.6
R P4	—	—	7.6	8.8
L P4	7.2	10.4	7.8	8.6
R M1	9.4	11.2	9.1	8.9
L M1	9.4	11.4	9.5	9.1
R M2	11.3	11.8	—	—
L M2	10.7	12.1	11.5	10.0
R M3	10.2	10.4	—	—

MD, mesiodistal; BL, buccolingual; R, right; L, left.

the posterior part of the C¹ (with the alveolar plane horizontal). Nasal aperture edges are vertical. The zygomatic root is moderately high and situated over the M¹. The anterior surface of the zygomatic root is downwardly inclined. The frontal sinus is well developed, filling the glabellar area and part of the frontal squama. The maxillary sinus is reduced, situated well above the roots of the molars, occupying a small area below the medial side of the orbit. The zygomatic root is not pneumatized. Coalescent temporal lines indicate the presence of a sagittal crest. Thin superciliary arches are evident. A large and open incisive foramen, with the posterior border located at the level of the P³, is shown. The palate is short, wide, and deep. The pyriform aperture is wide, widest close to the base. Dentition is characterized by thick enamel (relative enamel thickness, RET = 20) with low dentine penetrance. Low crowns show globulous cusps, blunt crests, and restricted basins with nonperipheralized cusps; there are remnants of cingula in lower teeth. Canines and P3 are low-crowned whereas upper canines are relatively small and very compressed. A robust mandible shows highly divergent rami and reduced mandibular length; strong and long inferior torus and weak superior torus that forms a simian shelf.

Differential Diagnosis. *Anoiapithecus* differs from all known Miocene Eurasian hominoids by the very orthognathous face, be-

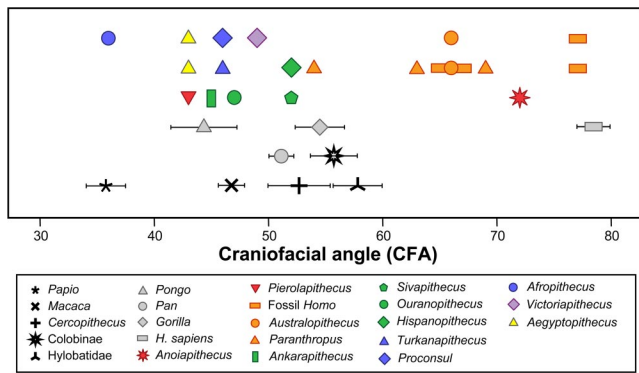


Fig. 2. Craniofacial angle (CFA) in living and fossil catarrhines. CFA is the angle formed by the line joining glabella and prosthion with the tooth row plane (in lateral view). Extinct taxa are represented by individual values, whereas living taxa are represented by the mean and the 95% confidence interval for the mean. Note that *Anoiapithecus* differs from both extant cercopithecoids and nonhuman hominoids by displaying a CFA well above 60°, most closely resembling members of the genus *Homo*.

cause of reduced mid- and lower facial prognathism, with the glabella and orbits situated very anteriorly (close to the premolars and C¹ on the vertical plane); it further differs from the above-mentioned taxa except *Oreopithecus* by the presence of a sagittal crest. More specifically, *Anoiapithecus* further differs from proconsulids and afropithecids by the possession of hominid facial synapomorphies, including the wide nasal aperture widest at the base, the high face, the deep palate, and the configuration of the nasals. With regard to kenyapithecins, it further differs from *Kenyapithecus* by the reduced heteromorphy of the upper premolars and low-crowned canines and from *Griphopithecus* by the strongly reduced cingula and the high zygomatic root. As compared to other Middle Miocene dryopithecins, among others it differs from *Pierolapithecus* by the presence of a frontal sinus, by the thicker enamel, the less peripheralized cusps, and the downward inclination of the zygomatic root; and from *Dryopithecus* by the lower degree of nasoalveolar prognathism and the more posteriorly situated anterior zygomatic root. Finally, as compared to the short-faced, Late Miocene *Oreopithecus*, *Anoiapithecus* further differs by the higher face, the shorter muzzle, the reduced maxillary sinus, the vertical nasals, the lack of a nasoalveolar clivus covering the palatine fenestra, and the morphology of the dentition.

Morphometric Analyses. Craniofacial angle. The most outstanding characteristic of *A. brevisrostris* is the strong reduction of the facial skeleton, because of the combination of an anteriorly positioned glabella with limited nasal and reduced alveolar prognathism. Measurements of the craniofacial angle (CFA) clearly show this pattern (Fig. 2; see also *SI Text* and *Tables S2 and S3*). In fossil and living catarrhines, CFA does not surpass 60°, with colobines and hylobatids displaying the highest values, because of their anteriorly placed glabella. The value of *A. brevisrostris* is even higher and only comparable to that of fossil *Homo*. The differences in CFA between *Anoiapithecus* and other fossil taxa included in the analysis clearly exceed the normal range of variation within extant taxa, as reflected by their 95% confidence intervals, thus confirming the distinctiveness of the unique taxon.

Geometric morphometrics. To further evaluate the uniqueness of the pattern of *Anoiapithecus*, we analyzed the shape of the facial profile using a geometric morphometrics approach (Fig. 3; see also *SI Text* and *Tables S4 and S5*). Extant great apes are characterized by strong alveolar prognathism, because of the posteriorly placed rhinion and nasion in relation to the more

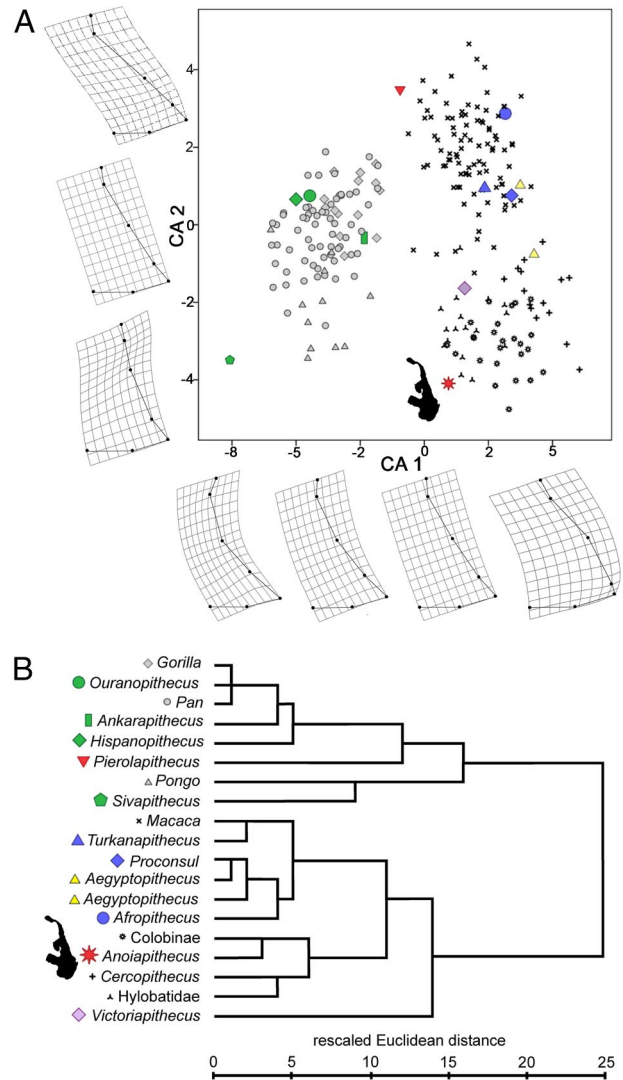


Fig. 3. Results of the geometric morphometrics analysis. (A) Scatter diagram showing the 2 first canonical axes (CA) of a canonical variate analysis (CVA), reflecting the differences in the facial profile of living and fossil catarrhines (see *Materials and Methods* and *SI Text* for further information). Visualizations of the shape changes along the CA are also shown; to facilitate the interpretation, the grids are rotated so that the alveolar plane is horizontal. CA1 reflects the degree of midfacial concavity, while CA2 reflects the degree of alveolar prognathism. Note that, regarding these axes, *Anoiapithecus* closely approaches hylobatids and colobines, far away from stem hominoids, extant great apes, and *Pierolapithecus*. (B) UPGMA cluster based on Euclidean distances computed from centroids (for extant taxa) and discriminant scores (for extinct taxa). Note that *Anoiapithecus* clusters with colobines, unlike both African stem hominoids (which cluster with *Macaca* and stem catarrhines) and Eurasian fossil great apes (which cluster with living great apes).

anterior glabella, thus forming the midfacial concavity typical of this group (Fig. 3A). Several Miocene great apes such as *Hispanopithecus*, *Ouranopithecus*, *Ankarapithecus*, and *Sivapithecus* fit this pattern. More primitive taxa, however, such as the stem hominoids *Afropithecus*, *Turkanapithecus*, and *Proconsul* rather match the pattern of extant cercopithecines, whose facial profile is characterized by strong alveolar and midfacial prognathism, with glabella placed posteriorly from nasion, and rhinion being much more anteriorly situated. The stem hominid *Pierolapithecus* displays a similar or even higher degree of alveolar prognathism, while the degree of midfacial concavity is intermediate between stem hominoids and living great apes. *Anoi-*

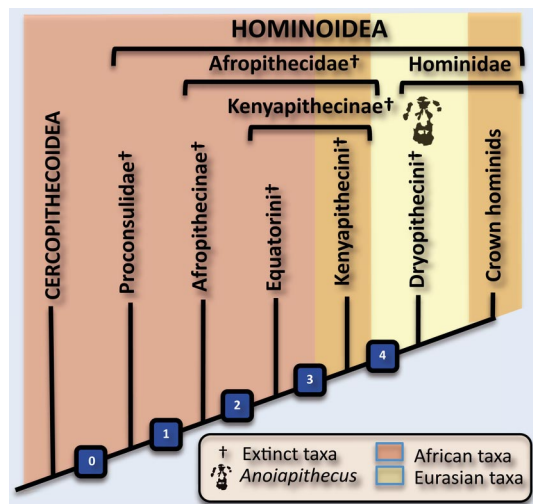


Fig. 4. Simplified cladogram depicting the phylogenetic hypothesis and biogeographic scenario favored in this paper. The Afropithecinae include the Afropithecini; the Equatorini include *Equatorius* and *Nacholapithecus*; the Kenyapithecini include *Kenyapithecus* and *Griphopithecus*; and the Dryopithecini include *Pierolapithecus*, *Dryopithecus* s.s., and *Anoiapithecus*. Nodes: 0, taillessness and other postcranial and cranial features; 1, thick enamel, dental morphology, robust mandible, procumbent premaxilla; 2, anterior position of the zygomatic root, strong mandibular inferior torus; 3, reduction of maxillary sinus, very deep canine fossa, reduced mandibular length; 4, high face, high zygomatic root, wide nasal aperture (widest at the base), flat nasals that project anteriorly beneath the level of the inferior orbital rim, orthograde-related features (as judged from *Pierolapithecus*). This hypothesis implies a back-to-Africa dispersal of the Homininae and a reversal of some features of node 3 in this group, but assumes that features of node 4 are homologous between pongines and hominines.

pithecus differs from great apes by the lack of midfacial concavity, but unlike *Pierolapithecus*, it displays a very orthognathous face, with rhinion situated very close to and vertically aligned with nasion. It, thus, approximates the pattern observed in colobines and, to a lesser extent, gibbons (Fig. 3B).

Given the distinctiveness of the facial morphology of *Anoiapithecus*, as compared to both living and fossil hominoids, it is likely that it represents an autapomorphically derived condition of this taxon. To ensure that great differences found by the canonical analysis between *Anoiapithecus* and other extinct taxa cannot be accommodated by the normal range of variation that is customarily found within extant hominoid genera, we followed a randomization approach on the basis of discriminant scores. The results of this analysis (SI Text) allow us to refute the hypothesis that differences between *Anoiapithecus* and *Pierolapithecus* might be attributable to interindividual variation within a single genus with $P < 0.001$, which confirms the need to erect a previously undescribed taxon.

Discussion

Despite its autapomorphic facial morphology, *A. brevis* retains primitive stem-hominoid features (1, 6–8), such as low-crowned teeth (especially the P₃ and canines), cheek teeth with flaring labial and lingual walls, short canine roots converging toward the midline, heteromorphic upper premolar cusps, and a frontal sinus that invades the glabella and the frontal squama. These features, like the autapomorphic facial pattern, are not phylogenetically informative (1, 9). However, *A. brevis* shares an array of significant features with both Middle Miocene afropithecids (here included within the Kenyapithecinae) and Middle to Late Miocene hominids (see SI Text and Table S1 for further details on the systematics used in this paper). These features are lacking in Early Miocene proconsu-

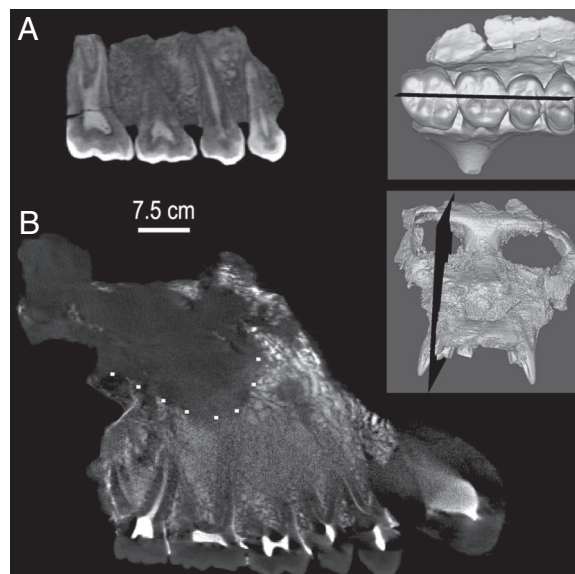


Fig. 5. CT scans in a parasagittal plane of (A) the left maxilla of *Anoiapithecus brevis* gen. et sp. nov. (IPS43000, holotype) and (B) the right maxilla of *Pierolapithecus catalaunicus* (IPS21350, holotype), to the same scale. Each CT scan is accompanied by a virtual model showing the plane represented by the scans. Note the lack of sinus over the molar roots in the preserved maxilla of *Anoiapithecus*. The more completely preserved *Pierolapithecus* specimen similarly shows a small and restricted maxillary sinus (the lower and anterior limits of the sinus are marked by white points), which does not reach the apices of the dental roots and anteriorly does not surpass the level of posterior M¹.

lids (1, 2, 6–8, 10) and can be hence interpreted as derived features that might reflect a phylogenetic link between kenyapithecines and stem Eurasian hominids (Fig. 4).

Among others, *Anoiapithecus* shares with all afropithecids a thick-enamelled condition (Fig. 1G), with a RET value of 20, which is in the upper range of *Griphopithecus alpani* from Paşalar (11). This feature is further combined with other shared denognathic features, such as low dentine penetration, globulous and nonperipheralized cusps with restricted basins, thick and rounded crests, a robust mandible, and a procumbent premaxilla. *Anoiapithecus* also shares derived features with the Kenyapithecinae (*Equatorius*, *Nacholapithecus*, *Kenyapithecus*, and *Griphopithecus*). These synapomorphies include the anterior position of the zygomatic root, indicating a shorter face than in the Afropithecinae, and a strong mandibular inferior torus entailing a simian shelf (1, 6–8, 10, 12–16). Moreover, *Anoiapithecus* shares with Eurasian Middle Miocene Kenyapithecini (*Kenyapithecus* and *Griphopithecus*) an extreme reduction of the maxillary sinus, which is situated well above the roots of the molars (Fig. 5A). The extent of the maxillary sinus should be interpreted with great care, because it can increase throughout life. Nevertheless, the holotype of *A. brevis* belongs to a fully adult individual, as evidenced by the fully erupted M³ and the presence of some dental wear on both M² and M³ (albeit with no dentine exposure, given the thick-enamelled condition of this taxon). Moreover, additional CT scans of the skull of *Pierolapithecus* (Fig. 5B) have revealed that this stem hominid also retains this kenyapithecini trait. Further synapomorphies of *Anoiapithecus* and kenyapithecines are a very deep canine fossa and reduced mandibular length with anteriorly placed mandibular rami (1, 6–7, 10, 12–17). The extreme shortening of the face in *Anoiapithecus* denotes a step further in the tendency toward facial reduction that characterizes kenyapithecines.

Significantly, *Anoiapithecus* also exhibits the basic facial hominid synapomorphies (8), indicating that this taxon is a stem

member of the great ape and human clade: high face, high zygomatic root, pyriform nasal aperture widest at the base, deep palate, and nasals that project slightly anteriorly beneath the level of the lower orbital rims (observed from the nasomaxillary sutures). The same modern facial pattern is also shared by *Pierolapithecus* (5), despite the striking differences in facial profile as compared to *Anoiapithecus*.

The retention of highly specialized, derived kenyapithecine features in a stem hominid such as *Anoiapithecus* has important implications for understanding the origin of the Hominidae. The presence in Eurasia of kenyapithecine hominoids (*Kenyapithecus* and *Griphopithecus*) of putative African origin by ≈ 16.5 Ma (18) or 15–14 Ma (19, 20) has led some authors to hypothesize that later Middle and Late Miocene Eurasian hominids evolved from these taxa (2, 7, 8, 10, 16, 18–24). Hitherto, however, the apparent lack of synapomorphies between both groups precluded testing this hypothesis (7). The unique facial specimen of *Anoiapithecus* provides strong support for a sister-group relationship between the Kenyapithecini and Hominidae. Additional support for this hypothesis comes from the association of kenyapithecine traits with cranial and postcranial great-ape synapomorphies in the stem hominid *Pierolapithecus* (5).

Kenyapithecus has been considered a good candidate for the ancestral form of the Hominidae because it shares several features with hominids, including the moderately high zygomatic root, the high-crowned canine, the reduced molar cingula, and distal humeral morphology (2, 6, 10, 13, 14, 16, 25). The hominids *Anoiapithecus* and *Pierolapithecus* retain plesiomorphic low-crowned canines and heteromorphic premolar cusps, although they do not exhibit the autapomorphies of *Kenyapithecus*. Furthermore, *Pierolapithecus catalaunicus* shares with *G. alpani* the highly distinctive spatulate central incisor with a lingual pillar continuous with the lingual cingulum. This is a feature shared with later, more derived, Eurasian hominoids (26–27). This contradictory evidence makes it difficult to determine which of the 2 kenyapithecine genera is more closely related to hominids, while it clearly stresses the role of homoplasy in hominoid evolution.

When currently available evidence is taken into account, the hypothesis suggesting a Eurasian origin for the Hominidae is favored, given the following facts: (i) the presence in the Eurasian Middle Miocene of both kenyapithecins and hominids, (ii) their likely sister-group relationships, and (iii) their remarkable consistent consecutive time span (kenyapithecins, 15–13 Ma; dryopithecins such as *Anoiapithecus* and *Pierolapithecus*, 11.9 Ma; and Late Miocene hominids, <11.1 Ma). Kenyapithecins retain not only a primitive facial pattern for hominids, but also—as far as it can be ascertained—a pronograde postcranial body plan (21–23, 28, 29). *Anoiapithecus* and other dryopithecins (*Dryopithecus* s.s. and *Pierolapithecus*) share with Late Miocene Eurasian hominids and extant great apes a derived facial morphology (4, 5) and, at least *Pierolapithecus*, an orthograde postcranial body plan (5). This combination of characters supports the view that crown hominids originated in Eurasia from more primitive, kenyapithecine ancestors and radiated in this continent into pongines and hominines (Fig. 4).

This scenario entails a subsequent “back to Africa” dispersal of the hominine clade (African apes and humans) (9, 18). Alternatively, the basic putative facial and postcranial synapomorphies of the Hominidae could be homoplastic between pongines and hominines, with both groups having independently evolved in Eurasia and Africa, respectively, from different afropithecine ancestors. Independent evolution of suspensory capabilities has been previously hypothesized (5). However, given the lack of both cranial and postcranial crown-hominid synapomorphies in afropithecids, this alternative, to the back-to-Africa hypothesis would entail a more pervasive role for homoplasy than previously suggested. If so, parallelism and

convergence would be far more common during hominoid evolution than the principle of parsimony, customarily applied to cladistic analyses, generally assumes. We expect that future discoveries, particularly in the long Middle to Late Miocene stratigraphic sections of Els Hostalets de Pierola section (Catalonia, Spain) (3, 4), may help to disentangle the complex question of the initial diversification of the great apes.

Materials and Methods

The Primate Sample. The facial profile of *A. brevisrostris* was compared to that of living and extinct catarrhines by means of univariate and multivariate techniques (see below). Several fossil specimens and many different individuals from several living genera (Table S6) were included in the analyses. Data were taken from photographs of crania in lateral view, taken with the lens parallel to the midsagittal plane. Regarding the extant comparative sample, photographs were taken by the authors at the Koninklijk Museum voor Midden-Africa (Tervuren, Belgium) and at the Anthropologisches Institut und Museum (Zürich, Switzerland), were kindly provided by Xavier Jordana (in the case of living humans from the Coleções Osteológicas Identificadas from the Museu Antropológico da Universidade de Coimbra), and were taken from the “Mammalian Crania Photographic Archive” Second Edition, which is available from the Internet (<http://1kai.dokkyomed.ac.jp/mammal/en/mammal.html>).

CFA. To quantify the degree of orthognathism/prognathism, we measured CFA as the angle comprised between the plane defined by the nasion–prosthion and that defined by the occlusal plane. It was measured in 256 individuals belonging to 11 extant genera (Table S6), including the 5 extant genera of hominoid primates, 3 cercopithecines (*Cercopithecus*, *Macaca*, and *Papio*) and 3 colobines (the latter being grouped into a single group Colobinae). Comparisons were carried out by means of ANOVA and post hoc multiple comparisons (Bonferroni method).

Geometric Morphometrics. We used a thin-plate spline approach with generalized least-squares (GLS) Procrustes superimposition. A canonical variate analysis (CVA) was performed on the resulting matrix of partial warp scores and the similarities between the several taxa were depicted by means of a cluster analysis based on centroids (extant taxa) and discriminant scores (extinct ones).

Seven landmarks, defined on the lateral facial profile and projected onto the midsagittal plane, were used (Fig. S2). Most of these landmarks (nos. 2–7) are located at intersections between bones or bone tissues and must be therefore considered type 1 landmarks following Bookstein’s classification (30), while landmark no. 1 (glabella) is of type 2. These landmarks were measured in 255 individuals from the same genera included in CFA analysis (Table S6) except for *Papio* and *Homo*, which were excluded given their extreme condition as compared to the remaining taxa; similarly, fossil Hominini were also excluded from the analysis. Landmarks were digitized using the tpsDig software (31). Landmark configurations were superimposed by means of GLS Procrustes superimposition (32). GLS was conducted using the tpsRelw program (33). A thin-plate spline approach (30, 34) was adopted for visualizing shape differences and producing a set of variables (the partial warps, including the uniform components of deformation) amenable to statistical analysis. The partial warp scores (weight matrix), indicating the position of each individual relative to the reference along the partial warps, were calculated using the program tpsRelw (33).

The canonical variate analysis was performed with SPSS 15.0 on the basis of the weight matrix for extant taxa alone, to define a morphospace reflecting the facial differences between living catarrhines. Groups were defined on the basis of the different genera included in the analysis, except for *Colobus*, *Presbytis*, and *Procolobus*, which were grouped as Colobinae. Extinct genera were left ungrouped and classified on the basis of squared Mahalanobis distances a posteriori. A cluster analysis was also performed with SPSS 15.0 on the basis of Euclidean distances computed from centroids (for extant taxa) and discriminant scores (for extinct taxa) for all canonical axes, by means of the unweighted pair group method with arithmetic mean (UPGMA) and by rescaling distances to values comprised between 0 and 25 (Tables S4 and S5).

To take into account the range of variation displayed by extant taxa when interpreting the differences found between different fossil individuals (particularly the holotypes of *Anoiapithecus* and *Pierolapithecus*) in the geometric morphometrics analysis, we followed a randomization approach. In particular, on the basis of the discriminant scores of the CVA, we computed the squared distance for each pair of individuals within several genera (*Pan*, *Gorilla*, *Pongo*, and *Macaca* separately). The distribution of these distances

was then used to test the null hypothesis that the distance between *Anoia-pithecus* and *Pierolapithecus* fits interindividual variation within a single extant genus. This null hypothesis was rejected when the probability of finding such a distance was lower than 5%, on the basis of the distribution of the selected extant genera separately.

Enamel Thickness. RET was measured in a coronal plane through the mesial cusps of the right M² as (area of the enamel cap/length of the dentinoenamel junction)/(area of the dentine)^{1/2} × 100 (35). The teeth were scanned with high-resolution computed tomography (Xylon Compact) at Burgos University (Spain). Images were analyzed with NIH Image software (developed at the U.S. National Institutes of Health and available from the Internet at <http://rsb.info.nih.gov/nihimage/>).

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