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Short Communication

New remains of the Miocene great ape *Anoiapithecus brevirostris* from Abocador de Can

Mata

David M. Alba^{a,*}, Florian Bouchet^a, Josep Fortuny^a, Josep M. Robles^a, Jordi Galindo^a, Àngel H. Luján^a, Salvador Moyà-Solà^{a,b,c}, Clément Zanolli^{d,*}

^a *Institut Català de Paleontologia Miquel Crusafont (ICP-CERCA), Universitat Autònoma de Barcelona, c/ Columnes s/n, 08193 Cerdanyola del Vallès, Barcelona, Spain*

^b *Institució Catalana de Recerca i Estudis Avançats (ICREA), Pg. Lluís Companys 23, 08010 Barcelona, Spain*

^c *Unitat d'Antropologia Biològica (Dept. BABVE), Universitat Autònoma de Barcelona, 08193 Cerdanyola del Vallès, Barcelona, Spain*

^d *Univ. Bordeaux, CNRS, MCC, PACEA, UMR 5199, F-33600 Pessac, France*

***Corresponding authors.**

E-mail addresses: david.alba@icp.cat (D.M. Alba); clement.zanolli@gmail.com (C. Zanolli).

1 Short Communication

2 New remains of the Miocene great ape *Anoiapithecus brevirostris* from Abocador de Can

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4

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6

7 1. Introduction

8 The local stratigraphic sequence of Abocador de Can Mata (ACM; Alba et al., 2006),
9 located in the Vallès-Penedès Basin (NE Iberian Peninsula) and spanning from ~12.6 to 11.1
10 Ma (Moyà-Solà et al., 2009b; Casanovas-Vilar et al., 2011, 2016a, 2016b; Alba et al., 2017,
11 2022), has yielded fossil hominoid remains attributed to three species: *Pierolapithecus*
12 *catalaunicus* from ACM/BCV1 (12.0 Ma; Moyà-Solà et al., 2004); *Anoiapithecus brevirostris*
13 from ACM/C3-Aj (12.0 Ma) and ACM/C1-E* (12.4–12.3 Ma; Moyà-Solà et al., 2009a; Alba et
14 al., 2013); and *Dryopithecus fontani* from ACM/C3-Ae, ACM/C4-Ap and, tentatively,
15 ACM/C3-Az (11.9 Ma; Moyà-Solà et al., 2009b; Alba and Moyà-Solà, 2012). Additional
16 remains of ‘*Sivapithecus*’ *occidentalis* (species inquirenda) have been recovered from Can
17 Vila and ACM/BCV4 (11.9 Ma; Alba et al., 2020), being potentially attributable to either *P.*
18 *catalaunicus* or *A. brevirostris*, while indeterminate dryopithecine remains have been also
19 recovered between 11.8 and 11.1 Ma (Alba et al., 2017, 2022). Here, we describe hominoid
20 upper teeth recovered in 2006 from locality ACM/C4-Cp, which has an estimated age of 11.9
21 Ma (Alba et al., 2022) and was located relatively close to, but stratigraphically 16 m below,
22 ACM/C4-Ap (Supplementary Online Material [SOM] Fig. S1), with an estimated age
23 difference of 70 kyr (Alba et al., 2022). The dental remains from ACM/C4-Cp were previously
24 reported by Alba (2012) as Hominidae indet. and by Alba et al. (2017, 2022) as *A.*

25 *brevirostris*, but remained unpublished. Here we describe and figure them for the first time
26 and provide morphological and morphometric comparisons to justify their attribution to *A.*
27 *brevirostris*.

28

29 **2. Materials and methods**

30 IPS41713a–e consists of five upper teeth (Table 1) that constitute a left C¹–M² series
31 from a single male adult individual (see SOM S1 and SOM Fig. S2 for further details). Dental
32 measurements of length (MD) and breadth (BL) were taken with a digital caliper to the
33 nearest 0.1 mm and used to compute a breadth/length index ($BLI = BL / MD \times 100$); to
34 measure the length of the C¹, the mesiodistal axis was defined as the maximum basal crown
35 diameter and the labiolingual one as perpendicular to it. The comparative sample includes
36 other Iberian dryopithecines, with emphasis on Middle Miocene taxa from the Vallès-
37 Penedès Basin (see measurements in SOM Table S1).

38 The cheek teeth were μ CT-scanned and segmented to generate three-dimensional (3D)
39 surface models of the outer enamel surface (OES) and the enamel-dentine junction (EDJ)—
40 see SOM S2.1 for details on scanning parameters and segmentation. The OES and EDJ 3D
41 surfaces are available from MorphoSource (SOM Table S2). Two-dimensional relative
42 enamel thickness (2DRET) was computed following standard procedures (e.g., Fortuny et al.,
43 2021; see SOM S2.2). The incomplete preservation of the crown base precluded computing
44 enamel thickness in 3D as well the application of alternative deformation-based methods of
45 shape analysis (e.g., Zanolli et al., 2023). However, a 3D geometric morphometric (3DGM)
46 analysis of EDJ shape of the M¹ was performed using (semi)landmarks (SOM Fig. S3) to
47 assess the closest morphometric affinities of the specimen. Shape coordinates were
48 subjected to two different statistical analyses: a canonical variate analysis (CVA) based on

49 extant great ape genera (Zanolli et al., 2023: SOM Table S2) and a principal component
50 analysis (PCA) based exclusively on Vallès-Penedès dryopithecines (Fortuny et al., 2021;
51 Zanolli et al., 2023; see SOM Table S3). For additional details on shape analysis and the
52 comparative sample, see SOM S2.3.

53

54 **3. Results**

55 *3.1. Description*

56 The upper canine The C¹ (Fig. 1a–e; Table 1) is labiolingually very compressed, more
57 markedly so at the crown (BLI = 63%) than at the root, which is somewhat stouter, higher,
58 and distally tilted relative to the apicobasal crown axis. The apex of the crown appears
59 almost unworn, with a preserved labial crown height of >14.6 mm (it cannot be measured
60 with certainty due to damage at the cervix). The crown displays a marked and deep
61 mesiolingual sulcus that does not extend onto the root through the cervix and apically fades
62 before reaching the crown apex. The crown curves lingually from base to apex and is thus
63 lingually tilted. The labial crown wall is markedly convex, while the distolingual one appears
64 basally concave due to honing against the P₃, which would have presumably maintained a
65 sharp distal margin (although this cannot be unambiguously confirmed due to damage).

66 The upper premolars The P³ (Fig. 1f, j) only shows minimal wear at the paracone apex but,
67 due to incomplete preservation, it is not informative about occlusal proportions. The
68 preparacrista is straighter and more mesiodistally aligned than the postparacrista, which is
69 not continuous with the distal marginal ridge. Moderately well-developed styles can be
70 discerned on the mesiobuccal and distobuccal corners of the crown. Two distinct transverse
71 crests originate from the buccal aspect of the protocone and reach the lingual base of the
72 paracone, delimiting a deep but restricted, rectangular (much broader than long) central

73 fovea, which is well distinct from the partially preserved mesial fovea and the more spacious
74 and deeper distal fovea. The latter shows some development of enamel wrinkling. At the
75 mesial fovea, a moderately distinct hypoparacrista of mesiolingual direction appears to
76 bifurcate at about its midway. The postprotocrista is curved and continuous with the distal
77 marginal ridge.

78 The P⁴ (Fig. 1g, l) is similarly worn but more completely preserved than the P³ and hence
79 enables a rough estimation of crown proportions. The crown displays a suboval occlusal
80 contour that is slightly longer lingually than buccally and much broader than long (BLI ≈
81 147%; Table 1). Although the lingual and buccal crown walls are not preserved at the crown
82 base, it can be ascertained that the protocone is subequal in size to the paracone and that
83 the buccal crown wall is only moderately flaring. As in the P³, there are two transverse
84 crests between the protocone and paracone that delimit a broader than long central fovea,
85 although less distinct than in the P³ because the crests are less well defined (maybe due to
86 damage). Also, as in the P³, an oblique (albeit less distinct) hypoparacrista divides the mesial
87 fovea, the curved postprotocrista merges with the distal marginal ridge, and the
88 postparacrista is more obliquely oriented than the protoparacrista and curves lingually
89 before reaching the distal marginal ridge (although the distobuccal style is less distinct than
90 in the P³). Although there are some indications of enamel wrinkling, they are difficult to
91 distinguish from damage on the OES.

92 The EDJ shape of the premolars (Fig. 1k, m) supports the descriptions provided above
93 based on the OES and shows some additional details. It confirms that the postparacrista
94 does not reach the distal marginal ridge but abruptly curves lingually before reaching it (in
95 the P⁴ merging with a short and lingually oriented secondary crest), that the two transverse
96 crests originate from the lingual aspect of the protocone dentine horn, and that in the P⁴

97 the distal transverse crest fades away clearly before reaching the postprotocrista. In the P⁴,
98 the oblique hypoparacrista reaches the mesial marginal ridge, completely isolating a
99 restricted mesiobuccal fovea from the rest of the mesial fovea. Enamel wrinkling is not
100 generally expressed at the EDJ, except for some tenuous secondary ridges.

101 The upper molars The M¹ (Fig. 1h, n) is only slightly worn (with no dentine exposure despite
102 some damage at the metacone apex) and displays tenuous mesial and distal interproximal
103 wear facets. The enamel is moderately thick (2DRET = 15.54; SOM Fig. S4; SOM Table S4).
104 The occlusal contour is subquadrangular (slightly broader than long; BLI ≈ 110%; Table 1)
105 and moderately distally tapering (albeit this might be attributable to the more incomplete
106 preservation of the distobuccal crown base). There are four main cusps, the lingual ones
107 (especially the protocone) slightly more distally located than the corresponding buccal
108 cusps. The hypocone is well developed (subequal in size to the trigon cusps) and slightly
109 more lingually located than the protocone. There is also a distinct but smaller protoconule
110 (=paraconule) located mesiobuccally from the paracone, at the junction between the short
111 and mesiobuccally oriented preprotocrista and the mesial marginal ridge. The latter is also
112 continuous with the short preparacrista. A thick and transversely aligned hypoparacrista
113 extends between the bases of the protoconule and the paracone, separating a fissure-like
114 mesial fovea (mostly located on the buccal half of the crown) from the subtriangular and
115 much more extensive deeper trigon basin. The latter is delimited distally by a straight, thick,
116 sharp, and continuous crista obliqua, and buccally by the similarly distinct but narrower
117 postparacrista and premetacrista, which are aligned to one another. The bases of the
118 protocone and hypocone are separated by a deep transverse groove that extends from the
119 buccal wall to the center of the distal fovea across the poorly-defined prehypocrista. A
120 short, thick, and blunt transverse crista extends between the bases of the hypocone and

121 metacone, dividing the distal fovea. The posthypocrista and postmetacrista are short,
122 curved, and continuous with the distal marginal ridge. Very narrow cingular remnants are
123 present mesiolingually and distolingually, while a narrow buccal cingulum was likely present
124 between the paracone and metacone (albeit this cannot be conclusively ascertained owing
125 to incomplete preservation). The occlusal morphology preserved by the partial M² (Fig. 1i, p)
126 is entirely comparable to that of the M¹ at a larger size, except for the more conspicuous
127 prehypocrista (even if partly interrupted by the aforementioned transverse groove) and the
128 more abundant development of secondary enamel wrinkling at the distal fovea.

129 The EDJ shape of the molars (Fig. 1o, q) further confirms the descriptions provided above
130 for the OES, including the presence of a well-developed protoconule horn tip, a distinct
131 hypoparacrasta separating the mesial from the central fovea, a continuous crista obliqua,
132 and a hypocone-metacone transverse crest dividing the distal fovea. The prehypocrista,
133 which is continuous and more clearly defined than at the OES level, is obliquely oriented
134 and does not join the apex of the protocone dentine horn but the origin of the
135 postprotocrista, where a poorly-developed secondary dentine horn can be discerned in the
136 M¹ but not in the M².

137

138 3.2. Comparisons

139 The upper canine Among the male C¹ sample of Middle Miocene dryopithecines from the
140 Vallès-Penedès Basin, IPS41713a (Fig. 2a) most closely resembles that of the *A. brevirostris*
141 holotype (Fig. 2b), which displays a slightly larger but similarly slender crown with an
142 elliptical and markedly labiolingually compressed occlusal contour (SOM Fig. S5a; SOM Table
143 S1) and a lingually tilted apex. Besides minor size differences, these two specimens only
144 slightly differ in the shape of the root, which is straighter in the holotype of *A. brevirostris*

145 (forming a more abrupt angle with the crown apicobasal axis than in IPS41713a). The male
146 C¹s of the *P. catalaunicus* holotype (Fig. 2e–f) show a similar degree of crown labiolingual
147 compression and a lingually tilted crown apex but display somewhat larger and less
148 labiolingually compressed crown basal dimensions (SOM Fig. S5a; SOM Table S1), a less
149 elliptical occlusal contour (more constricted at about mid-length), and a stouter root. The
150 male C¹s of *D. fontani* (Fig. 2d) display larger dimensions (SOM Fig. S5a; SOM Table S1),
151 especially breadth, resulting in a much broader crown than in *A. brevirostris*, further
152 displaying a clearly suboval instead of elliptical occlusal contour that is broadest toward the
153 mesial side and more distally tapering than in the remaining specimens. Furthermore, in *D.*
154 *fontani* the crown apex is not lingually tilted as in IPS41713a and the holotypes of *A.*
155 *brevirostris* and *P. catalaunicus*.

156 The upper premolars The upper cheek teeth of IPS41713 and its M¹ OES and EDJ are
157 compared with those of Middle Miocene dryopithecines from the Vallès-Penedès Basin in
158 Figure 2 and SOM Figure S6, respectively, while dental size and proportions (SOM Table S1)
159 can be ascertained from bivariate plots depicted in SOM Figure S5b–c.

160 The upper premolars show a similar occlusal pattern to those of other Middle Miocene
161 dryopithecines, characterized by the presence of two transverse crests between the
162 protocone and the paracone, although further comparisons are restricted to the P⁴ due to
163 the incomplete preservation of the P³. The described P⁴ (IPS41713b) is larger than female
164 specimens of *A. brevirostris* and more closely resembles in size those of other male
165 dryopithecines (SOM Fig. S5b). However, its proportions most closely approach those of the
166 *A. brevirostris* male holotype, whereas the P⁴s of *D. fontani* and especially *P. catalaunicus*—
167 which display a more flaring buccal crown wall at the level of the paracone—are relatively
168 broader (SOM Fig. S5b; SOM Table S1). The newly described P⁴ apparently differs from

169 those in the comparative sample because the distal transverse crest does not join the
170 postparacrista, where it usually forms a cusplike thickening, but this is difficult to
171 ascertain at the OES level due to damage.

172 The upper molars In dental size and proportions, the M¹ from ACM/C4-Cp resembles those
173 of Middle Miocene dryopithecine male individuals included in the comparative sample and
174 is larger than those of female specimens of *A. brevirostris* (SOM Fig. S5c; SOM Table S1). All
175 these M¹s show a similar occlusal pattern at the OES and EDJ levels (Fig. 2; SOM Fig. S6),
176 including the presence of a distinct protoconule, a small buccal cingulum between the
177 paracone and metacone (not confidently ascertainable in IPS41713d owing to incomplete
178 preservation), and a hypocone-metacone crest. Nevertheless, IPS41713d differs from the
179 holotype of *P. catalaunicus* in the slightly more lingual position of the hypocone and the
180 somewhat less inflated crests. Another possible difference refers to the orientation of the
181 hypocone-metacone crista, which in IPS41713d is transversely oriented from the hypocone
182 toward the metacone base, as in previously described specimens of *A. brevirostris*. By
183 contrast, this crest is more obliquely oriented (i.e., directed toward the end of the
184 postmetacrista) in *P. catalaunicus* and *D. fontani*. The 2DRET displayed by the M¹ from
185 ACM/C4-Cp is higher than that of African apes and more similar to that of orangutans, more
186 closely approaching the condition of *A. brevirostris* and *P. catalaunicus* than the thinner-
187 enameled condition of *D. fontani* (SOM Fig. S7; Fortuny et al., 2021).

188 The 3DGM analyses of EDJ shape confirm that the M¹ from ACM/C4-Cp displays closest
189 morphometric affinities with other dryopithecines from the Vallès-Penedès Basin. The CVA
190 (Fig. 3a), which maximizes the distinction among extant great ape genera and correctly
191 classifies 97% of original cases (93% after cross-validation; SOM Table S5), indicates that all
192 dryopithecines occupy an intermediate position in the morphospace along the first

193 canonical variate (CV1) but overlap with extant great apes in the second (CV2)—see SOM
194 S3.1, SOM Table S6, and SOM Figure S8 for a more detailed description of the results. The
195 Late Miocene *Hispanopithecus* shows moderately negative CV2 scores, while the Middle
196 Miocene genera show slightly more positive scores along this axis. IPS41713 shows slightly
197 less negative scores than the other analyzed dryopithecines along CV1, whereas it only
198 overlaps with *Anoiapithecus* specimens along CV2, being approximately equidistant from
199 the holotype of the latter species and the single specimen of *Dryopithecus*. Typicality
200 probabilities indicate that none of the fossil specimens (including IPS41713) fit with the
201 variation of any extant genus (SOM Table S7). The PCA focused on dryopithecines (Fig. 3b
202 zzz), which does not distort the morphospace to maximize the variance among taxa, shows
203 some differences between Late and Middle Miocene taxa along the first principal
204 component (PC1) with only slight overlap, while PC2 separates *Anoiapithecus* from other
205 taxa (see SOM S3.2 and SOM Table S8 for further details of the PCA results). Overall, the M¹
206 from ACM/C4-Cp appears approximately equidistant to *Hispanopithecus laietanus* and the
207 holotypes of *A. brevisrostris* and *P. catalaunicus*, and most distinctive from both *D. fontani*
208 and *Hispanopithecus crusafonti*.

209

210 **4. Discussion and conclusions**

211 Middle and Late Miocene dryopithecines from Iberia have been variously recovered by
212 cladistic analyses as crown hominids of uncertain affinities (Nengo et al., 2017; Gilbert et al.,
213 2020), as stem hominids (Alba et al., 2015; Pugh, 2022), or as stem hominines (Sevim-Erol et
214 al., 2023). Given such contradictory results (for further discussion, see Alba, 2012; Almécija
215 et al., 2021; Urciuoli and Alba, 2023), coupled with taxonomic controversies about the
216 distinctiveness of the Middle Miocene genera (Begun, 2009, 2015) and the scarcity of fossil

217 great ape remains from Europe, every bit of new information is important. For example,
218 analyses of tooth endostructural morphology of these dryopithecines (Alba et al., 2010,
219 2013, 2020; Fortuny et al., 2021; Zanolli et al., 2023) have supported the presence of some
220 differences in enamel thickness and EDJ shape among Iberian dryopithecine genera, in
221 further agreement with differences in OES (Alba and Moyà-Solà, 2012; Alba et al., 2013,
222 2020; Pérez de los Ríos et al., 2013) and cranial (Moyà-Solà et al., 2004, 2009a, 2009b; Pérez
223 de los Ríos et al., 2012; Pugh et al., 2023) morphology. Nevertheless, all these analyses
224 suffer from the problem of small sample sizes, which, coupled with their likely close
225 phylogenetic relationships, hinder adequately evaluating intra- vs. interspecific variation.

226 The description and analysis of the hominoid dental remains from ACM/C4-Cp modestly
227 enlarge the previously available upper tooth samples and reinforce previous purported
228 differences noted among Middle Miocene dryopithecine genera from the Vallès-Penedès
229 Basin. According to previous accounts of the dental morphology of these taxa (Alba and
230 Moyà-Solà, 2012; Alba et al., 2013), *Anoiapithecus* would differ from *Pierolapithecus* in the
231 less inflated cheek tooth crests, less developed enamel wrinkling, and the more lingually
232 located hypocone in the upper molars, from *Dryopithecus* in the thicker molar enamel, and
233 from both genera in the size and proportions of the male C¹ and the lower-crowned upper
234 molars. The latter feature cannot be reliably measured in the newly described specimens
235 due to incomplete preservation, and differences in enamel wrinkling are difficult to
236 ascertain in the M¹ due to differential wear. Nevertheless, the M¹ from ACM/C4-Cp most
237 closely resembles those attributed to *A. brevirostris* in some features, differing from
238 *Pierolapithecus* in the less inflated crests and the more lingually located hypocone, from
239 *Dryopithecus* in the thicker enamel, and from both genera in the more transversely aligned
240 hypocone-metacone crest. Our 3DGM analyses of M¹ EDJ shape are not entirely conclusive,

241 but confidently rule out an attribution to *D. fontani*. The P⁴ occlusal proportions and contour
242 further support an attribution to *A. breviostris*, like the male C¹, which displays closest
243 similarities in both shape (labiolingual crown compression and lingual tilt of the apex) and
244 size to that of the *A. breviostris* and, to a lesser extent, that of the *P. catalaunicus*, most
245 clearly discounting an alternate attribution to *D. fontani* (which displays larger size, broader
246 proportions, and a less lingually tilted apex). We therefore conclude that, when all available
247 evidence from the upper teeth is taken into account, an attribution of IPS41713 *A.*
248 *breviostris* is warranted.

249

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267

268 **References**

269

270 Alba, D.M., 2012. Fossil apes from the Vallès-Penedès Basin. *Evol. Anthropol.* 21, 254–269.

271 Alba, D.M., Moyà-Solà, S., 2012. On the identity of a hominoid male upper canine from the
272 Vallès-Penedès Basin figured by Pickford (2012). *Estud. Geol.* 68, 149–153.

273 Alba, D.M., Moyà-Solà, S., Casanovas-Vilar, I., Galindo, J., Robles, J.M., Rotgers, C., Furió, M.,
274 Angelone, C., Köhler, M., Garcés, M., Cabrera, L., Almécija, S., Obradó, P., 2006. Los
275 vertebrados fósiles del Abocador de Can Mata (els Hostalets de Pierola, l’Anoia,
276 Catalunya), una sucesión de localidades del Aragoniense superior (MN6 y MN7+8) de la
277 cuenca del Vallès-Penedès. Campañas 2002-2003, 2004 y 2005. *Estud. Geol.* 62, 295–312.

278 Alba, D.M., Fortuny, J., Moyà-Solà, S., 2010. Enamel thickness in Middle Miocene great apes
279 *Anoiapithecus*, *Pierolapithecus* and *Dryopithecus*. *Proc. R. Soc. B* 277, 2237–2245.

280 Alba, D.M., Fortuny, J., Pérez de los Ríos, M., Zanolli, C., Almécija, S., Casanovas-Vilar, I.,
281 Robles, J.M., Moyà-Solà, S., 2013. New dental remains of *Anoiapithecus* and the first
282 appearance datum of hominoids in the Iberian Peninsula. *J. Hum. Evol.* 65, 573–584.

283 Alba, D.M., Almécija, S., DeMiguel, D., Fortuny, J., Pérez de los Ríos, M., Pina, M., Robles,
284 J.M., Moyà-Solà, S., 2015. Miocene small-bodied ape from Eurasia sheds light on
285 hominoid evolution. *Science* 350, aab2625.

286 Alba, D.M., Casanovas-Vilar, I., Garcés, M., Robles, J.M., 2017. Ten years in the dump: An
287 updated review of the Miocene primate-bearing localities from Abocador de Can Mata
288 (NE Iberian Peninsula). *J. Hum. Evol.* 102, 12–20.

289 Alba, D.M., Fortuny, J., Robles, J.M., Bernardini, F., Pérez de los Ríos, M., Tuniz, C., Moyà-
290 Solà, S., Zanolli, C., 2020. A new dryopithecine mandibular fragment from the middle
291 Miocene of Abocador de Can Mata and the taxonomic status of '*Sivapithecus*'
292 *occidentalis* from Can Vila (Vallès-Penedès Basin, NE Iberian Peninsula). *J. Hum. Evol.* 145,
293 102790.

294 Alba, D.M., Robles, J.M., Casanovas-Vilar, I., Beamud, E., Bernor, R.L., Cirilli, O., DeMiguel,
295 D., Galindo, J., Llopart, I., Pons-Monjo, G., Sánchez, I.M., Vinuesa, V., Garcés, M., 2022. A
296 revised (earliest Vallesian) age for the hominoid-bearing locality of Can Mata 1 based on
297 new magnetostratigraphic and biostratigraphic data from Abocador de Can Mata (Vallès-
298 Penedès Basin, NE Iberian Peninsula). *J. Hum. Evol.* 170, 103237.

299 Almécija, S., Hammond, A.S., Thompson, N.E., Pugh, K.D., Moyà-Solà, S., Alba, D.M., 2021.
300 Fossil apes and human evolution. *Science* 372, eabb4363.

301 Begun, D.R., 2009. Dryopithecins, Darwin, de Bonis, and the European origin of the African
302 apes and human clade. *Geodiversitas* 31, 789–816.

303 Begun, D.R., 2015. Fossil record of Miocene hominoids. In: Henke, W., Tattersall, I. (Eds.),
304 *Handbook of Paleoanthropology*, 2nd ed. Springer, Heidelberg, pp. 1261–1332.

305 Casanovas-Vilar, I., Alba, D.M., Garcés, M., Robles, J.M., Moyà-Solà, S., 2011. Updated
306 chronology for the Miocene hominoid radiation in Western Eurasia. *Proc. Natl. Acad. Sci.*
307 *USA* 108, 5554–5559.

308 Casanovas-Vilar, I., Madern, A., Alba, D.M., Cabrera, L., García-Paredes, I., Van den Hoek
309 Ostende, L.W., DeMiguel, D., Robles, J.M., Furió, M., Van Dam, J., Garcés, M., Angelone,
310 C., Moyà-Solà, S., 2016a. The Miocene mammal record of the Vallès-Penedès Basin
311 (Catalonia). *C. R. Palevol* 15, 791–812.

312 Casanovas-Vilar, I., Garcés, M., Van Dam, J., García-Paredes, I., Robles, J.M., Alba, D.M.,
313 2016b. An updated biostratigraphy for the late Aragonian and the Vallesian of the Vallès-
314 Penedès Basin (Catalonia). *Geol. Acta* 14, 195–217.

315 Fortuny, J., Zanolli, C., Bernardini, F., Tuniz, C., Alba, D.M., 2021. Dryopithecine
316 palaeobiodiversity in the Iberian Miocene revisited on the basis of molar endostructural
317 morphology. *Palaeontology* 64, 531–554.

318 Gilbert, C.C., Ortiz, A., Pugh, K.D., Campisano, C.J., Patel, B.A., Singh, N.P., Fleage, J.G.,
319 Patnaik, R., 2020. New middle Miocene ape (Primates: Hylobatidae) from Ramnagar,
320 India fills major gaps in the hominoid fossil record. *Proc. R. Soc. B* 287, 20201655.

321 Moyà-Solà, S., Köhler, M., Alba, D.M., Casanovas-Vilar, I., Galindo, J., 2004. *Pierolapithecus*
322 *catalaunicus*, a new Middle Miocene great ape from Spain. *Science* 306, 1339–1344.

323 Moyà-Solà, S., Alba, D.M., Almécija, S., Casanovas-Vilar, I., Köhler, M., De Esteban-Trivigno,
324 S., Robles, J.M., Galindo, J., Fortuny, J., 2009a. A unique Middle Miocene European
325 hominoid and the origins of the great ape and human clade. *Proc. Natl. Acad. Sci. USA*
326 106, 9601–9606.

327 Moyà-Solà, S., Köhler, M., Alba, D.M., Casanovas-Vilar, I., Galindo, J., Robles, J.M., Cabrera,
328 L., Garcés, M., Almécija, S., Beamud, E., 2009b. First partial face and upper dentition of
329 the Middle Miocene hominoid *Dryopithecus fontani* from Abocador de Can Mata (Vallès-
330 Penedès Basin, Catalonia, NE Spain): Taxonomic and phylogenetic implications. *Am. J.*
331 *Phys. Anthropol.* 139, 126–145.

332 Nengo, I., Tafforeau, P., Gilbert, C.C., Fleagle, J.G., Miller, E.R., Feibel, C., Fox, D.L., Feinberg,
333 J., Pugh, K.D., Berruyer, C., Mana, S., Engle, Z., Spoor, F., 2017. New infant cranium from
334 the African Miocene sheds light on ape evolution. *Nature* 548, 169–174.

335 Pérez de los Ríos, M., Moyà-Solà, S., Alba, D.M., 2012. The nasal and paranasal architecture
336 of the Middle Miocene ape *Pierolapithecus catalaunicus* (Primates: Hominidae):
337 Phylogenetic implications. *J. Hum. Evol.* 63, 497–506.

338 Pickford, M., 2012. Hominoids from Neuhausen and other Bohnerz localities, Swabian Alb,
339 Germany: Evidence for a high diversity of apes in the Late Miocene of Germany. *Estud.*
340 *Geol.* 68, 113–147.

341 Pugh, K.D., 2022. Phylogenetic analysis of Middle-Late Miocene apes. *J. Hum. Evol.* 165,
342 103140.

343 Pugh, K.D., Catalano, S.A., Pérez de los Ríos, M., Fortuny, J., Shearer, B.M., Vecino Gazabón,
344 A., Hammond, A.S., Moyà-Solà, S., Alba, D.M., Almécija, S., 2023. The reconstructed
345 cranium of *Pierolapithecus* and the evolution of the great ape face. *Proc. Natl. Acad. Sci.*
346 *USA* 120, e2218778120.

347 Sevim-Erol, A., Begun, D.R., Sönmez Sözer, Ç., Mayda, S., van den Hoek Ostende, L.W.,
348 Martin, R.M.G., Cihat Alçiçek, M., 2023. A new ape from Türkiye and the radiation of late
349 Miocene hominines. *Commun. Biol.* 6, 842.

350 Urciuoli, A., Alba, D.M., 2023. Systematics of Miocene apes: State of the art of a
351 neverending controversy. *J. Hum. Evol.* 175, 103309.

352 Zanolli, C., Bouchet, F., Fortuny, J., Bernardini, F., Tuniz, C., Alba, D.M., 2023. A reassessment
353 of the distinctiveness of dryopithecine genera from the Iberian Miocene based on
354 enamel-dentine junction geometric morphometric analyses. *J. Hum. Evol.* 177, 103326.

355

356 **Figure captions**

357

358 **Figure 1.** Dental remains of *Anoiapithecus brevirostris* from ACM/C4-Cp, including
359 photographs (a–i) and three-dimensional model renders of the outer enamel surface (j, l, n,
360 p) and enamel-dentine junction (k, m, o, q): a–e) IPS41713a, left C¹ in occlusal (a), labial (b),
361 mesial (c), lingual (d), and distal (e) views; f, j, k) IPS41713c, left partial P³ in occlusal view; g,
362 l, m) IPS41713b, left P⁴ crown in occlusal view; h, n, o) IPS41713d, left M¹ crown in occlusal
363 view; i, p, q) IPS41713e, left M² lingual crown fragment in occlusal view. In occlusal views,
364 mesial is on top. See Figure 2 and SOM Figure S6 for comparison with other Middle Miocene
365 dryopithecine specimens from the same area. The 3D models can be accessed from
366 MorphoSource (see SOM Table S2).

367
368 **Figure 2.** The male C¹ (a) and P³–M² (g) of *Anoiapithecus brevirostris* described in this paper
369 as compared with male C¹s (b–f) and upper cheek teeth (h–q) of Middle Miocene
370 dryopithecines from Abocador de Can Mata: a) IPS41713a, *A. brevirostris* from ACM/C4-Cp;
371 b) IPS43000, *A. brevirostris* (holotype) from ACM/C3-Aj (mirrored); c) IPS41714, *D. fontani*
372 from ACM/C4-Ap; d) IPS35026, *Dryopithecus fontani* from ACM/C3-Ae (reversed); e–f)
373 IPS21350, *Pierolapithecus catalaunicus* (holotype) from ACM/BCV1 (panel f is reversed); g)
374 IPS41713b–e, P³–M² of *A. brevirostris* from ACM/C4-Cp; h–i) IPS43000, P³–M² of *A.*
375 *brevirostris* (holotype) from ACM/C3-Aj (panel i is reversed); j–k) IPS35027, P⁴–M¹ (j) and
376 M¹–M² (k, reversed) of *A. brevirostris* from ACM/C1-E*; l) IPS41712, P³–M¹ of *A. brevirostris*
377 from ACM/C3-Aj; m) MGSB48486, M² of *D. fontani* from Can Mata s.l. (reversed); n–o)
378 IPS35026, P³–M² (n) and P³–M¹ (o, reversed) of *D. fontani* from ACM/C3-Ae; p–q) IPS21350,
379 P³–M² of *P. catalaunicus* from ACM/BCV1 (panel k is reversed). All specimens are depicted
380 as from the left side (indicated when mirrored). Canines are shown in occlusal (left top),

381 mesial (left bottom or middle), and labial (right) views, whereas cheek teeth are shown in
382 occlusal view (mesial on top).

383

384 **Figure 3.** Results of the three-dimensional geometric morphometric analyses of M¹ enamel-
385 dentine junction shape in *Anoiapithecus brevirostris* from ACM/C4-Cp as compared with
386 other Middle Miocene dryopithecine specimens from the same area based on the
387 (semi)landmark configuration after Procrustes alignment (see Materials and methods for
388 further details). a) Canonical variate (CV) analysis based on extant great ape genera, with
389 fossil specimens projected a posteriori, as depicted by a bivariate plot of CV2 vs. CV1. b)
390 Principal component (PC) analysis based exclusively on the same fossil specimens, as
391 depicted by a bivariate plot of PC2 vs. PC1. The maximum and minimum landmark
392 configurations are depicted along each axis in occlusal and buccal views, while the
393 percentage of variance accounted by each axis is reported within parentheses.

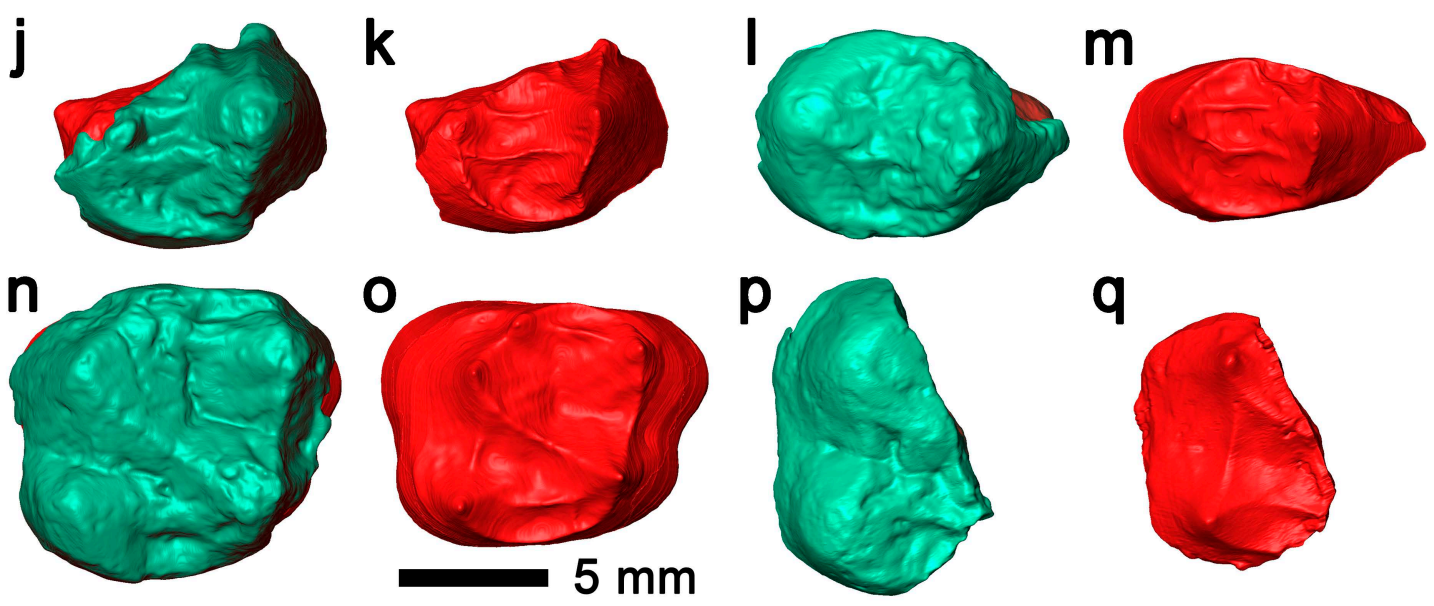
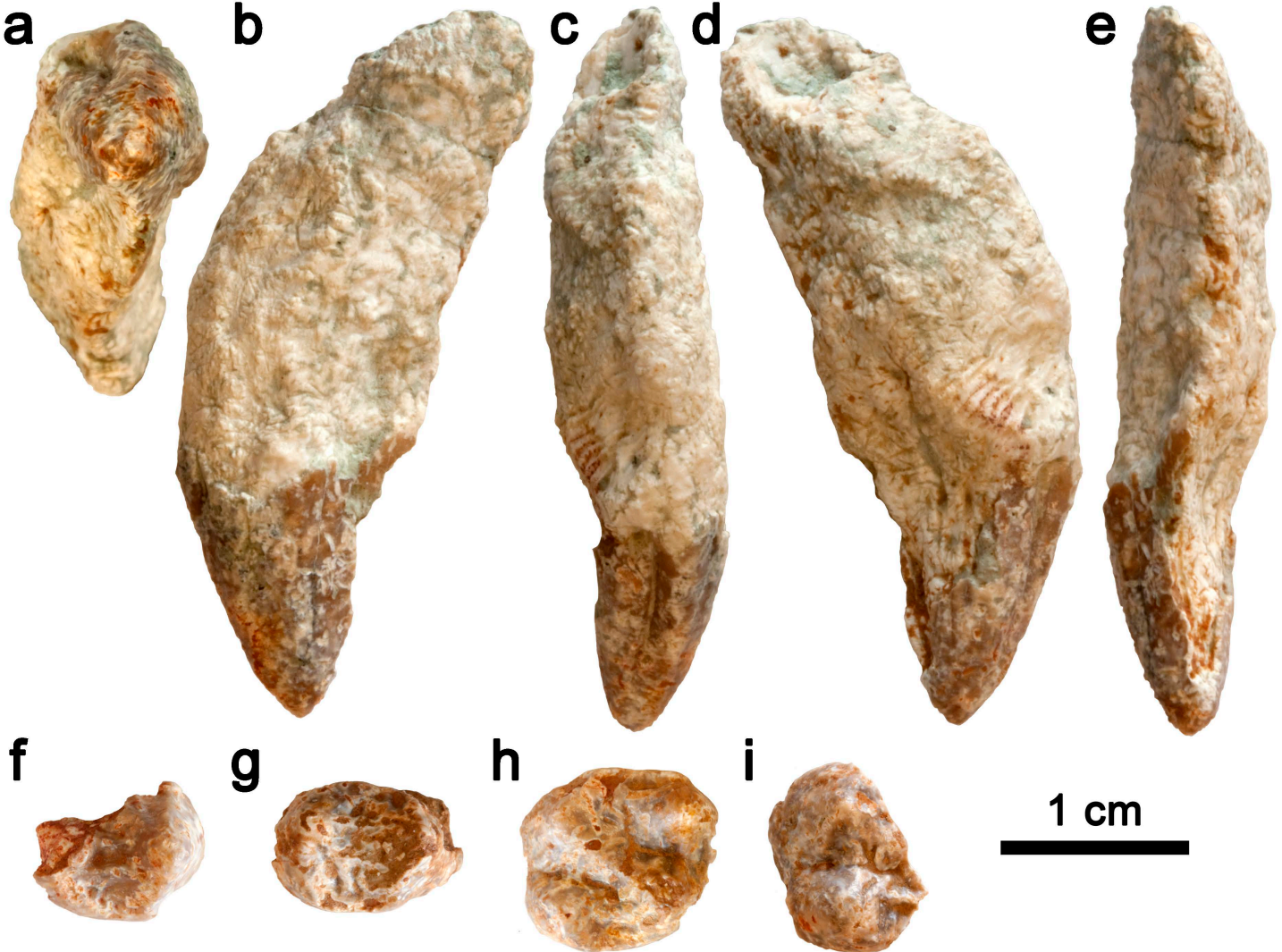
Table 1

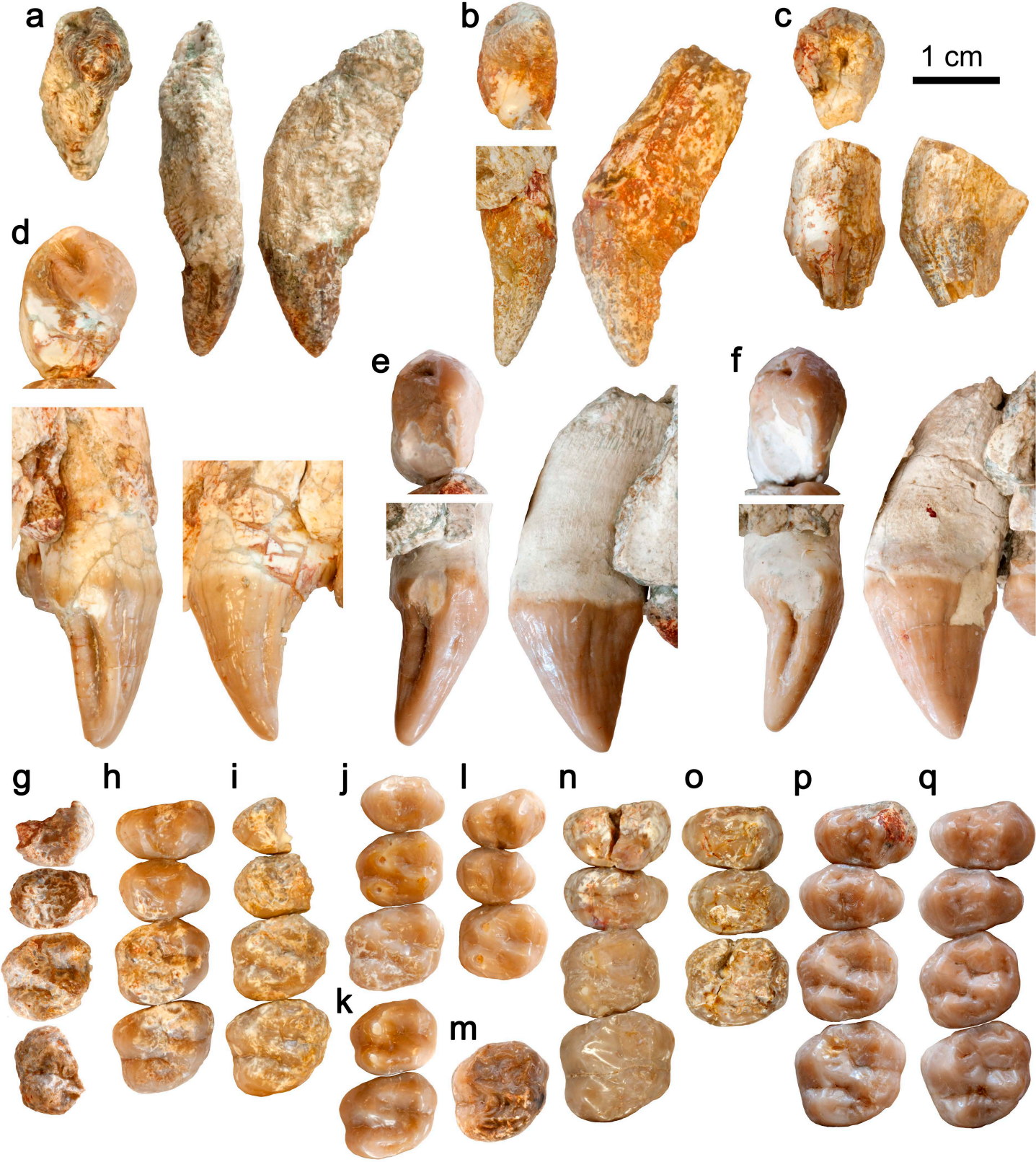
Measurements^a of left upper tooth series of *Anoiapithecus brevirostris* from ACM/C4-Cp.

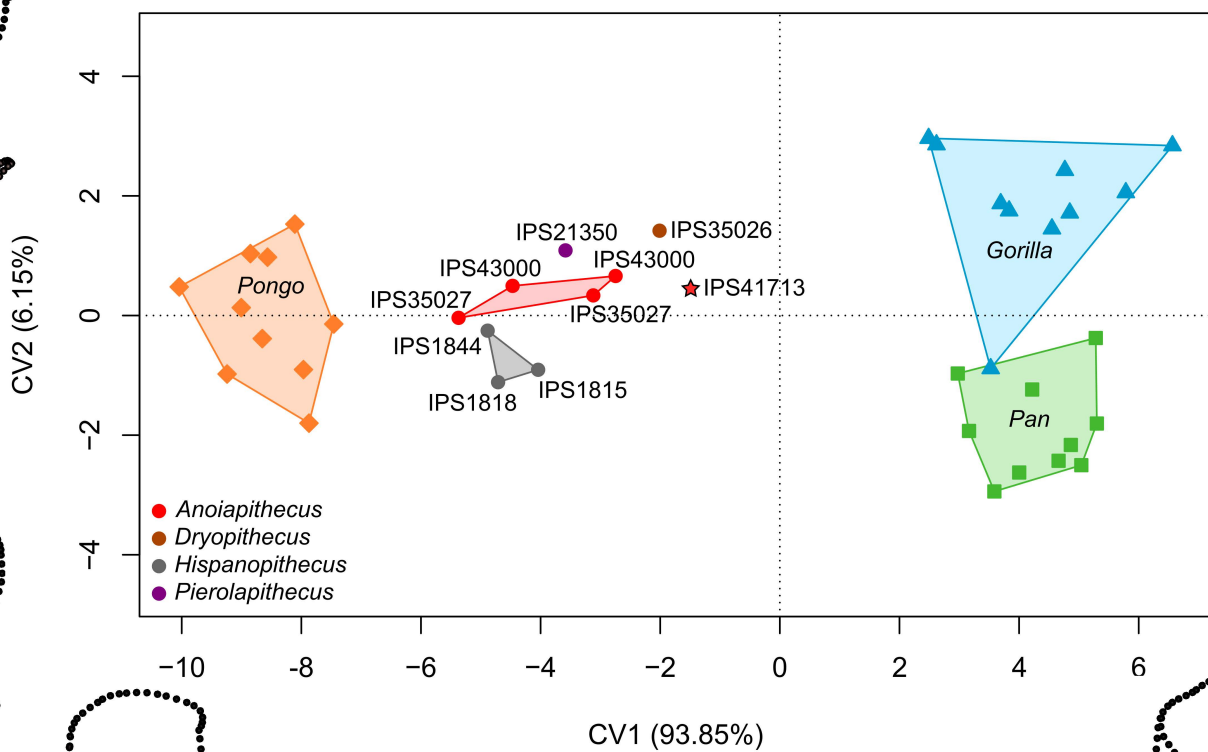
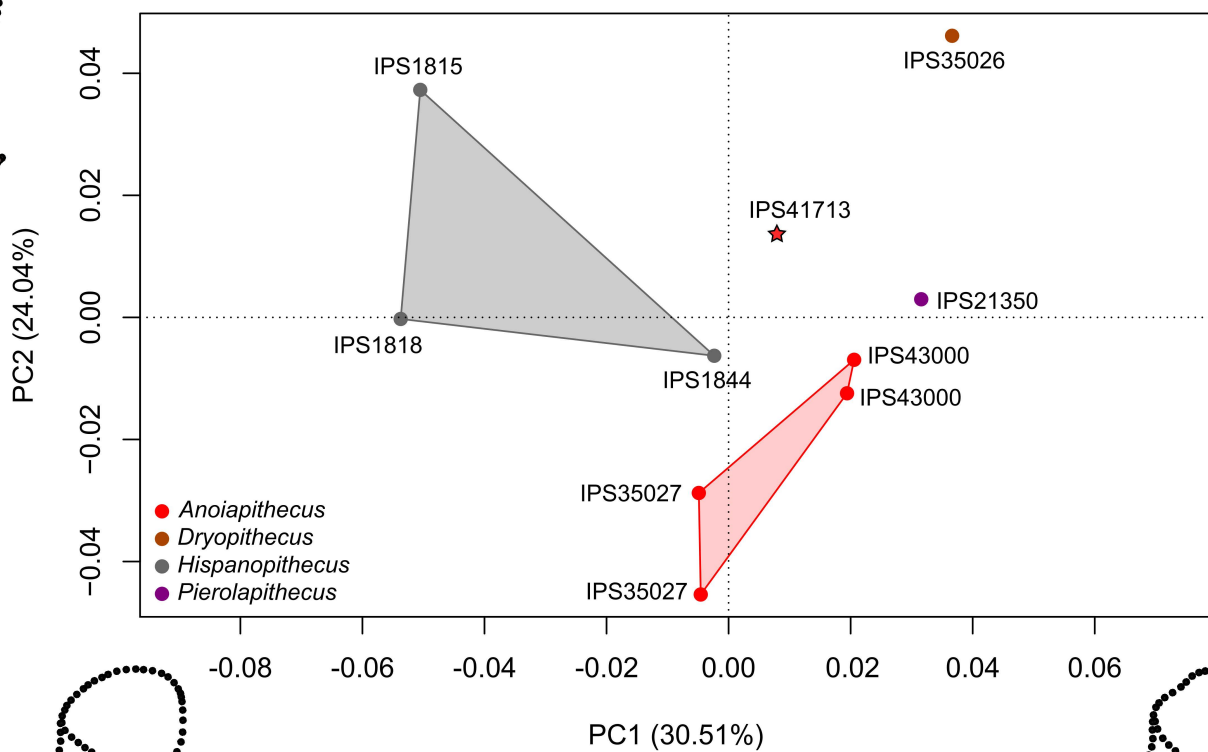
Catalog no.	Tooth locus	MD	BL	BLm	BLd	BLI
IPS41713a	C ¹	12.6	8.0	—	—	63.5
IPS41713c	P ³	>7.3	>9.9	—	—	—
IPS41713b	P ⁴	7.5	(11.0)	—	—	(146.7)
IPS41713d	M ¹	10.3	(11.3)	(11.3)	>9.5	(109.7)
IPS41713e	M ²	>10.3	—	—	—	—

Abbreviations: MD = mesiodistal length (in mm); BL = buccolingual (or labiolingual) breadth (in mm), distinguishing between the mesial (BLm) and the distal (BLd) lobes in the case of molars; BLI = breadth/length index (in %), computed as maximum BL / MD × 100.

^a Measurements between parentheses are estimates while those preceded by the 'greater than' symbol are lower than the original dimension due to incomplete preservation.





a**b**

Supplementary Online Material (SOM):

New remains of the Miocene great ape *Anoiapithecus brevirostris* from Abocador de Can Mata

David M. Alba ^{a,*}, Florian Bouchet ^a, Josep Fortuny ^a, Josep M. Robles ^a, Jordi Galindo ^a, Àngel H. Luján ^a, Salvador Moyà-Solà ^{a,b,c}, Clément Zanolli ^{d,*}

^a *Institut Català de Paleontologia Miquel Crusafont (ICP-CERCA), Universitat Autònoma de Barcelona, c/ Columnes s/n, 08193 Cerdanyola del Vallès, Barcelona, Spain*

^b *Institució Catalana de Recerca i Estudis Avançats (ICREA), Pg. Lluís Companys 23, 08010 Barcelona, Spain*

^c *Unitat d'Antropologia Biològica (Dept. BABVE), Universitat Autònoma de Barcelona, 08193 Cerdanyola del Vallès, Barcelona, Spain*

^d *Univ. Bordeaux, CNRS, MCC, PACEA, UMR 5199, F-33600 Pessac, France*

***Corresponding authors.**

E-mail addresses: david.alba@icp.cat (D.M. Alba); clement.zanolli@gmail.com (C. Zanolli).

SOM S1

Preservation

The dental sample from ACM/C4-Cp includes five isolated specimens from the left side: an almost complete C¹ (IPS41713a), partial P³ (IPS41713c) and M² (IPS41713e) crowns, and almost complete P⁴ (IPS41713b) and M¹ (IPS41713d) crowns. No maxillary bone is preserved except for small, isolated fragments (IPS41713f), but the teeth were found in close spatial association and, in all probability, belong to a single individual. Based on canine size and shape, this individual can be sexed as male, probably corresponding to a young adult given the degree of wear of the upper molars and canine.

The teeth are poorly preserved due to taphonomic processes, as can be observed from the photograph of the C¹ taken in the field (SOM Fig. S2). This is probably attributable to acid corrosion during and/or soon after burial, as the fossil was recovered from a fresh claystone matrix not affected by recent edaphic processes. The C¹ preserves the crown and most of the root, except for its apical-most portion (Fig. 1a–e). However, the enamel surface is cracked and corroded, with chips of enamel missing, particularly close to the cervix. The root surface is even more affected by cracking and corrosion and, on its mesiolingual portion close to the cervix, it seemingly displays rodent gnawing marks. The roots of the cheek teeth (Figs. 1f–i and 2) are missing and the crowns display abundant acidic corrosion. The crowns of the P⁴ and M¹ preserve most of the occlusal surface but are missing most of their basal-most portions toward the cervix, whereas those of the P³ and M² are very incomplete. The P³ preserves the paracone and the central and distal portions of the crown, but is missing the lingual and mesial walls as well as the basal-most portion of the buccal wall, while the M² consists of the buccal half of the crown.

SOM S2

Supplementary methods

2.1. Scanning and segmentation

The cheek teeth of IPS41713 were μ CT-scanned at the Centro Nacional de Investigación sobre la Evolución Humana in Burgos (Spain) with a high-resolution X-ray μ CT scanner model V|Tome|X s 240 (GE Sensing & Inspections Technologies). The μ CT acquisition was carried out at 160 kV with a current of 120 μ A, obtaining a voxel size of 18.50 μ m. The X-ray beam was filtered by a 0.2 mm-thick copper absorber. Using the commercial software Avizo v. 7.1 (FEI Visualization Sciences Group, Hillsboro), a semiautomatic, threshold-based segmentation was carried out using a combination of the half-maximum height method (Spoor et al., 1993) and of the region of interest thresholding protocol (Fajardo et al., 2002; Coleman and Colbert, 2007).

2.2. Relative enamel thickness

Orientation and reconstruction Two-dimensional relative enamel thickness (2DRET) is a dimensionless variable devised to compare enamel thickness among species irrespective of size (Martin, 1985). In previous studies of 2DRET in Iberian dryopithecines (Alba et al., 2013, 2020; Fortuny et al., 2021), measurements were taken on a buccolingual virtual cross section passing through the tips of the mesial dentine horns and perpendicular to the best-fit plane of the cervical line (Benazzi et al., 2014). However, given that the cervix is not completely preserved in IPS41713d, we relied instead on the developmental plane (defined by placing a landmark on the apex of each trigon cusps) to generate a buccolingual cross section perpendicular to it. Results obtained with either the developmental plane or the cervical plane were previously shown to be comparable (Smith et al., 2012). Furthermore, it was necessary to reconstruct the basal portion of the dentine and enamel cap, as well as the

enamel at the apex of the protocone, to account for light wear as in previous studies (e.g., Fortuny et al., 2021). Following previously established protocols (e.g., Smith et al., 2012), enamel was reconstructed following the natural curve of the crown and only minimal reconstructions were made. Two independent reconstructions were made by two authors of the paper (F.B. and C.Z.) and the average value was then taken.

Computation of relative enamel thickness Two-dimensional relative enamel thickness was computed following Martin's (1985) protocol on a virtual buccolingual section passing through the mesial dentine horns, reconstructed as described above. The following formulas was used (Martin, 1985; Smith et al., 2005; Fortuny et al., 2021): $2DRET = 2DAET \times 100/b^{1/2}$ and $2DAET = c/e$, where $2DAET$ = bidimensional average enamel thickness (in mm), b = dentine and pulp area (in mm^2), c = enamel cap area (in mm^2), and e = enamel-dentine junction length (in mm).

2.3. Shape analysis

(Semi)landmark protocol The three-dimensional geometric morphometric analysis of enamel-dentine junction (EDJ) virtual surfaces was performed using a protocol based on four landmarks placed at the apices of the main cusp dentine horns plus 75 semilandmarks placed along occlusal crests and the mesial and distal marginal ridges (SOM Fig. S3): 10 on the prehypocrista, 10 on the postparacrista + premetacrista, 20 on the preprotocrista + mesial marginal ridge + preparacrista, 20 on the postmetacrista + distal marginal ridge + posthypocrista, and 15 on the crista obliqua. Landmark data were imported into R v. 4.1.1 (R Core Team, 2021) to perform Procrustes alignments using the 'ProcSym' function of the R package 'Morpho' v. 2.9 (Schlager, 2021).

Comparative sample The comparative sample of Iberian dryopithecines for the morphometric analysis consists of nine M^1 s for which the EDJ was previously analyzed (Fortuny et al.,

2021; Zanolli et al., 2023; see SOM Table S3): the right and left antimeres of two individuals of *Anoiapithecus brevirostris* (IPS43000 [holotype] and IPS35027); a single specimen of *Pierolapithecus catalaunicus* (IPS21350 [holotype]) and another of *Dryopithecus fontani* (IPS35026); and three specimens of *Hispanopithecus*, including two of *Hispanopithecus crusafonti* (IPS1815 and IPS1818) and another of *Hispanopithecus laietanus* (IPS1844). In turn, the extant hominid comparative sample consists of 10 M¹s for each of the three living great ape genera *Pan*, *Gorilla*, and *Pongo* (i.e., 30 M¹s in total; for details of the extant comparative sample composition, see Zanolli et al., 2023: SOM Table S2).

Multivariate analyses The multivariate analyses were performed on landmark data taken from the EDJ surface after Procrustes alignment. A canonical variate analysis (CVA) was performed from a prior principal component analysis (PCA), with three groups (corresponding to the three extant genera) defined a priori and the fossils projected a posteriori. Another PCA based exclusively on the fossil specimens was also performed. The CVA allows to ascertain the portion of the morphospace occupied by dryopithecines relative to extant taxa but has the problem that the fossils do not participate in the definition of the morphospace and that the latter is distorted to maximize the distinction among extant genera but not extinct ones. In contrast, the PCA defines the morphospace exclusively on the basis of fossil specimens and is thus arguably more suitable to ascertain the closest similarities of the newly described specimen to dryopithecine genera. Given that CVA requires a smaller number of variables than specimens, it was based on a subset of the first principal component (PC) scores that maximized correct classification (e.g., Zanolli et al., 2023). The first seven PCs (accounting for 93% of variance) were selected to run the CVA (see the first two PCs in SOM Fig. S10), whose accuracy was ascertained based on the percentage of correctly classified extant cases (both without and with cross validation). For fossil specimens, typicality probabilities were reported to ascertain if they fit with the variation of the extant

great ape genera separately. The PCAs and CVA were computed using the R packages ‘ade4’ v. 1.7-18 (Dray and Dufour, 2007) and ‘Morpho’, respectively.

SOM S3

Supplementary results of the shape analyses

3.1. Canonical variate analysis

The CVA based on M¹ EDJ shape of extant great ape genera correctly classifies 96.7% of the original cases (93.3% after cross-validation; SOM Table S5). Dryopithecines display an intermediate position between orangutans and African apes along the first canonical variate (CV1; Fig. 3a; SOM Table S6). This axis, which explains most of the variance (94%), discriminates between orangutans (very negative scores) and African apes (positive scores), with dryopithecines displaying moderately negative scores. It is mainly driven by dentine horn height (and hence occlusal relief) and other occlusal details, with orangutans displaying toward negative scores lower dentine horns and shallower relief, as well as a relatively broader trigon basin with slightly more peripheral paracone and protocone horns and a more prominent protoconule, and a relatively narrower distal fovea with less peripheral metacone and hypocone horns (Fig. 3a).

In turn, CV2 (6% of variance) only discriminates between chimpanzees (negative scores) and gorillas (generally positive scores), with only minimal overlap with one another but extensive overlap with orangutans at intermediate scores (Fig. 3; SOM Table S6). This axis is driven by the relative width of the occlusal basins, with gorillas displaying relatively narrower foveae with a slightly less peripheral metacone toward positive scores. Along this axis, dryopithecines are intermediate between chimpanzees and gorillas (i.e., they display moderately positive or negative scores), completely overlapping with orangutans and to some extent with either gorillas or chimpanzees. Overall, dryopithecines occupy their own portion of the morphospace—distinct from any extant great ape genus but to a large extent intermediate among them—with extinct genera overlapping along CV1 but not CV2.

Typicality probabilities clearly show that none of the dryopithecine specimens, including IPS41713d, fits well with the variation of any extant taxon (SOM Table S7).

3.2. Principal component analysis

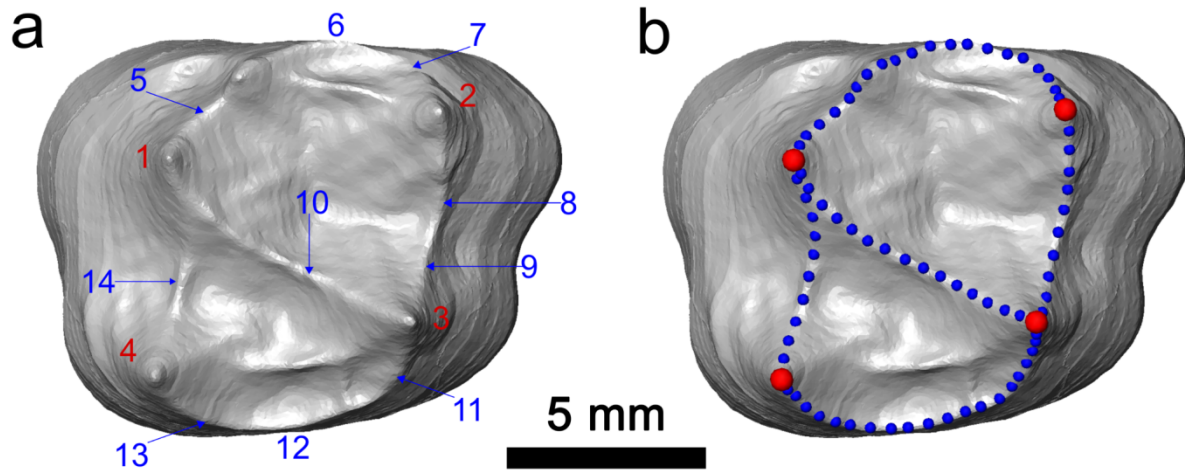
This analysis (Fig. 3b) denotes some differences between Middle and Late Miocene dryopithecines along the first principal component (PC1), which accounts for 31% of variance and is driven by multiple occlusal details, including the arrangement of the main cusps (more peripheral and mesial paracone, more median protocone, and more distal hypocone), the less marked protoconule, and the narrower distal fovea toward negative scores. Along this component, *Hispanopithecus* shows negative PC1 scores while the Middle Miocene specimens display positive or minimally negative scores, with only slight overlap between some specimens of *Anoiapithecus* and the single *H. laietanus* specimen. In turn, PC2 embeds 24% of variance and is driven by different occlusal details than PC1, including the higher paracone, the lower protocone, the more distal metacone with a more oblique crista obliqua, and the relatively shorter distal fovea toward positive scores. This axis separates *Anoiapithecus* (negative scores) from other M¹s, although almost overlapping with the single specimen of *H. laietanus*. The single M¹ of *Dryopithecus* most clearly differs from the rest of the sample by displaying the highest PC1 and PC2 scores, while IPS41713d displays moderately positive PC1 and PC2 scores—the former only overlapping with *Anoiapithecus* and the latter with *Hispanopithecus*. The next two components (PC3 and PC4) explain respectively 15% and 14% of variance but do not clearly discriminate among taxa. All the PC scores are reported in SOM Table S8.



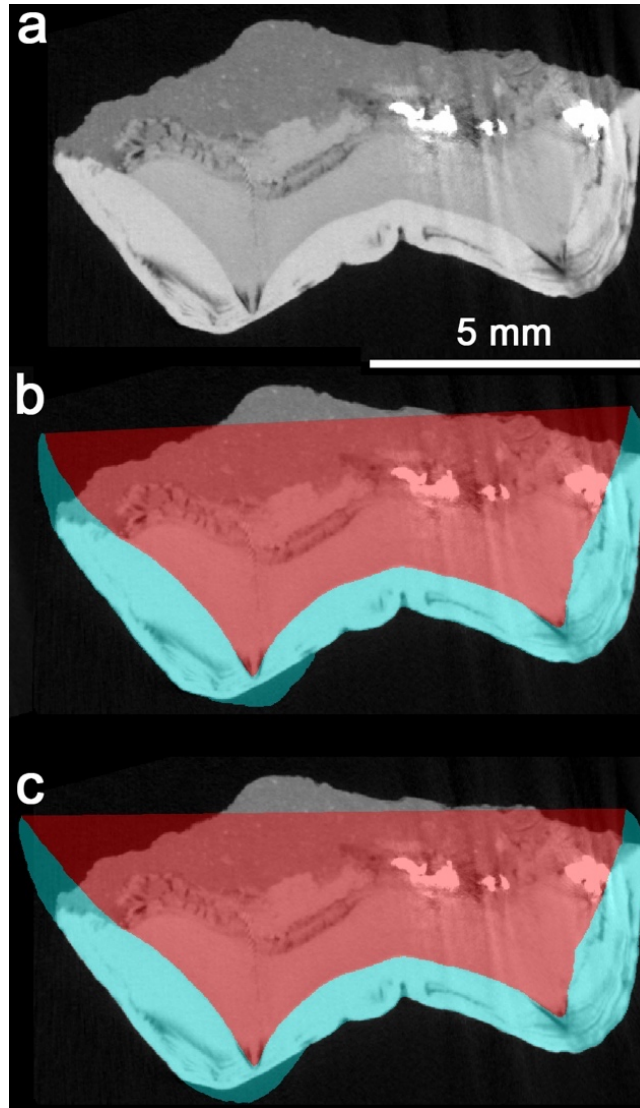
SOM Figure S1. Photograph of the construction of the Can Mata landfill and associated paleontological fieldwork in February 2006, showing the location of localities ACM/C4-Cp and C4-Ap. Photograph © Institut Català de Paleontologia Miquel Crusafont.



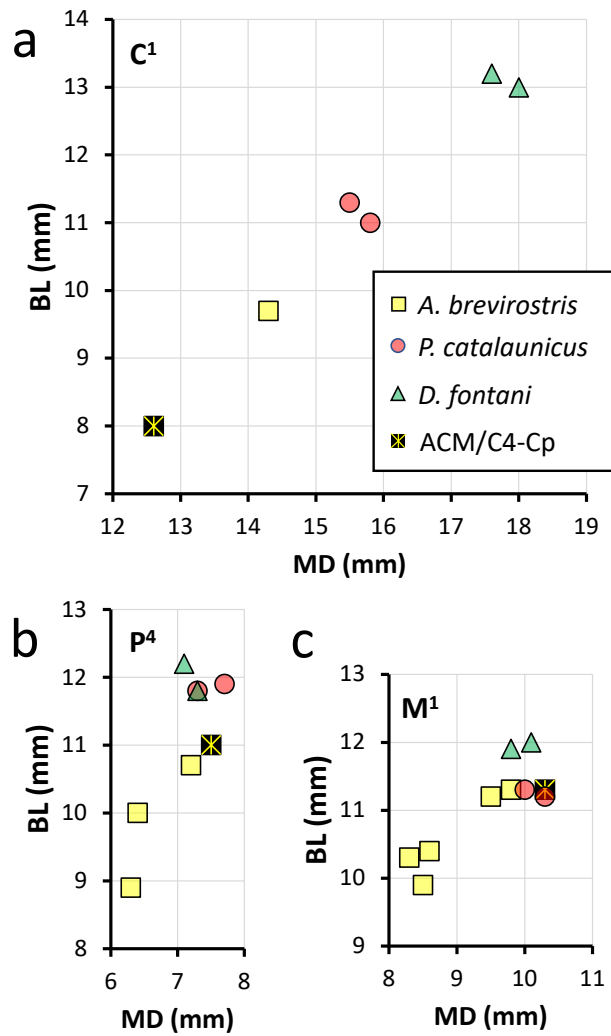
SOM Figure S2. Photograph of the male C¹ IPS41713a as found at the field before being prepared. Photograph © Institut Català de Paleontologia Miquel Crusafont.



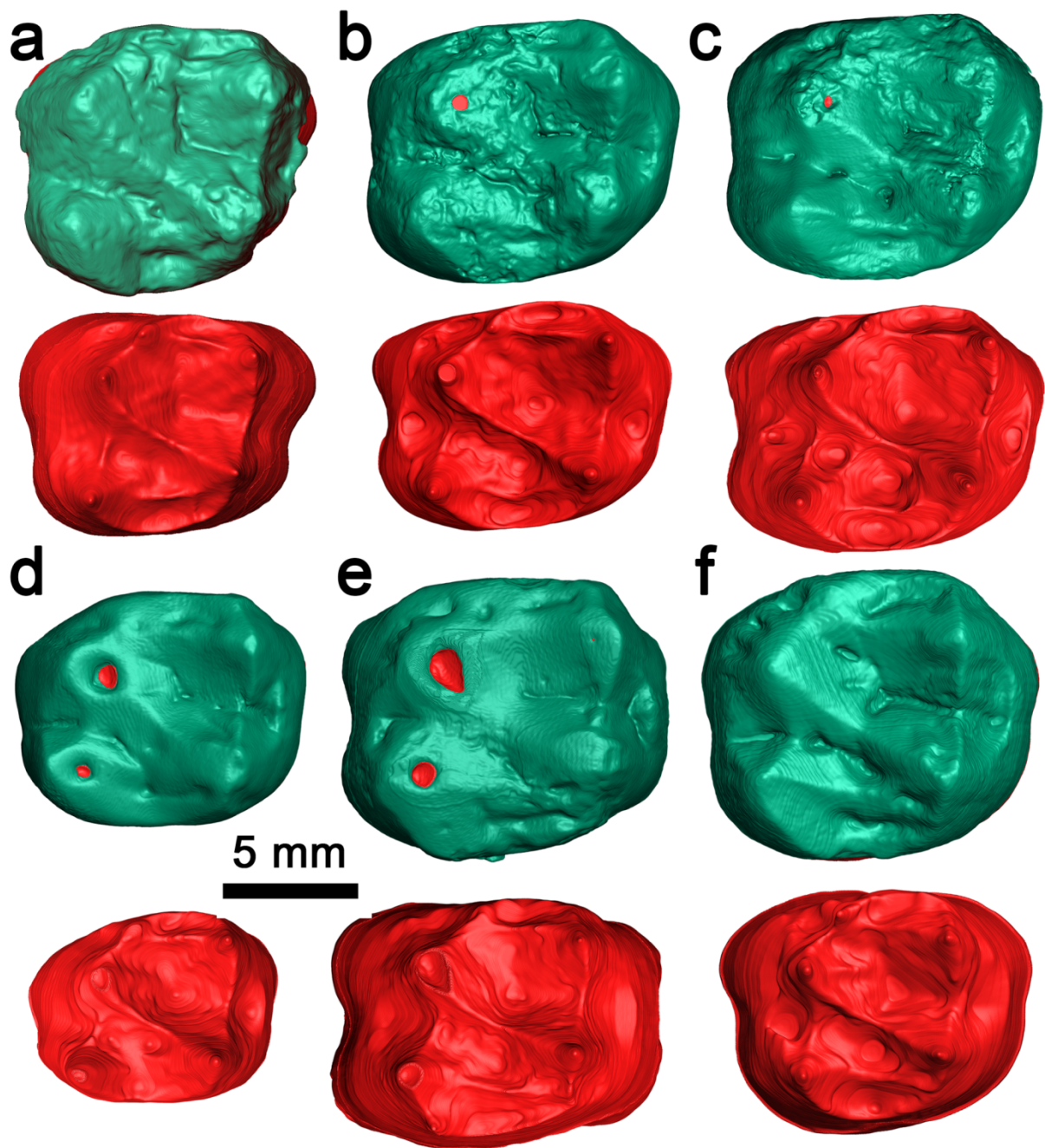
SOM Figure S3. Landmark protocol used for the analysis of M¹ enamel-dentine junction (EDJ) shape in dryopithecines from the Vallès-Penedès Basin, as exemplified by a rendering in occlusal view of the EDJ surface in IPS41713 from ACM/C4-Cp. a) EDJ dentine horns (red numbers) and crests/ridges (blue numbers) used for landmarking. b) Placement of landmarks (red dots) and semilandmarks (blue dots). 1 = protocone; 2 = paracone; 3 = metacone; 4 = hypocone; 5 = preprotocrista; 6 = mesial marginal ridge; 7 = preparacrista; 8 = postparacrista; 9 = premetacrista; 10 = crista obliqua; 11 = postmetacrista; 12 = distal marginal ridge; 13 = posthypocrista; 14 = prehypocrista.



SOM Figure S4. The μ CT buccolingual section of the left M¹ of *Anoiapithecus brevirostris* from ACM/C4-Cp (IPS41713d) used to compute relative enamel thickness, in mesial view (i.e., lingual is on the left): a) virtual section passing through the dentine horn apices of the mesial cusps and perpendicular to the developmental plane; b–c) reconstruction of the enamel (cyan) and dentine (red) in semitransparency and overlapping the aforementioned section, independently performed by C.Z. (b) and F.B. (c).

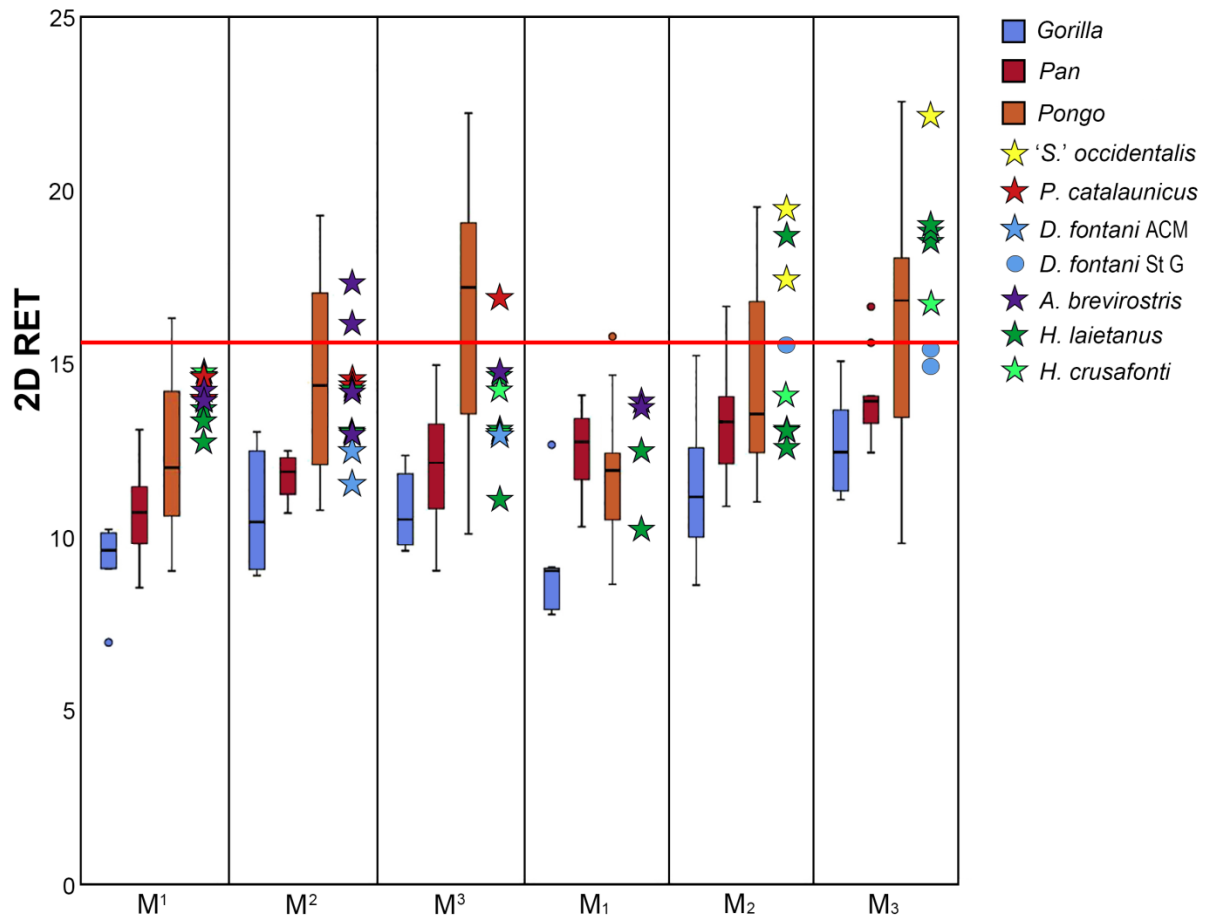


SOM Figure S5. Bivariate plots of buccolingual breadth (BL) vs. mesiodistal length (MD) in the male C^1 (a), the P^4 (b), and the M^1 (c) of *Anoiapithecus brevirostris* from ACM/C4-Cp as compared with other Middle Miocene dryopithecines from the Vallès-Penedès Basin. See SOM Table S1 for measurements.

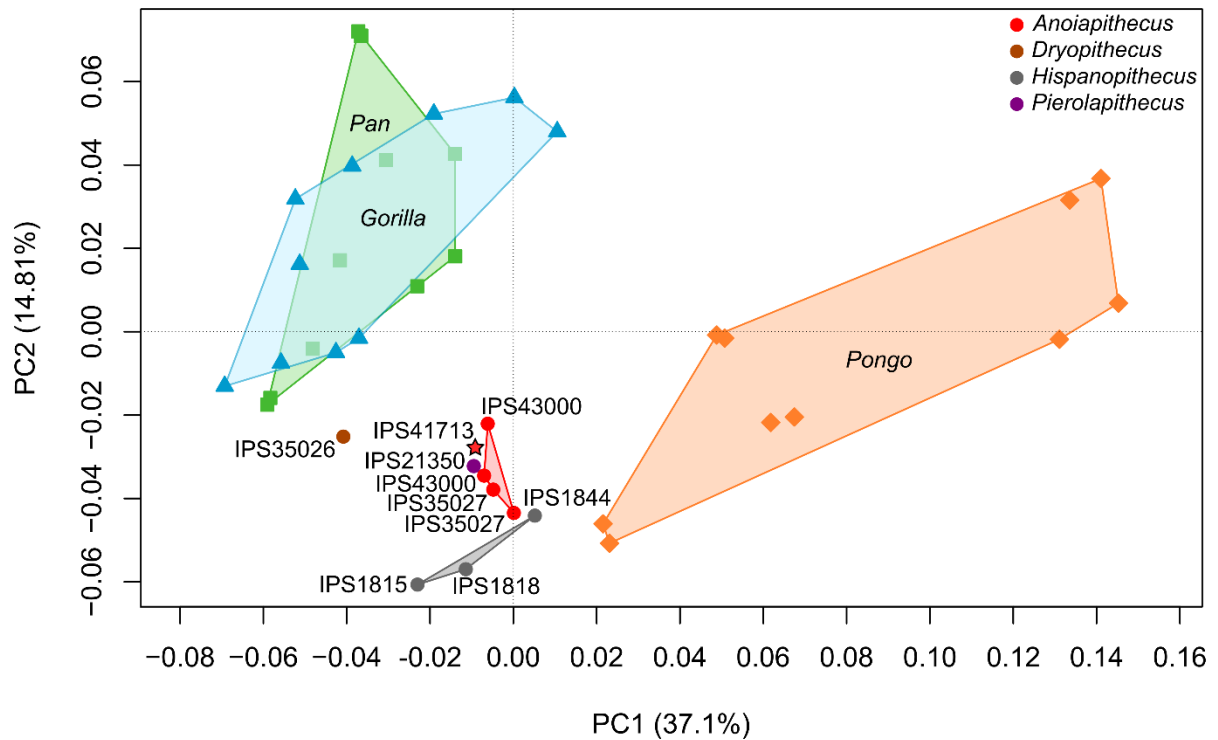


SOM Figure S6. Outer enamel surface (OES, in green) and enamel-dentine junction (EDJ, in red) three-dimensional surface renders of the M¹ of *Anoiapithecus brevirostris* described in this paper as compared with homologous teeth of Middle Miocene dryopithecines from the same area (reproduced from Fortuny et al., 2021: Fig. 4 and Supplementary Fig. 9): a) IPS41713d, left M¹ of *A. brevirostris* from ACM/C4-Cp; b–c) IPS43000 (holotype), left (b) and right (c, reversed) M¹ of *A. brevirostris* from ACM/C3-Aj; d) IPS35027, left M¹ of *A. brevirostris* from ACM/C1-E*; e) IPS35026, left M¹ of *Dryopithecus fontani* from ACM/C3-

Ae; f) IPS21350 (holotype), left M¹ of *Pierolapithecus catalaunicus* from ACM/BCV1. All specimens are depicted as from the left side (indicated when mirrored) in occlusal view (mesial on top).



SOM Figure S7. Box-and-whisker plots of molar two-dimensional relative enamel thickness (2DRET) in the M¹ (IPS41713d) of *Anoiapithecus brevirostris* from ACM/C4-Cp (red horizontal line) as compared with dryopithecines from Spain and southern France as well as extant great apes. Boxes represent the interquartile range (IQR), centerline is the median, whiskers denote the maximum and minimum values within 1.5 times the IQR, and dots are outliers. Abbreviations: ACM = Abocador de Can Mata; St G = Saint-Gaudens.



SOM Figure S8. Principal component (PC) analysis of M¹ enamel-dentine junction shape in extant great ape genera based on the (semi)landmark configuration after Procrustes alignment, with fossil specimens projected a posteriori. Only the first two axes (PC2 vs. PC1, with the percentage of variance accounted by each axis reported within parentheses) are shown. However, the first seven PCs (accounting for 93% of variance) were selected to run the canonical variate analysis depicted in Figure 3a.

SOM Table S1

Measurements^a of left upper tooth series IPS41713 from Abocador de Can Mata locality ACM/C4-Cp as compared with those of the same tooth loci of other dryopithecine specimens from the same area.

Species	Locality	Catalog no.	Tooth locus	Side	MD	BL	BLI	Source ^b
<i>Anoiapithecus brevirostris</i>	ACM/C4-Cp	IPS41713a	C ¹	L	12.6	8.0	63.5	This study
<i>Anoiapithecus brevirostris</i>	ACM/C3-Aj	IPS43000	C ¹	R	14.3	9.7	67.8	Moyà-Solà et al. (2009a)
<i>Pierolapithecus catalaunicus</i>	ACM/BCV1	IPS21350	C ¹	R	15.5	11.3	72.9	Moyà-Solà et al. (2004)
<i>Pierolapithecus catalaunicus</i>	ACM/BCV1	IPS21350	C ¹	L	15.8	11.0	69.6	Moyà-Solà et al. (2004)
<i>Dryopithecus fontani</i>	ACM/C3-Ae	IPS35026	C ¹	R	18.0	13.0	72.2	Moyà-Solà et al. (2009b)
<i>Dryopithecus fontani</i>	ACM/C3-Ae	IPS35026	C ¹	L	17.6	13.2	75.0	Moyà-Solà et al. (2009b)
<i>Dryopithecus fontani</i>	ACM/C4-Ap	IPS41714	C ¹	L	>13.8	12.4	—	Alba and Moyà-Solà (2012) ^c
<i>Anoiapithecus brevirostris</i>	ACM/C4-Cp	IPS41713c	P ³	L	>7.3	>9.9	—	This study
<i>Anoiapithecus brevirostris</i>	ACM/C3-Aj	IPS43000	P ³	L	7.0	11.7	167.1	Moyà-Solà et al. (2009a)
<i>Anoiapithecus brevirostris</i>	ACM/C3-Aj	IPS41712	P ³	L	6.4	9.4	146.9	Alba et al. (2013)
<i>Pierolapithecus catalaunicus</i>	ACM/BCV1	IPS21350	P ³	R	7.9	11.9	150.6	Moyà-Solà et al. (2004)
<i>Pierolapithecus catalaunicus</i>	ACM/BCV1	IPS21350	P ³	L	7.4	11.5	155.4	Moyà-Solà et al. (2004)
<i>Dryopithecus fontani</i>	ACM/C3-Ae	IPS35026	P ³	R	7.5	12.0	160.0	Moyà-Solà et al. (2009b)

<i>Dryopithecus fontani</i>	ACM/C3-Ae	IPS35026	P ³	L	8.0	12.0	152.5	Moyà-Solà et al. (2009b)
<i>Anoiapithecus brevirostris</i>	ACM/C4-Cp	IPS41713b	P ⁴	L	7.5	(11.0)	(146.7)	This study
<i>Anoiapithecus brevirostris</i>	ACM/C3-Aj	IPS43000	P ⁴	R	7.3	>9.2	—	Moyà-Solà et al. (2009a)
<i>Anoiapithecus brevirostris</i>	ACM/C3-Aj	IPS43000	P ⁴	L	7.2	10.7	148.6	Moyà-Solà et al. (2009a)
<i>Anoiapithecus brevirostris</i>	ACM/C3-Aj	IPS41712	P ⁴	L	6.3	8.9	141.3	Alba et al. (2013)
<i>Anoiapithecus brevirostris</i>	ACM/C1-E*	IPS35027	P ⁴	L	6.4	10.0	156.3	Alba et al. (2013)
<i>Pierolapithecus catalaunicus</i>	ACM/BCV1	IPS21350	P ⁴	R	7.7	11.9	154.5	Moyà-Solà et al. (2004)
<i>Pierolapithecus catalaunicus</i>	ACM/BCV1	IPS21350	P ⁴	L	7.3	11.8	161.6	Moyà-Solà et al. (2004)
<i>Dryopithecus fontani</i>	ACM/C3-Ae	IPS35026	P ⁴	R	7.3	11.8	161.6	Moyà-Solà et al. (2009b)
<i>Dryopithecus fontani</i>	ACM/C3-Ae	IPS35026	P ⁴	L	7.1	12.2	171.8	Moyà-Solà et al. (2009b)
<i>Anoiapithecus brevirostris</i>	ACM/C4-Cp	IPS41713d	M ¹	L	10.3	(11.3)	(109.7)	This study
<i>Anoiapithecus brevirostris</i>	ACM/C3-Aj	IPS43000	M ¹	R	9.5	11.2	117.9	Moyà-Solà et al. (2009a)
<i>Anoiapithecus brevirostris</i>	ACM/C3-Aj	IPS43000	M ¹	L	9.8	11.3	115.3	Moyà-Solà et al. (2009a)
<i>Anoiapithecus brevirostris</i>	ACM/C3-Aj	IPS41712	M ¹	L	8.5	9.9	116.5	Alba et al. (2013)
<i>Anoiapithecus brevirostris</i>	ACM/C1-E*	IPS35027	M ¹	R	8.6	10.4	120.9	Alba et al. (2013)
<i>Anoiapithecus brevirostris</i>	ACM/C1-E*	IPS35027	M ¹	L	8.3	10.3	124.1	Alba et al. (2013)
<i>Pierolapithecus catalaunicus</i>	ACM/BCV1	IPS21350	M ¹	R	10.3	11.2	108.7	Moyà-Solà et al. (2004)

<i>Pierolapithecus catalaunicus</i>	ACM/BCV1	IPS21350	M ¹	L	10.0	11.3	113.0	Moyà-Solà et al. (2004)
<i>Dryopithecus fontani</i>	ACM/C3-Ae	IPS35026	M ¹	R	10.1	12.0	118.8	Moyà-Solà et al. (2009b)
<i>Dryopithecus fontani</i>	ACM/C3-Ae	IPS35026	M ¹	L	9.8	11.9	119.0	Moyà-Solà et al. (2009b)
<i>Anoiapithecus brevirostris</i>	ACM/C4-Cp	IPS41713e	M ²	L	>10.3	—	—	This study
<i>Anoiapithecus brevirostris</i>	ACM/C3-Aj	IPS43000	M ²	R	11.3	12.2	109.0	Moyà-Solà et al. (2009a)
<i>Anoiapithecus brevirostris</i>	ACM/C3-Aj	IPS43000	M ²	L	10.9	12.2	111.9	Moyà-Solà et al. (2009a)
<i>Anoiapithecus brevirostris</i>	ACM/C1-E*	IPS35027	M ²	R	9.3	11.7	125.8	Alba et al. (2013)
<i>Anoiapithecus brevirostris</i>	ACM/C1-E*	IPS35027	M ²	L	9.5	11.6	122.1	Alba et al. (2013)
<i>Pierolapithecus catalaunicus</i>	ACM/BCV1	IPS21350	M ²	R	11.3	12.4	109.7	Moyà-Solà et al. (2004)
<i>Pierolapithecus catalaunicus</i>	ACM/BCV1	IPS21350	M ²	L	11.3	12.5	110.6	Moyà-Solà et al. (2004)
<i>Dryopithecus fontani</i>	ACM/C3-Ae	IPS35026	M ²	L	12.7	13.8	108.7	Moyà-Solà et al. (2009b)
<i>Dryopithecus fontani</i>	Can Mata s.l.	MGSB48486	M ²	R	11.4	11.6	101.8	Van der Made and Ribot, 1999

Abbreviations: R = right; L = left; MD = mesiodistal length (in mm); BL = maximum buccolingual (or labiolingual) breadth (in mm); BLI = breadth/length index (in %), computed as $BL / MD \times 100$; ACM = Abocador de Can Mata; BCV1 = Barranc de Can Vila 1; C1 = Cell 1; C3 = Cell 3; C4 = Cell 4.

^a Measurements between parentheses are estimates while those preceded by the ‘greater than’ symbols are lower than the original dimension due to incomplete preservation.

^b All the measurements were taken or confirmed by D.M.A. to ensure consistency, as in some cases there are small discrepancies with those provided in the original descriptions cited in the last column.

^c This specimen was figured and cursorily described by Alba and Moyà-Solà (2012) in response to Pickford (2012), but no measurements were provided by the former.

SOM Table S2

Digital object identifiers (DOIs) of the three-dimensional models of the outer enamel surface (OES) and enamel-dentine junction (EDJ) of the cheek teeth of *Anoiapithecus brevirostris* from ACM/C4-Cp.

Catalog no.	Tooth locus	Type of model	DOI
IPS41713c	P ³	OES	https://doi.org/10.17602/M2/M575286
IPS41713c	P ³	EDJ	https://doi.org/10.17602/M2/M575289
IPS41713b	P ⁴	OES	https://doi.org/10.17602/M2/M575272
IPS41713b	P ⁴	EDJ	https://doi.org/10.17602/M2/M575283
IPS41713d	M ¹	OES	https://doi.org/10.17602/M2/M575292
IPS41713d	M ¹	EDJ	https://doi.org/10.17602/M2/M575295
IPS41713e	M ²	OES	https://doi.org/10.17602/M2/M575299
IPS41713e	M ²	EDJ	https://doi.org/10.17602/M2/M575302

SOM Table S3

Comparative sample of Miocene dryopithecine M¹s from the Vallès-Penedès Basin used in the shape analysis of enamel-dentine junction (available from MorphoSource after Fortuny et al., 2021).

Species	Catalog no.	Side	Site	Age	DOI
<i>A. brevirostris</i>	IPS43000	R	ACM/C3-Aj	12.0 Ma	https://doi.org/10.17602/M2/M166408
<i>A. brevirostris</i>	IPS43000	L	ACM/C3-Aj	12.0 Ma	https://doi.org/10.17602/M2/M166414
<i>A. brevirostris</i>	IPS35027	R	ACM/C1-E*	12.4–12.3 Ma	https://doi.org/10.17602/M2/M166403
<i>A. brevirostris</i>	IPS35027	L	ACM/C1-E*	12.4–12.3 Ma	https://doi.org/10.17602/M2/M166405
<i>D. fontani</i>	IPS35026	L	ACM/C3-Ae	11.9 Ma	https://doi.org/10.17602/M2/M166397
<i>P. catalaunicus</i>	IPS21350	L	ACM/BCV1	12.0 Ma	https://doi.org/10.17602/M2/M166321
<i>H. crusafonti</i>	IPS1815	L	CP1	10.4–10.0 Ma	https://doi.org/10.17602/M2/M166372
<i>H. crusafonti</i>	IPS1818	L	CP1	10.4–10.0 Ma	https://doi.org/10.17602/M2/M166229
<i>H. laietanus</i>	IPS1844	R	CLL1	9.8 Ma	https://doi.org/10.17602/M2/M166318

Abbreviations: DOI = digital object identifier; R = right; L = left; ACM = Abocador de Can Mata macrosite; BCV1 = Barranc de Can Vila 1; C1 = Cell 1; C3 = Cell 3; CLL1 = Can Llobateres 1; CP1 = Can Poncic 1.

SOM Table S4

Measurements taken on the reconstructed M¹ of *Anoiapithecus brevirostris* from ACM/C4-Cp (IPS41713d) to compute enamel thickness.^a

	Reconstruction 1	Reconstruction 2	Average
Enamel area (c, in mm ²)	14.65	14.90	14.78
Dentine and pulp area (b, in mm ²)	30.74	30.43	30.59
Enamel-dentine junction length (e, in mm)	17.20	17.19	17.20
Average enamel thickness (in mm): 2DAET = c / e	0.85	0.87	0.86
Relative enamel thickness (2DRET = 2DAET × 100/b ^{1/2})	15.36	15.72	15.54

^a Measurements were taken from two reconstructions, which were independently performed by C.Z. (reconstruction 1) and F.B. (reconstruction 2; see the virtual sections used in SOM Fig. S4), yielding very similar results. The average values were then used to compute 2DRET.

SOM Table S5

Classification results of the canonical variate analysis of M¹ enamel-dentine junction shape in extant great ape genera ($n = 30$).^a

Without cross validation	<i>Gorilla</i>	<i>Pan</i>	<i>Pongo</i>	Total correct
<i>Gorilla</i>	9 (90.0%)	1 (10.0%)	0 (0.0%)	9 (90.0%)
<i>Pan</i>	0 (0%)	10 (100%)	0 (0.0%)	10 (100%)
<i>Pongo</i>	0 (0%)	0 (0%)	10 (100%)	10 (100%)
Total	9 (30.0%)	11 (36.7%)	10 (33.3%)	29 (96.7%)
With cross validation	<i>Gorilla</i>	<i>Pan</i>	<i>Pongo</i>	Total correct
<i>Gorilla</i>	9 (90.0%)	1 (10.0%)	0 (0%)	9 (90.0%)
<i>Pan</i>	1 (10.0%)	9 (90.0%)	0 (0%)	9 (90%)
<i>Pongo</i>	0 (0%)	0 (0%)	10 (100%)	10 (100%)
Total	10 (33.3%)	10 (33.3%)	10 (33.3%)	28 (93.3%)

^a Percentage classification results are given within parentheses.

^b The total of correctly classified cases is bolded.

SOM Table S6

Canonical variate (CV) scores for IPS41713d from ACM/C4-Cp, other dryopithecines from the Vallès-Penedès Basin, and the centroids of the three groups defined a priori (extant great ape genera) resulting from a canonical variate analysis of M¹ enamel-dentine junction shape. The percentage of variance explained by each CV is reported within parentheses.

Species	Catalog no.	CV1 (93.85%)	CV2 (6.15%)
<i>A. brevirostris</i>	IPS41713	-1.490195	0.463888
<i>A. brevirostris</i>	IPS35027	-5.370976	-0.038744
<i>A. brevirostris</i>	IPS35027	-3.118701	0.335988
<i>A. brevirostris</i>	IPS43000	-2.745946	0.660717
<i>A. brevirostris</i>	IPS43000	-4.467845	0.495539
<i>P. catalaunicus</i>	IPS21350	-3.583646	1.088764
<i>D. fontani</i>	IPS35026	-2.010734	1.417876
<i>H. crusafonti</i>	IPS1815	-4.040992	-0.907053
<i>H. crusafonti</i>	IPS1818	-4.710648	-1.114975
<i>H. laietanus</i>	IPS1844	-4.885182	-0.253428
<i>Gorilla</i> centroid	—	4.266756	1.904310
<i>Pan</i> centroid	—	4.309286	-1.898025
<i>Pongo</i> centroid	—	-8.576042	-0.006286

SOM Table S7

Classification results for IPS41713d from ACM/C4-Cp and other Middle Miocene dryopithecines from the Vallès-Penedès Basin based on a canonical variate analysis of M¹ enamel-dentine junction shape in extant great ape genera, including typicality probabilities^a and the Mahalanobis squared distances to extant group centroids.

Catalog no.	Species	Typicality probabilities		
		<i>Gorilla</i>	<i>Pan</i>	<i>Pongo</i>
IPS41713	<i>A. brevisrostris</i>	<0.01	<0.01	<0.01
IPS35027 (left)	<i>A. brevisrostris</i>	<0.01	<0.01	0.03
IPS35027 (right)	<i>A. brevisrostris</i>	<0.01	<0.01	<0.01
IPS43000 (left)	<i>A. brevisrostris</i>	<0.01	<0.01	<0.01
IPS43000 (right)	<i>A. brevisrostris</i>	<0.01	<0.01	<0.01
IPS35026	<i>D. fontani</i>	<0.01	<0.01	<0.01
IPS1815	<i>H. crusafonti</i>	<0.01	<0.01	<0.01
IPS1818	<i>H. crusafonti</i>	<0.01	<0.01	<0.01
IPS1844	<i>H. laietanus</i>	<0.01	<0.01	0.01
IPS21350	<i>P. catalaunicus</i>	<0.01	<0.01	<0.01

Catalog no.	Species	Distances		
		<i>Gorilla</i>	<i>Pan</i>	<i>Pongo</i>
IPS41713	<i>A. brevisrostris</i>	5.93	6.26	7.10
IPS35027 (left)	<i>A. brevisrostris</i>	9.83	9.85	3.21
IPS35027 (right)	<i>A. brevisrostris</i>	7.55	7.75	5.47
IPS43000 (left)	<i>A. brevisrostris</i>	7.12	7.50	5.87
IPS43000 (right)	<i>A. brevisrostris</i>	8.85	9.10	4.14
IPS35026	<i>D. fontani</i>	6.30	7.13	6.72

IPS1815	<i>H. crusafonti</i>	8.77	8.41	4.62
IPS1818	<i>H. crusafonti</i>	9.47	9.05	4.02
IPS1844	<i>H. laietanus</i>	9.40	9.34	3.70
IPS21350	<i>P. catalaunicus</i>	7.89	8.44	5.11

Abbreviations: R = right; L = left.

^a Typicality probabilities, which add to unity, denote the probability of having the given score assuming the specimen belongs to a particular group, and hence indicate if a fossil specimen fits well with the variation of each extant group (rejected when $p < 0.05$).

SOM Table S8

Principal component (PC) scores for IPS41713d from ACM/C4-Cp and other dryopithecines from the Vallès-Penedès Basin, resulting from a principal component analysis of M¹ enamel-dentine junction shape. The percentage of variance explained by each PC is reported within parentheses.

Species	Catalog no.	PC1 (30.5%)	PC2 (24.0%)	PC3 (15.4%)	PC4 (13.6%)	PC5 (6.0%)	PC6 (4.4%)	PC7 (3.1%)	PC8 (1.9%)	PC9 (1.1%)
<i>A. brevirostris</i>	IPS41713	0.0078740	0.0136901	0.0193508	-0.0337240	-0.0143747	0.0059635	0.0046638	-0.0118356	0.0038692
<i>A. brevirostris</i>	IPS35027	-0.0045621	-0.0454002	0.0270590	0.0158740	0.0102334	-0.0060722	-0.0076233	-0.0094472	-0.0035005
<i>A. brevirostris</i>	IPS35027	-0.0048789	-0.0287682	0.0166910	0.0114523	-0.0021312	0.0068738	0.0162866	0.0102727	0.0065877
<i>A. brevirostris</i>	IPS43000	0.0194095	-0.0124312	-0.0199514	0.0061576	-0.0166729	0.0131280	0.0025595	0.0010361	-0.0115351
<i>A. brevirostris</i>	IPS43000	0.0205686	-0.0069459	-0.0152722	0.0071349	-0.0108491	0.0025095	-0.0196284	0.0036523	0.0087131
<i>P. catalaunicus</i>	IPS21350	0.0315652	0.0029753	0.0018880	-0.0188488	-0.0012008	-0.0263331	0.0022653	0.0074333	-0.0031079
<i>D. fontani</i>	IPS35026	0.0366237	0.0461426	-0.0001280	0.0315652	0.0127305	0.0011791	0.0054048	-0.0048270	0.0011856
<i>H. crusafonti</i>	IPS1815	-0.0505218	0.0372798	0.0257830	0.0015282	-0.0023431	0.0030270	-0.0083608	0.0075355	-0.0040949
<i>H. crusafonti</i>	IPS1818	-0.0537303	-0.0002556	-0.0364222	0.0079002	-0.0040345	-0.0115364	0.0062168	-0.0062058	0.0022849
<i>H. laietanus</i>	IPS1844	-0.0023479	-0.0062867	-0.0189979	-0.0290395	0.0286423	0.0112609	-0.0017843	0.0023857	-0.0004021

SOM References

- Alba, D.M., Moyà-Solà, S., 2012. On the identity of a hominoid male upper canine from the Vallès-Penedès Basin figured by Pickford (2012). *Estud. Geol.* 68, 149–153.
- 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. *J. Hum. Evol.* 65, 573–584.
- Alba, D.M., Fortuny, J., Robles, J.M., Bernardini, F., Pérez de los Ríos, M., Tuniz, C., Moyà-Solà, S., Zanolli, C., 2020. A new dryopithecine mandibular fragment from the middle Miocene of Abocador de Can Mata and the taxonomic status of ‘*Sivapithecus*’ *occidentalis* from Can Vila (Vallès-Penedès Basin, NE Iberian Peninsula). *J. Hum. Evol.* 145, 102790.
- Benazzi, S., Panetta, D., Fornai, C., Toussaint, M., Gruppioni, G., Hublin, J.-J., 2014. Technical Note: Guidelines for the digital computation of 2D and 3D enamel thickness in hominoid teeth. *Am. J. Phys. Anthropol.* 153, 305–313.
- Coleman, M.N., Colbert, M.W., 2007. Technical note: CT thresholding protocols for taking measurements on three-dimensional models. *Am. J. Phys. Anthropol.* 133, 723–725.
- Dray, S., Dufour, A.-B., 2007. The ade4 package: Implementing the duality diagram for ecologists. *J. Stat. Softw.* 22(4), 1–20.
- Fajardo, R.J., Ryan, T.M., Kappelman, J., 2002. Assessing the accuracy of high-resolution X-ray computed tomography of primate trabecular bone by comparisons with histological sections. *Am. J. Phys. Anthropol.* 118, 1–10.
- Fortuny, J., Zanolli, C., Bernardini, F., Tuniz, C., Alba, D.M., 2021. Dryopithecine palaeobiodiversity in the Iberian Miocene revisited on the basis of molar endostructural morphology. *Palaeontology* 64, 531–554.

- Martin, L., 1985. Significance of enamel thickness in hominoid evolution. *Nature* 314, 260–263.
- R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Schlager, S., 2021. Morpho: Calculations and visualizations related to geometric morphometrics. R package version 2.9. <http://cran.r-project.org/web/packages/Morpho/index.html>.
- Smith, T.M., Olejniczak, A.J., Martin, L.B., Reid, D.J., 2005. Variation in hominoid molar enamel thickness. *J. Hum. Evol.* 48, 575–592.
- Smith, T.M., Olejniczak, A.J., Zermeno, J.P., Tafforeau, P., Skinner, M.M., Hoffmann, A., Radovicic, J., Toussaint, M., Kruszynski, R., Menter, C., Moggi-Cecchi, J., Glasmacher, U.A., Kullmer, O., Schrenk, F., Stringer, C., Hublin, J.-J., 2012. Variation in enamel thickness within the genus *Homo*. *J. Hum. Evol.* 62, 395–411.
- Smith, T.M., Tafforeau, P., Pouech, J., Begun, D.R., 2019. Enamel thickness and dental development in *Rudapithecus hungaricus*. *J. Hum. Evol.* 136, 102649.
- Spoor, C.F., Zonneveld, F.W., Macho, G.A., 1993. Linear measurements of cortical bone and dental enamel by computed tomography: Applications and problems. *Am. J. Phys. Anthropol.* 91, 469–484.
- van der Made, J., Ribot, F., 1999. Additional hominoid material from the Miocene of Spain and remarks on hominoid dispersals into Europe. *Contrib. Tert. Quat. Geol.* 36, 25–39.
- Zanoli, C., Bouchet, F., Fortuny, J., Bernardini, F., Tuniz, C., Alba, D.M., 2023. A reassessment of the distinctiveness of dryopithecine genera from the Iberian Miocene based on enamel-dentine junction geometric morphometric analyses. *J. Hum. Evol.* 177, 103326.