

Supporting Information

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SI Text

Systematic Framework. In Table S1 we provide a systematic classification of living and fossil Hominoidea to the tribe level, by further including extant taxa and extinct genera discussed in this paper. Hominoidea are defined as the group constituted by Hylobatidae and Hominidae, plus all extinct taxa more closely related to them than to Cercopithecoidea. Hominidae, in turn, are defined as the group containing Ponginae and Homininae, plus all extinct forms more closely related to them than to Hylobatidae. While this broad concept of Hominidae is currently used by many paleoprimatologists (e.g., refs. 1–2), the systematic position of primitive (or archaic) putative hominoids is far from clear (see below). Begun (3–5) employs the terms “Eohominoidea” and “Euhominoidea” to informally refer to hominoids of primitive and modern aspect, respectively. These terms, however, are roughly equivalent to stem-lineage and crown-group hominoids, respectively, and are not further used here.

The systematic status of many Late Oligocene and Early-Middle Miocene fossil catarrhines, lacking both cercopithecooid synapomorphies and crown hominoid synapomorphies, has been subject to different interpretations (6–8). Harrison (8) argues that most fossil “apes” from the Late Oligocene and Early Miocene of Africa have not crossed the hominoid “cladistic threshold” and classifies them into 2 distinct superfamilies (Dendropithecoidea and Proconsuloidea), which he considers to be successive sister taxa of stem catarrhines, more derived than propliopithecoids and pliopithecoids, but presumably preceding the cercopithecooid–hominoid split (8–12). On the other extreme, a few authors have considered that proconsuloids might be stem hominoids (13–15). Although the latter view is apparently abandoned (16), most authors consider that Early Miocene forms, especially *Proconsul*, are more closely related to extant hominoids than to cercopithecooids (3, 6–7, 16–20). The systematic scheme used here (Table S1) follows Harrison (8) in recognizing that proconsulids and dendropithecids are distinct clades, but considers that at least the former are stem hominoids. These putative stem hominoids lack crown hominoid synapomorphies, in particular, features functionally related to orthograde that are presumably homologous between hylobatids and hominids. Yet stem hominoids already share with both hylobatids and hominids some facial (16) and several postcranial (17–18, 21) synapomorphies. Prominently, the lack of external tail in *Proconsul* (17, 19, 21), albeit disputed by some authors (22), is now firmly established (23) and has been further ascertained in the putative stem hominoid *Nacholapithecus* (24).

Among putative stem hominoids, the position of *Afropithecus* and other related taxa is the most problematic. Harrison (8) distinguishes a single family Proconsulidae with 3 distinct subfamilies (Proconsulinae, Nyanzapithecinae, and Afropithecinae), while other authors (20) take an opposite approach by classifying their Afropithecinae (including *Nacholapithecus* and *Equatorius*) within the Hominidae, and others (2) consider the former to be a distinct family. Especially problematic is the placement of *Kenyapithecus* and *Griphopithecus*: in some systematic schemes (20, 25), the latter taxa are classified into the subfamily Kenyapithecinae within the Hominidae; others (2) distinguish a subfamily Griphopithecinae (for *Griphopithecus*) within the Afropithecidae; and Begun reunites both Kenyapithecinae and Griphopithecinae into a distinct family Griphopithecidae (2) or combines these taxa into an informal grouping (“griphopithecids”) of stem hominoids (5). The systematic scheme followed in this paper (Table S1) recognizes the close phyloge-

netic relationships between all these taxa by classifying them all into a single family Afropithecidae with 2 subfamilies (Kenyapithecinae and Afropithecinae).

The systematic scheme used here requires several nomenclatural decisions, which deserve further explanation. The nomina Kenyapithecini and Kenyapithecinae are adopted instead of Griphopithecinae and Griphopithecini (see also ref. 25) merely because the former have priority. It is unclear why neither Begun (1) nor Kelley (2) specify the authorship of Griphopithecinae (or Griphopithecidae), but, to our knowledge, the authorship of the latter nomina must be attributed to Begun (ref. 4, p. 232: Table 10.1), which therefore do not have priority over Kenyapithecinae Andrews, 1992. Griphopithecinae thus remains potentially valid only if *Kenyapithecus* (and *Afropithecus*, see below) are excluded from it. This notwithstanding, there has been some confusion regarding the authorship of the nomen Kenyapithecinae. Both Begun (1) and Ward and Duren (20) attribute its authorship to Leakey (26). However, the earliest usage of a suprageneric nomen with *Kenyapithecus* as the type genus is attributable to Andrews (6), who erected it as a previously undescribed tribe, Kenyapithecini, in the same paper that he erected Afropithecini (27). To our knowledge, *Kenyapithecus* and *Afropithecus* have not been previously included into a single family with the exclusion of Hominidae (as in ref. 20), but we have chosen the nomen Afropithecidae (instead of Kenyapithecidae) because the former has been already used at the family level—albeit with a different meaning—by some previous workers (2, 5). If, as suggested in this paper, there is a close phylogenetic relationship between Kenyapithecinae (in particular, the Kenyapithecini) and Hominidae, Afropithecidae as conceived here would be paraphyletic. Transferring the Kenyapithecinae into the Hominidae (25), however, would not solve this problem, since the remaining Afropithecidae (including only the Afropithecinae) would remain paraphyletic in excluding the Kenyapithecinae. Paraphyly can be transferred from one group or rank to another, but cannot be completely eliminated unless Linnean ranks are abandoned—a view that is not advocated here.

The Late Miocene genera *Hispanopithecus* and *Ouranopithecus* are not classified here at the tribe level. Both genera have been previously suggested to be either pongines (28) or hominines (4), but this issue is not definitively resolved and lies outside the scope of this paper. Nevertheless, it is worth mentioning that *Hispanopithecus* was recently resurrected (29) for Late Miocene species previously included in *Dryopithecus*, so that the latter genus is restricted to its type species, *Dryopithecus fontani*. As a result, the tribe Dryopithecini is here used with a different meaning from previous usages, to refer to Middle Miocene stem hominids that apparently do not belong to any of the 2 crown-hominid subfamilies; this tribe includes *Pierolapithecus*, *Dryopithecus* s.s., and *Anoiapithecus* gen. nov., but most likely excludes *Hispanopithecus*. Given the uncertain phylogenetic relationships between the several dryopithecine genera, it is currently unclear whether this tribe is paraphyletic or represents a clade of stem European hominids.

Results

Morphometric Analyses. ANOVA comparisons show that there are significant differences ($P < 0.001$; $F = 178.6$) among several extant catarrhines regarding the CFA (Table S2 and S3), with gorillas, colobines, and hylobatids displaying the highest values, which nevertheless generally do not surpass 60°. Living humans, on the contrary, differ from all of the remaining taxa ($P < 0.001$)

by the much higher CFA of the former, while extinct hominins display intermediate values. Most extinct catarrhines clearly fall within the ranges of extant nonhuman cercopithecoids and hominoids, with the exception of *Anoiapithecus*. The latter taxa display values of CFA beyond the maximum value recorded in extant nonhuman catarrhines, and $\approx 20^\circ$ higher than other fossil apes, most closely resembling the values displayed by extinct members of the genus *Homo*.

The canonical variate analysis (CVA) indicates that *Anoiapithecus* displays a unique morphology, previously unknown among living and fossil hominoids, which confirms the need to erect a previously undescribed genus. This analysis (Table S4 and Table S5) correctly classifies 93% of the original cases, only with minor confusion between some chimpanzees and gorillas and between very few colobines, cercopithecines, and hylobatids. Stem catarrhines, stem hominoids, and even the stem great ape *Pierolapithecus* most closely resemble cercopithecines, whereas all previously known putative crown hominids show a more derived condition that closely resembles one of the several extant great ape genera (Table S5). *Anoiapithecus* differs from crown hominids not only by the lack of facial concavity (as reflected by CA1, which explains 66% of variance), but also by the highly verticalized (orthognathous) facial profile (as reflected by CA2, which explains 23% of variance). *Anoiapithecus*, in particular, displays a vertical alignment of glabella, nasion, rhinion, and nasospinale in relation to the alveolar plane. Glabella and rhinion are more anteriorly situated, whereas rhinion and nasospinale are slightly more posteriorly placed. Thus, in *Anoiapithecus*, the rhinion is situated very close and only slightly more anterior than the nasion. In regard to the latter, *Anoiapithecus* shows the opposite condition from *Pierolapithecus*, most closely resembling hylobatids and colobines. In fact, *Anoiapithecus* clusters with colobines when the several canonical axes are taken into account simultaneously. It is thus the only known fossil great

ape to have ever displayed a colobine-like facial profile, to which it may have autapomorphically converged from an ancestral condition more similar to that displayed by stem hominoids and living cercopithecines.

Squared distances based on the CVA discriminant scores, and computed for pairs of fossil individuals included (Table S5), indicate that *Anoiapithecus* is particularly far from the 2 other Miocene hominoids from Spain included in the analysis (*Pierolapithecus* and *Hispanopithecus*); *D. fontani* could not be included in the analysis because of incomplete preservation, although a previous analysis of facial morphology based on new remains from Abocador de Can Mata indicates a gorilla-like morphology (29), which is thus quite different from the *Anoiapithecus* condition. The results of the randomization approach further confirm that differences between *Anoiapithecus* and other fossil individuals cannot be accommodated within the range of variation of a single genus. When the chimpanzee, the orangutan, or the gorilla distributions of intrageneric individual pair differences are used, the null hypothesis can be rejected with at least $P < 0.05$ with the single exception of *Ankarapithecus*. The latter is the fossil individual closest to *Anoiapithecus* when all canonical axes are taken into account (Table S5), although both taxa display a different facial profile—as shown by the highly divergent discriminant scores for CA1 and, especially, CA2 (Fig. 3A)—and cluster very far from one another (Fig. 3B). In any case, when the macaque distribution is used, the null hypothesis can be rejected with $P < 0.05$ in all instances, including *Ankarapithecus*. With regard to *Pierolapithecus* and *Hispanopithecus*, the null hypothesis can be rejected with $P < 0.001$ in all instances, i.e., irrespective of the distribution used. All this evidence clearly indicates that differences between *Anoiapithecus* and other fossil individuals cannot be interpreted as representing the extremes of the range of variation within a single taxon, so that the erection of a genus is fully justified.

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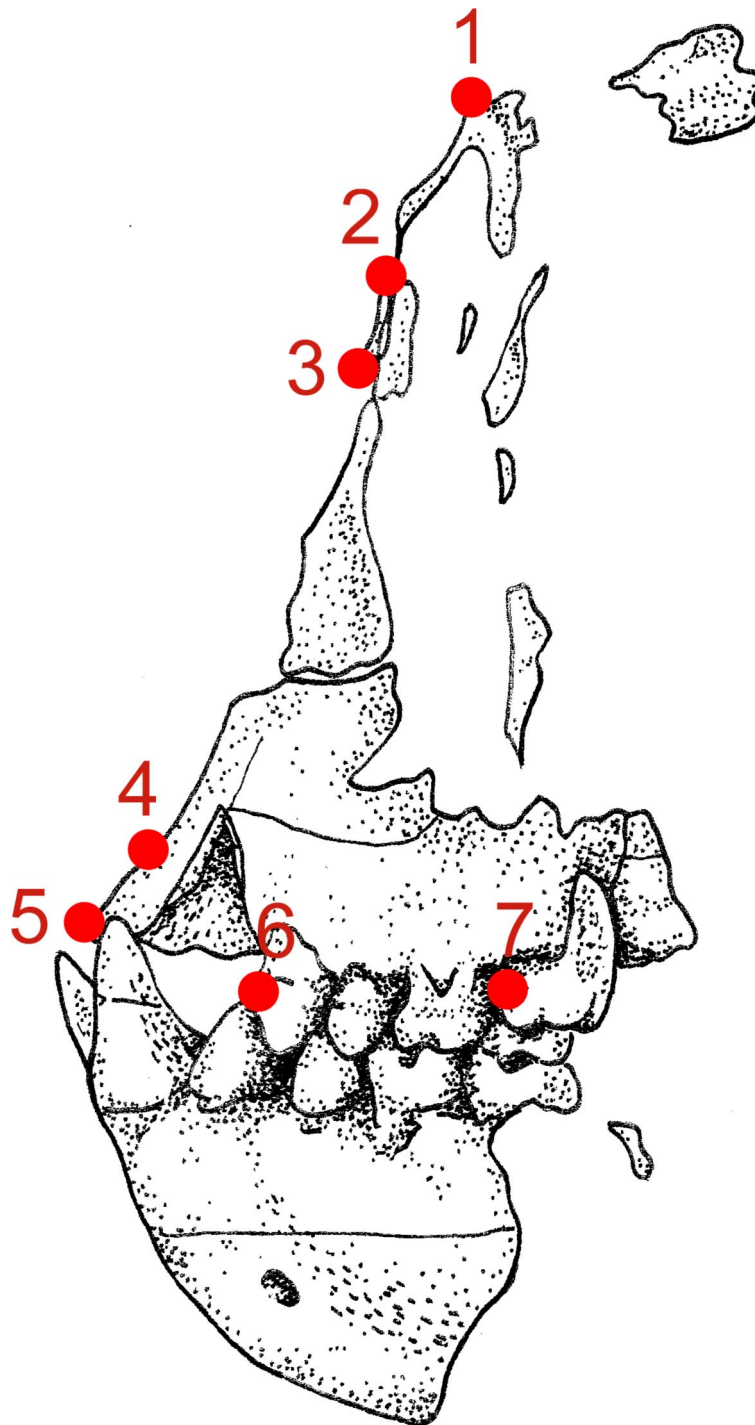


Fig. S2. Composite polarity stratigraphy of the ACM local series and correlation with the astronomically tuned geomagnetic polarity timescale ATNTS2004. The stratigraphic situation of the classical sites of Can Mata I and III, together with that of the published hominoid-bearing localities, is indicated. Stratigraphy is modified from ref. 5.

Table S2. Descriptive statistics of the craniofacial angle (CFA) in extant genera and values for extinct taxa included in the analysis

Taxon	<i>N</i>	Mean	SD	95% CI		Range	
<i>Macaca</i>	55	46.8	4.3	45.6	47.9	35	56
<i>Cercopithecus</i>	16	52.7	5.1	50.0	55.4	37	61
Colobinae	26	55.7	5.1	53.7	57.8	48	65
<i>Pongo</i>	17	44.4	5.6	41.5	47.2	34	52
<i>Hylobates s.l.</i>	21	57.8	4.7	55.7	60.0	50	67
<i>Pan</i>	63	51.1	4.3	50.0	52.2	40	59
<i>Gorilla</i>	14	54.5	3.8	52.3	56.7	47	58
<i>Homo</i>	31	78.5	3.9	77.0	79.9	68	85
<i>Papio</i>	13	35.8	2.9	34.0	37.5	30	40
<i>Anoiapithecus</i>	1	72					
<i>Ankarapithecus</i>	1	45					
<i>Proconsul</i>	1	46					
<i>Pierolapithecus</i>	1	43					
<i>Sivapithecus</i>	1	52					
<i>Aegyptopithecus</i>	2	43	0.0	43.0	43.0	43	43
<i>Ouranopithecus</i>	1	47					
<i>Afropithecus</i>	1	36					
<i>Hispanopithecus</i>	1	52					
<i>Turkanapithecus</i>	1	46					
<i>Victoriapithecus</i>	1	49					
<i>Paranthropus</i>	3	62.0	7.5	43.2	80.8	54	69
<i>Australopithecus</i>	2	66.0	0.0	66.0	66.0	66	66
Fossil <i>Homo</i>	4	71.5	6.4	61.3	81.7	65	77

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

Table S3. ANOVA and Bonferroni results for comparisons of the craniofacial angle (CFA) among extant taxa

Taxon	<i>Macaca</i>	<i>Cercopithecus</i>	Colobinae	<i>Pongo</i>	<i>Hylobates</i>	<i>Pan</i>	<i>Gorilla</i>	<i>Homo</i>
<i>Cercopithecus</i>	0.000							
Colobinae	0.000	0.000						
<i>Pongo</i>	0.000	1.000	0.000					
<i>Hylobates</i> s.l.	1.000	0.000	0.000	0.000				
<i>Pan</i>	0.000	0.026	0.000	1.000	0.000			
<i>Gorilla</i>	0.000	1.000	0.000	0.001	0.000	0.000		
<i>Homo</i>	0.000	1.000	0.000	1.000	0.000	1.000	0.424	
<i>Papio</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Cercopithecus</i>	***							
Colobinae	***	NS						
<i>Pongo</i>	NS	***	***					
<i>Hylobates</i> s.l.	***	*	NS	***				
<i>Pan</i>	***	NS	***	***	***			
<i>Gorilla</i>	***	NS	NS	***	NS	NS		
<i>Homo</i>	***	***	***	***	***	***	***	
<i>Papio</i>	***	***	***	***	***	***	***	***

***, significant at $P < 0.001$; *, significant at $P < 0.05$; NS, nonsignificant.

Table S4. Main results of the canonical variate analysis (CVA) performed on the matrix of partial warp scores (PW), including the uniform component (UNI)

	Discriminant functions (canonical axes)					
	CA1	CA2	CA3	CA4	CA5	CA6
Eigenvalues	9.512	3.355	0.870	0.436	0.143	0.067
% of variance	66.1	23.3	6.0	3.0	1.0	0.5
Cumulative %	66.1	89.5	95.5	98.5	99.5	100.0
Canonical correlation	0.951	0.878	0.682	0.551	0.354	0.251
Standardized coefficients of the canonical discriminant functions						
	CA1	CA2	CA3	CA4	CA5	CA6
X1-PW1	-0.162	0.391	-0.417	0.253	0.088	0.522
Y1-PW2	0.503	-0.185	0.046	0.405	-0.230	-0.106
X2-PW3	-0.098	-0.186	0.616	0.790	0.187	-0.123
Y2-PW4	0.442	-0.215	0.521	0.157	0.738	0.363
X3-PW5	0.136	-0.106	-0.125	-0.453	-0.336	0.423
Y3-PW6	-0.17	-0.099	-0.327	-0.146	-0.108	0.242
X4-PW7	-0.842	-0.232	0.502	0.056	0.162	0.348
Y4-PW8	-0.029	0.401	0.069	0.425	0.517	0.007
X5-UNI1	0.617	0.059	0.37	0.273	-0.288	0.707
Y5-UNI2	-0.214	0.573	0.841	-0.134	-0.353	-0.058
Functions at group centroids						
	CA1	CA2	CA3	CA4	CA5	CA6
<i>Cercopithecus</i>	4.513	-1.819	0.261	1.059	0.300	-0.747
<i>Colobinae</i>	3.025	-3.100	0.228	-1.366	-0.185	0.041
<i>Gorilla</i>	-2.898	0.554	-1.596	-0.770	1.160	-0.057
<i>Hylobates s.l.</i>	1.698	-2.631	-1.656	1.239	-0.055	0.505
<i>Pan</i>	-4.017	-0.171	-0.189	0.041	-0.316	-0.131
<i>Pongo</i>	-4.035	-2.131	3.175	0.592	0.659	0.359
<i>Macaca</i>	1.819	1.848	0.207	-0.004	-0.036	0.073
Discriminant scores for fossil taxa						
	CA1	CA2	CA3	CA4	CA5	CA6
<i>Afropithecus turkanensis</i>	3.157	2.870	2.584	-0.566	-1.345	-0.574
<i>Anoiapithecus brevirostris</i>	0.942	-4.093	1.834	-1.603	0.750	-0.457
<i>Hispanopithecus laietanus</i>	-5.002	0.657	-1.852	-0.981	-2.609	-0.077
<i>Ouranopithecus macedoniensis</i>	-4.465	0.749	-1.860	-0.514	0.349	0.045
<i>Sivapithecus indicus</i>	-7.581	-3.490	1.281	1.675	0.255	-2.144
<i>Turkanapithecus kalakolensis</i>	2.351	0.948	-1.142	-1.004	-0.450	-1.899
<i>Victoriapithecus macinnesi</i>	1.573	-1.636	3.830	-2.987	-3.589	-2.354
<i>Proconsul heseloni</i>	3.400	0.757	0.690	-0.558	-2.790	-0.130
<i>Pierolapithecus catalaunicus</i>	-0.947	3.489	2.773	-0.810	-0.079	0.023
<i>Aegyptopithecus zeuxis</i>	4.279	-0.764	0.868	-0.673	-2.931	-1.547
<i>Ae. zeuxis</i>	3.741	1.020	1.497	0.525	-2.845	-2.297
<i>Ankarapithecus meteai</i>	-2.343	-0.334	1.222	-1.732	-0.289	-0.259

Table S5. Classification results of the canonical variate analysis and squared Mahalanobis distance of *Anoiapithecus* to extant centroids and fossil taxa

Classification of fossil taxa				
	Predicted group (first)	Squared Mahalanobis distance to centroid	Predicted group (second)	Squared Mahalanobis distance to centroid
<i>Afropithecus turkanensis</i>	Macaca	10.932	Cercopithecus	34.6
<i>Anoiapithecus brevirostris</i>	Colobinae	9.082	Hylobates s.l.	24.539
<i>Hispanopithecus laietanus</i>	Pan	10.726	Gorilla	18.75
<i>Ouranopithecus macedoniensis</i>	Gorilla	3.296	Pan	4.618
<i>Sivapithecus indicus</i>	Pongo	25.611	Pan	32.928
<i>Turkanapithecus kalakolensis</i>	Macaca	7.971	Cercopithecus	20.44
<i>Victoriapithecus macinnesi</i>	Colobinae	37.176	Macaca	52.733
<i>Proconsul heseloni</i>	Macaca	11.859	Cercopithecus	20.601
<i>Pierolapithecus catalaunicus</i>	Macaca	17.577	Pan	32.397
<i>Aegyptopithecus zeuxis</i>	Cercopithecus	15.613	Colobinae	17.98
<i>Ae. zeuxis</i>	Macaca	19.838	Cercopithecus	22.766
<i>Ankarapithecus metei</i>	Pan	7.985	Gorilla	12.108

Classification of original cases (extant taxa)							
	<i>Cercopithecus</i>	Colobinae	<i>Gorilla</i>	<i>Hylobates</i> s.l.	<i>Pan</i>	<i>Pongo</i>	<i>Macaca</i>
<i>Cercopithecus</i>	14 (93.4%)	1 (6.7%)					
Colobinae	1 (4.0%)	24 (96.0%)					
<i>Gorilla</i>			15 (100%)				
<i>Hylobates</i> s.l.	1 (5.9%)			16 (94.1%)			
<i>Pan</i>			10 (15.6%)		54 (84.4%)		
<i>Pongo</i>						11 (100%)	
<i>Macaca</i>	1 (1.1%)	1 (1.1%)		1 (1.1%)			92 (96.8%)

Squared Mahalanobis distance of *Anoiapithecus* to extant centroids and fossil taxa

<i>Cercopithecus</i>	Colobinae	<i>Gorilla</i>	<i>Hylobates</i> s.l.
27.77	9.08	49.13	24.54
<i>Pan</i>	<i>Pongo</i>	<i>Macaca</i>	<i>Afropithecus</i>
48.01	35.91	42.17	59.43
<i>Hispanopithecus</i>	<i>Ouranopithecus</i>	<i>Sivapithecus</i>	<i>Turkanapithecus</i>
83.29	67.92	87.15	40.13
<i>Victoriapithecus</i>	<i>Proconsul</i>	<i>Pierolapithecus</i>	<i>Aegyptopithecus</i>
34.76	44.60	63.48	38.75
<i>Aegyptopithecus</i>	<i>Ankarapithecus</i>		
55.93	26.43		

Table S6. Composition of the extant comparative sample employed in the morphometric analyses

Genus	<i>N</i> (craniofacial angle)	<i>N</i> (geometric morphometrics)
<i>Cercopithecus</i>	16	15
<i>Colobus</i>	10	9
<i>Gorilla</i>	14	15
<i>Homo</i>	31	
<i>Hylobates</i> s.l.	21	17
<i>Macaca</i>	55	95
<i>Pan</i>	63	64
<i>Papio</i>	13	
<i>Pongo</i>	17	11
<i>Presbytis</i>	12	12
<i>Procolobus</i>	4	4

N, sample size.