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Short Communication

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

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

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25 *brevirostris*, but remained unpublished.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 C<sup>1</sup>–M<sup>2</sup> 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 × 100); to  
34 measure the length of the C<sup>1</sup>, 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 µCT-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 M<sup>1</sup> 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 C<sup>1</sup> (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 P<sub>3</sub>, which would have presumably maintained a  
65 sharp distal margin (although this cannot be unambiguously confirmed due to damage).

66 The upper premolars The P<sup>3</sup> (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  $P^4$  (Fig. 1g, l) is similarly worn but more completely preserved than the  $P^3$  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  $\approx$   
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  $P^3$ , 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  $P^3$  because the crests are less well defined (maybe due to  
86 damage). Also, as in the  $P^3$ , 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  $P^3$ ). 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  $P^4$  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  $P^4$

97 the distal transverse crest fades away clearly before reaching the postprotocrista. In the  $P^4$ ,  
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  $M^1$  (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  $\approx$  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  $M^2$  (Fig. 1i, p)  
126 is entirely comparable to that of the  $M^1$  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 hypoparacrista 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  $M^1$  but not in the  $M^2$ .

137

### 138 3.2. Comparisons

139 The upper canine Among the male  $C^1$  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 C<sup>1</sup>s 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 C<sup>1</sup>s 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 M<sup>1</sup> 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 P<sup>4</sup> due to  
163 the incomplete preservation of the P<sup>3</sup>. The described P<sup>4</sup> (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 P<sup>4</sup>s 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 P<sup>4</sup> 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 cuspule-like 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  $M^1$  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  $M^1$ s 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  $M^1$  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  $M^1$  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 M<sup>1</sup>  
206 from ACM/C4-Cp appears approximately equidistant to *Hispanopithecus laietanus* and the  
207 holotypes of *A. brevirostris* 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 C<sup>1</sup> 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 M<sup>1</sup> due to differential wear. Nevertheless, the M<sup>1</sup> 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 M<sup>1</sup> EDJ shape are not entirely conclusive,

241 but confidently rule out an attribution to *D. fontani*. The P<sup>4</sup> occlusal proportions and contour  
242 further support an attribution to *A. brevirostris*, like the male C<sup>1</sup>, 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. brevirostris* 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 *brevirostris* is warranted.

249

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267

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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 C<sup>1</sup> in occlusal (a), labial (b),  
361 mesial (c), lingual (d), and distal (e) views; f, j, k) IPS41713c, left partial P<sup>3</sup> in occlusal view; g,  
362 l, m) IPS41713b, left P<sup>4</sup> crown in occlusal view; h, n, o) IPS41713d, left M<sup>1</sup> crown in occlusal  
363 view; i, p, q) IPS41713e, left M<sup>2</sup> 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 C<sup>1</sup> (a) and P<sup>3</sup>–M<sup>2</sup> (g) of *Anoiapithecus brevirostris* described in this paper  
369 as compared with male C<sup>1</sup>s (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, P<sup>3</sup>–M<sup>2</sup> of *A. brevirostris* from ACM/C4-Cp; h–i) IPS43000, P<sup>3</sup>–M<sup>2</sup> of *A.*  
375 *brevirostris* (holotype) from ACM/C3-Aj (panel i is reversed); j–k) IPS35027, P<sup>4</sup>–M<sup>1</sup> (j) and  
376 M<sup>1</sup>–M<sup>2</sup> (k, reversed) of *A. brevirostris* from ACM/C1-E\*; l) IPS41712, P<sup>3</sup>–M<sup>1</sup> of *A. brevirostris*  
377 from ACM/C3-Aj; m) MGSB48486, M<sup>2</sup> of *D. fontani* from Can Mata s.l. (reversed); n–o)  
378 IPS35026, P<sup>3</sup>–M<sup>2</sup> (n) and P<sup>3</sup>–M<sup>1</sup> (o, reversed) of *D. fontani* from ACM/C3-Ae; p–q) IPS21350,  
379 P<sup>3</sup>–M<sup>2</sup> 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  $M^1$  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.

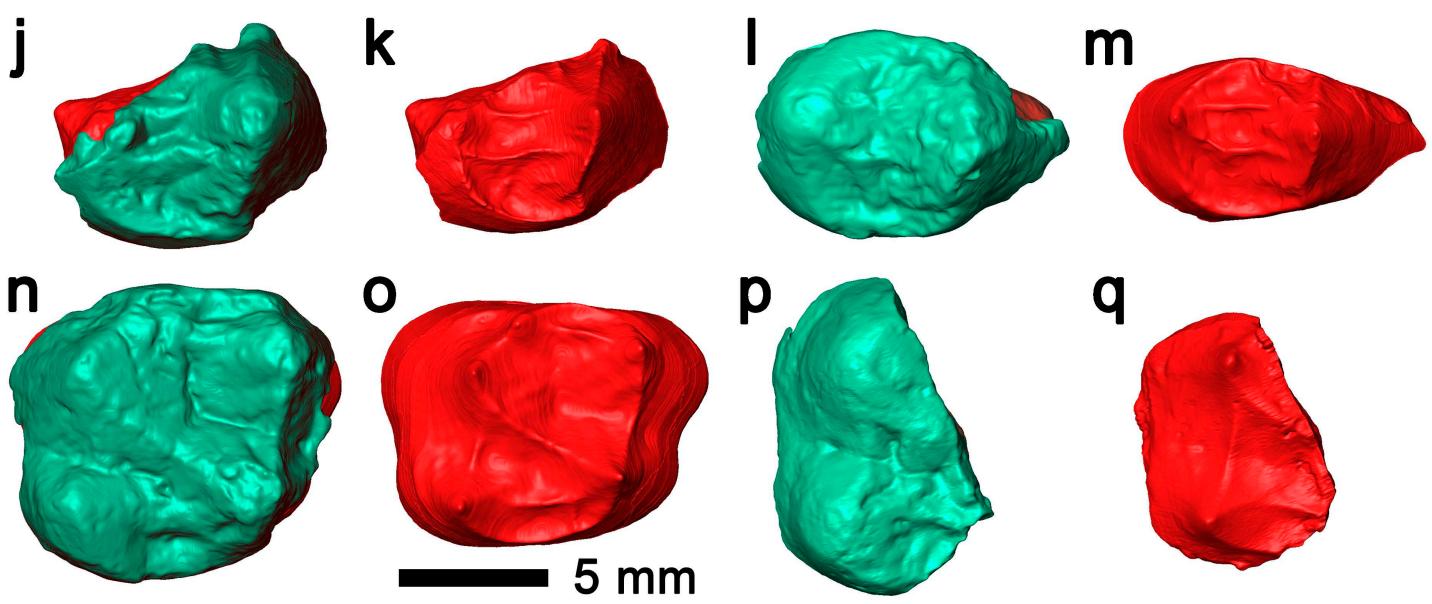
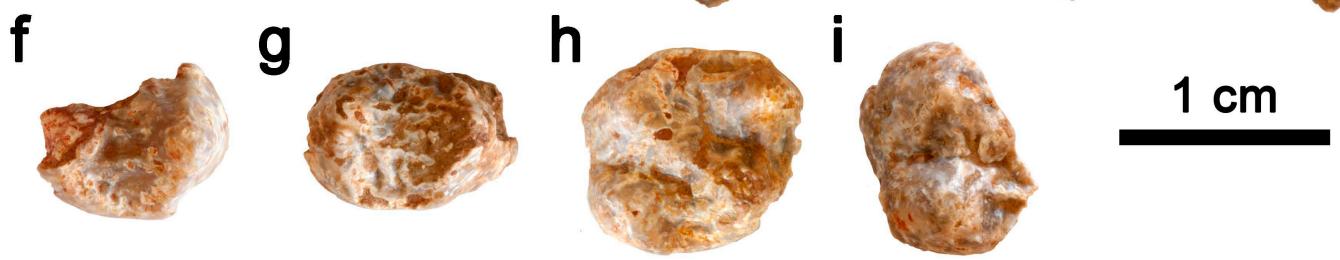
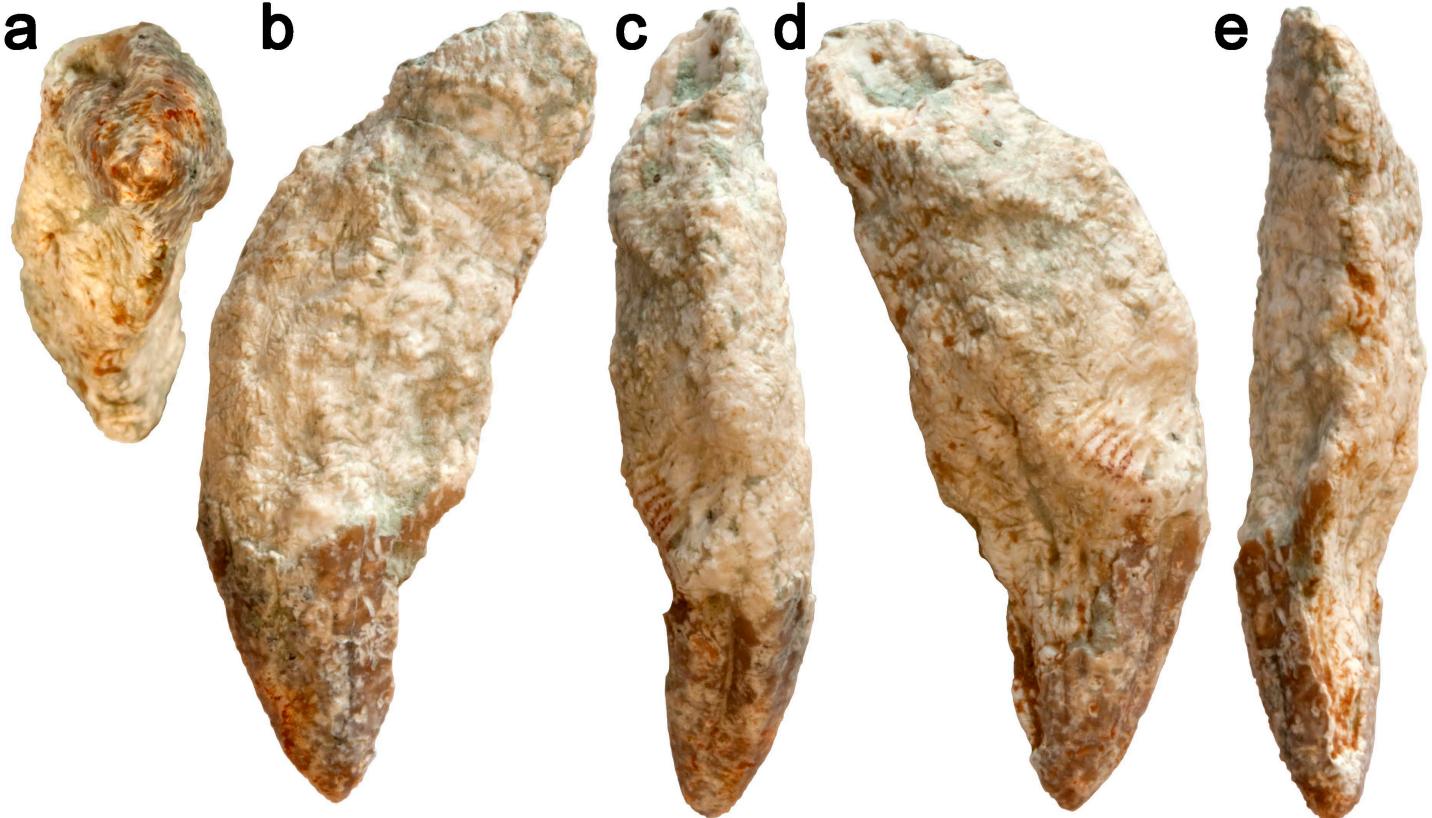
**Table 1**

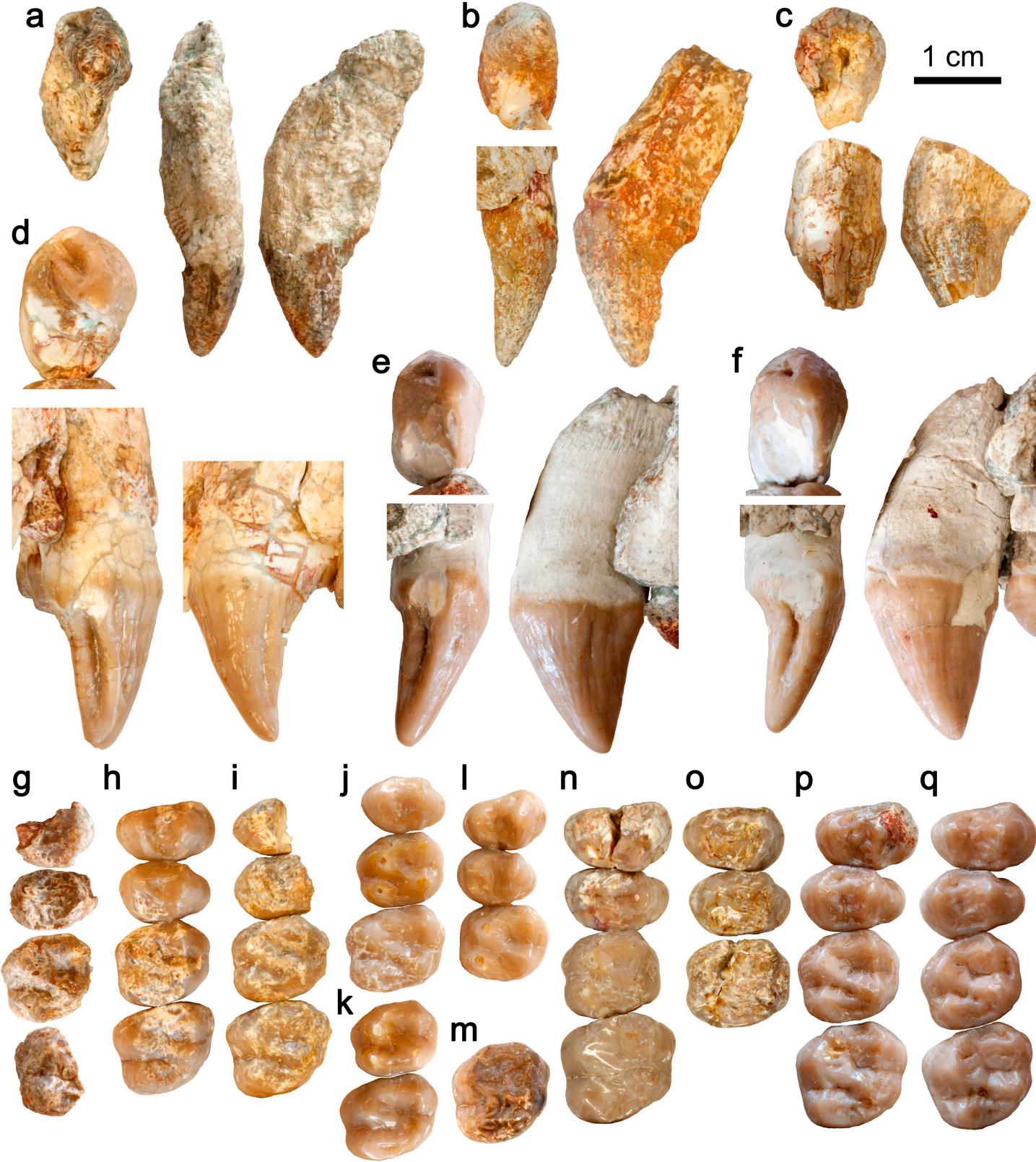
Measurements<sup>a</sup> of left upper tooth series of *Anoiapithecus brevirostris* from ACM/C4-Cp.

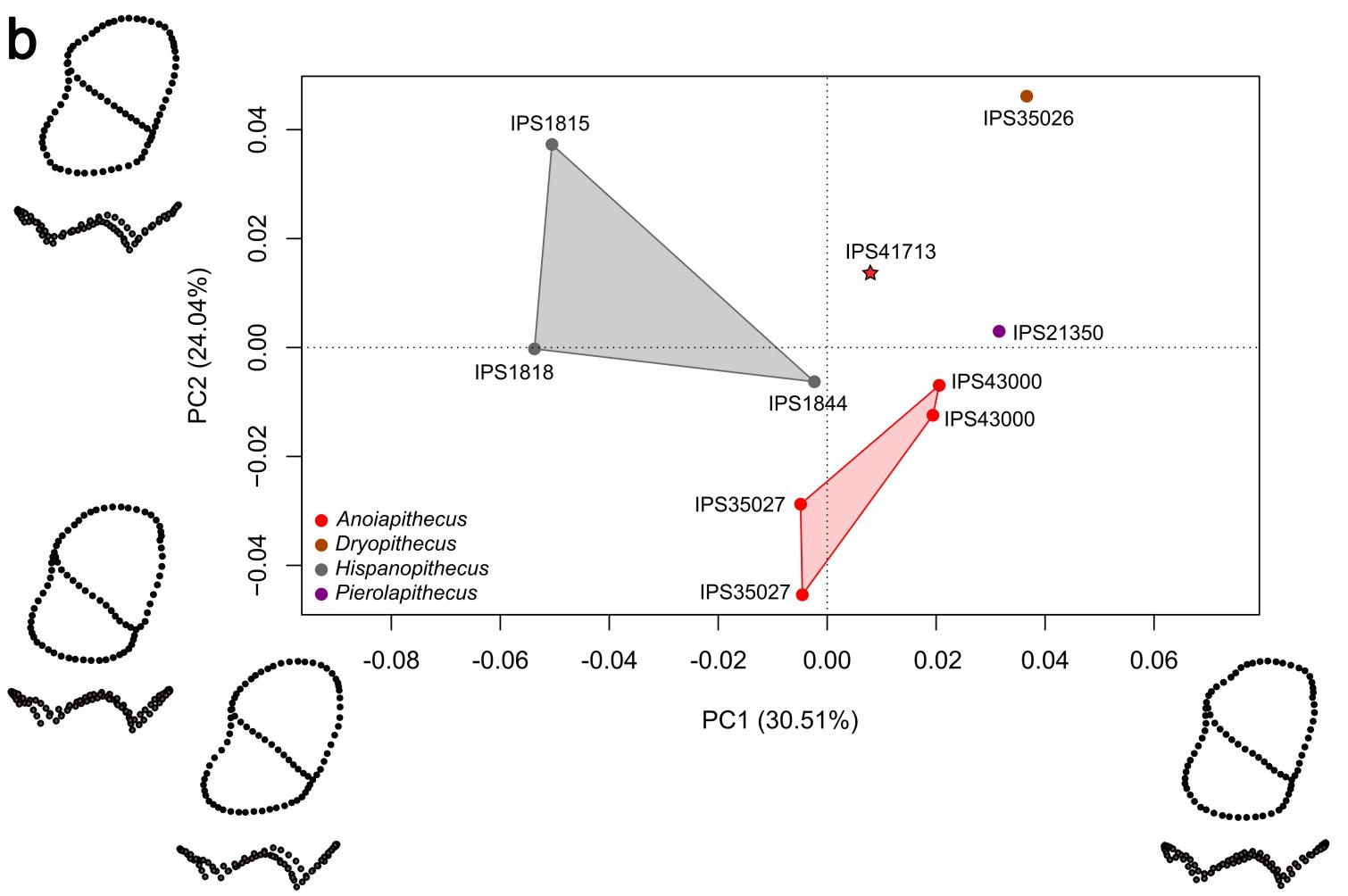
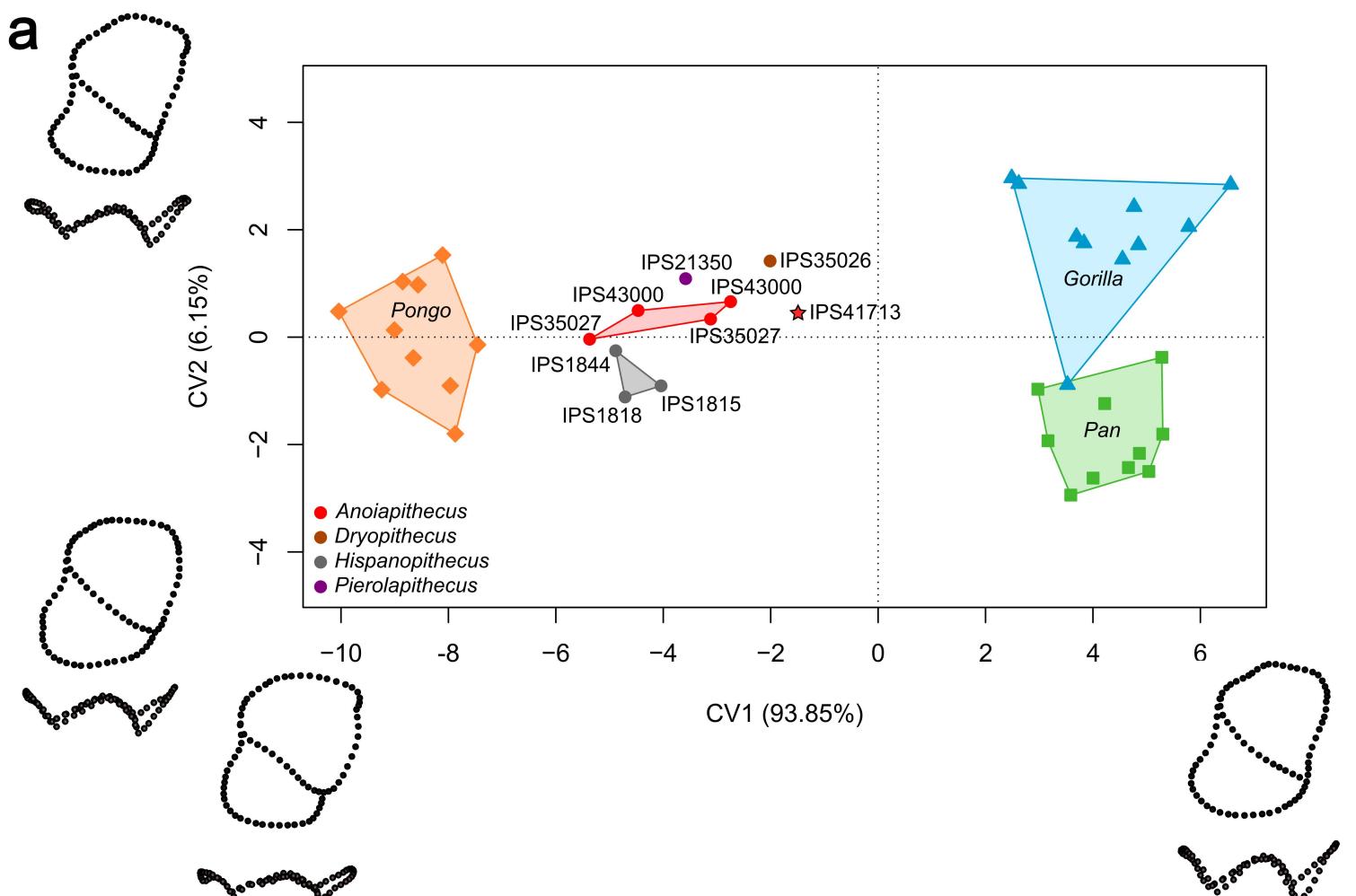
Catalog no.	Tooth locus	MD	BL	BLm	BLd	BLI
IPS41713a	C <sup>1</sup>	12.6	8.0	—	—	63.5
IPS41713c	P <sup>3</sup>	>7.3	>9.9	—	—	—
IPS41713b	P <sup>4</sup>	7.5 (11.0)	—	—	(146.7)	—
IPS41713d	M <sup>1</sup>	10.3 (11.3)	(11.3)	>9.5	(109.7)	—
IPS41713e	M <sup>2</sup>	>10.3	—	—	—	—

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.

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







**Supplementary Online Material (SOM):**

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

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## SOM S1

### Preservation

The dental sample from ACM/C4-Cp includes five isolated specimens from the left side: an almost complete C<sup>1</sup> (IPS41713a), partial P<sup>3</sup> (IPS41713c) and M<sup>2</sup> (IPS41713e) crowns, and almost complete P<sup>4</sup> (IPS41713b) and M<sup>1</sup> (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 C<sup>1</sup> 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 C<sup>1</sup> 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 P<sup>4</sup> and M<sup>1</sup> preserve most of the occlusal surface but are missing most of their basal-most portions toward the cervix, whereas those of the P<sup>3</sup> and M<sup>2</sup> are very incomplete. The P<sup>3</sup> 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 M<sup>2</sup> consists of the buccal half of the crown.

## SOM S2

### Supplementary methods

#### 2.1. Scanning and segmentation

The cheek teeth of IPS41713 were  $\mu$ CT-scanned at the Centro Nacional de Investigación sobre la Evolución Humana in Burgos (Spain) with a high-resolution X-ray  $\mu$ CT scanner model V|Tome|X s 240 (GE Sensing & Inspections Technologies). The  $\mu$ CT acquisition was carried out at 160 kV with a current of 120  $\mu$ A, obtaining a voxel size of 18.50  $\mu$ 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 M<sup>1</sup>s for each of the three living great ape genera *Pan*, *Gorilla*, and *Pongo* (i.e., 30 M<sup>1</sup>s 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

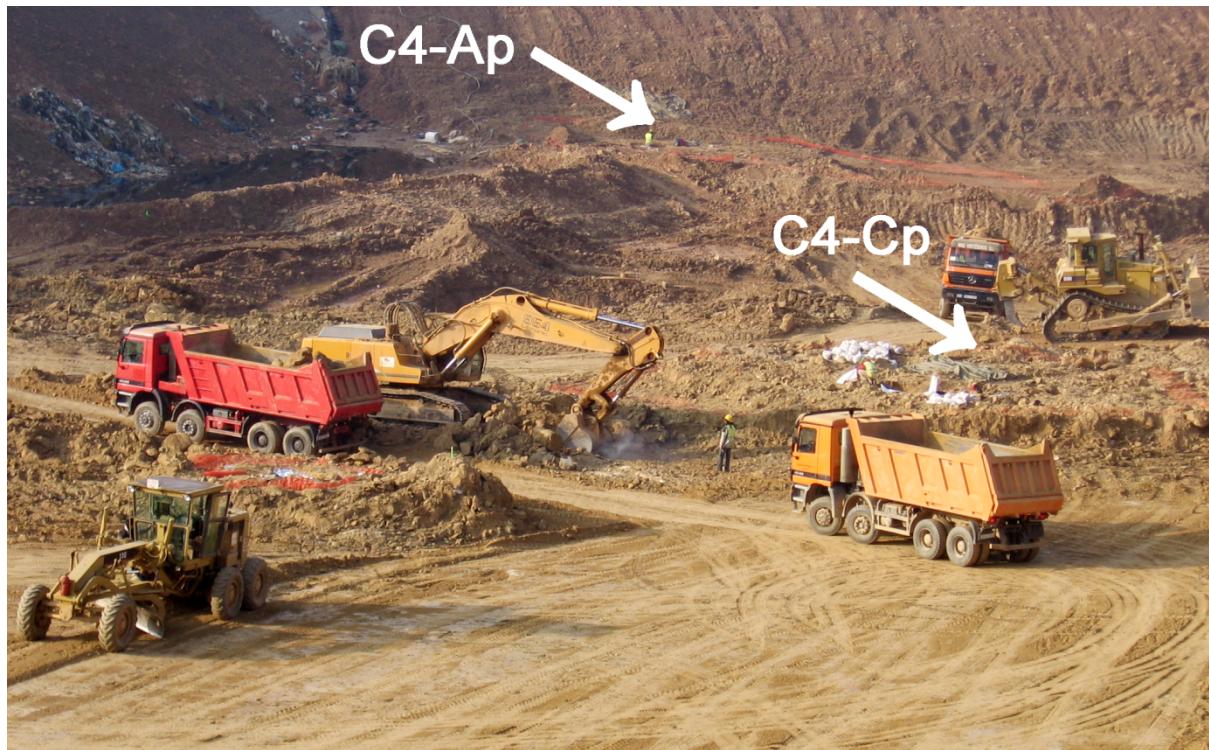
The CVA based on M<sup>1</sup> EDJ shape of extant great ape genera correctly classifies 96.7% of the original cases (93.3% after cross-validation; SOM Table S5). Dryopithecines display an intermediate position between orangutans and African apes along the first canonical variate (CV1; Fig. 3a; SOM Table 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.

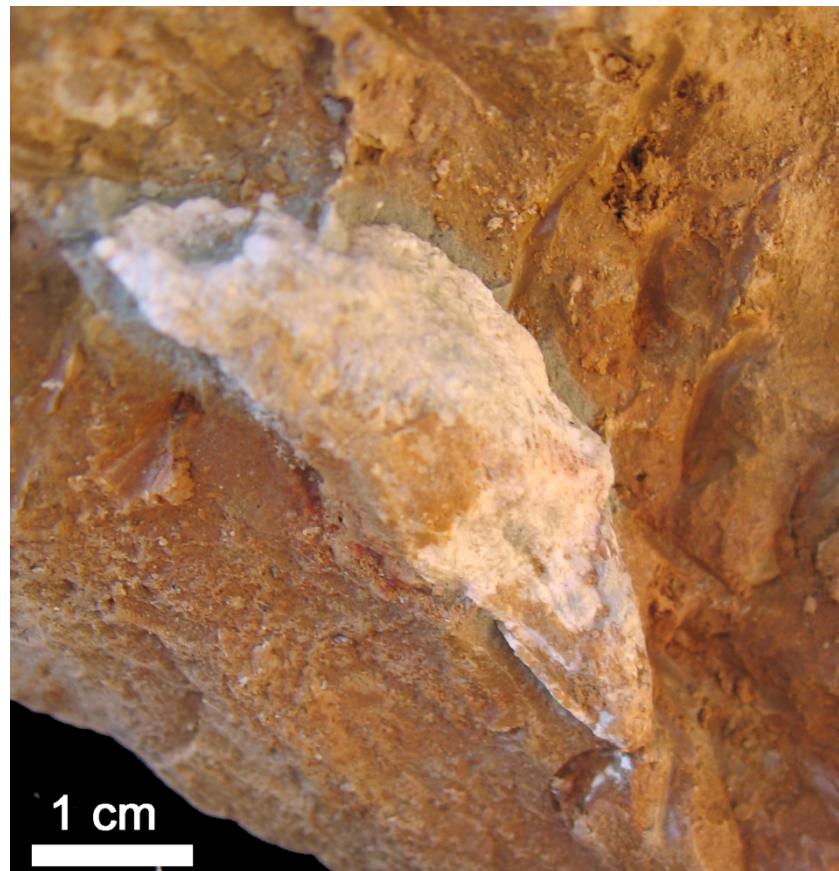
Typicality probabilities clearly show that none of the dryopithecine specimens, including IPS41713d, fits well with the variation of any extant taxon (SOM Table S7).

### 3.2. Principal component analysis

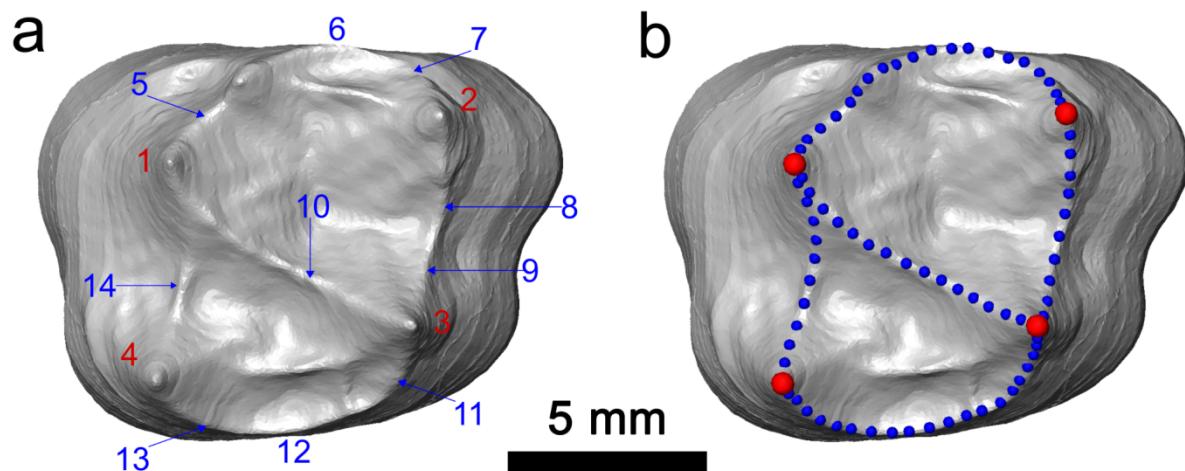
This analysis (Fig. 3b) denotes some differences between Middle and Late Miocene dryopithecines along the first principal component (PC1), which accounts for 31% of variance and is driven by multiple occlusal details, including the arrangement of the main cusps (more peripheral and mesial paracone, more 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 M<sup>1</sup>s, although almost overlapping with the single specimen of *H. laietanus*. The single M<sup>1</sup> 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.



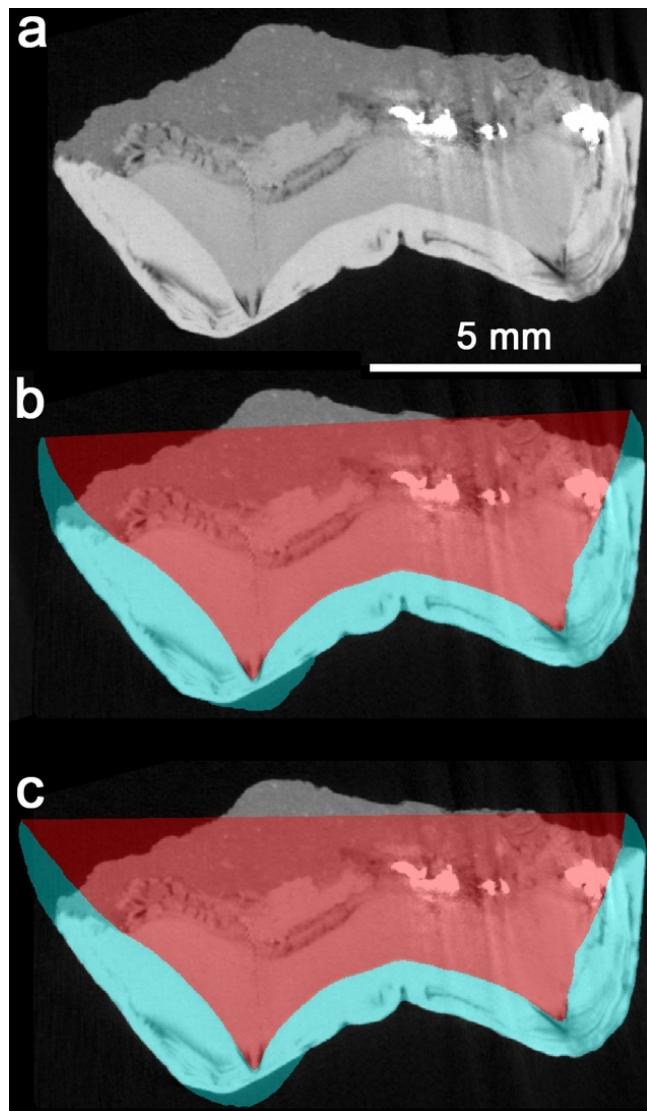
**SOM Figure S1.** Photograph of the construction of the Can Mata landfill and associated paleontological fieldwork in February 2006, showing the location of localities ACM/C4-Cp and C4-Ap. Photograph © Institut Català de Paleontologia Miquel Crusafont.



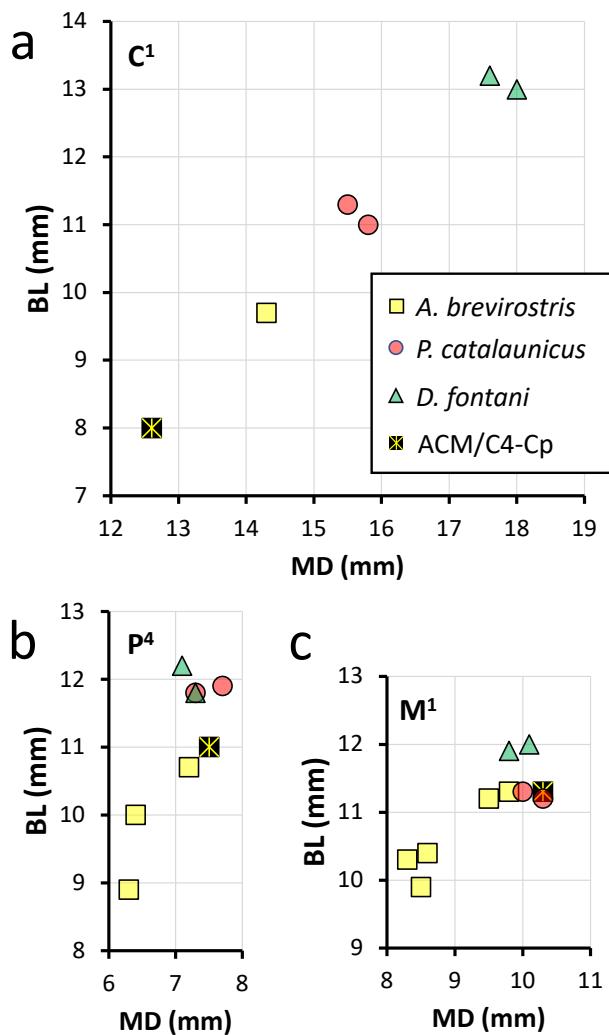
**SOM Figure S2.** Photograph of the male C<sup>1</sup> IPS41713a as found at the field before being prepared. Photograph © Institut Català de Paleontologia Miquel Crusafont.



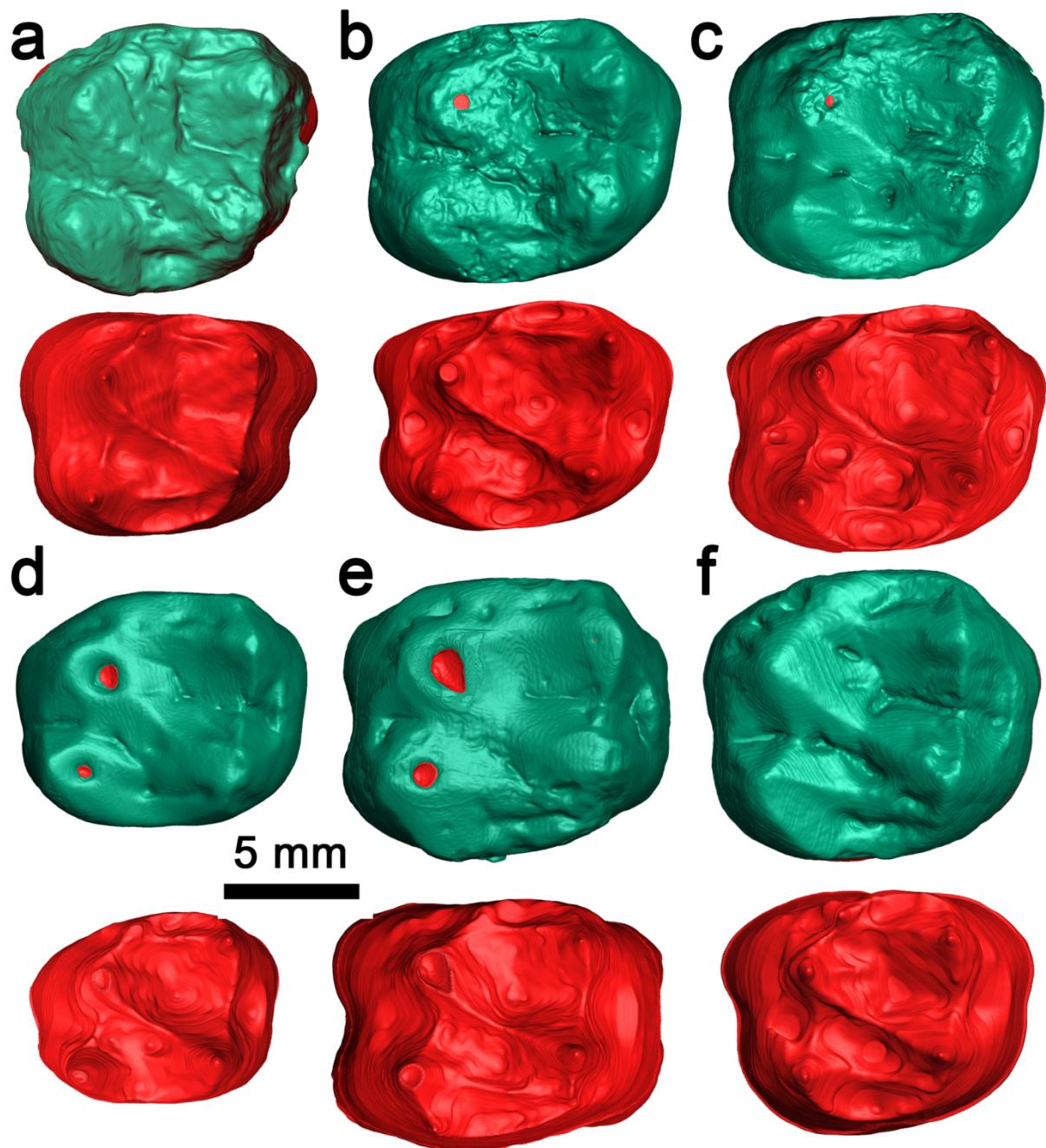
**SOM Figure S3.** Landmark protocol used for the analysis of  $M^1$  enamel-dentine junction (EDJ) shape in dryopithecines from the Vallès-Penedès Basin, as exemplified by a rendering in occlusal view of the EDJ surface in IPS41713 from ACM/C4-Cp. a) EDJ dentine horns (red numbers) and crests/ridges (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 µCT buccolingual section of the left  $M^1$  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).

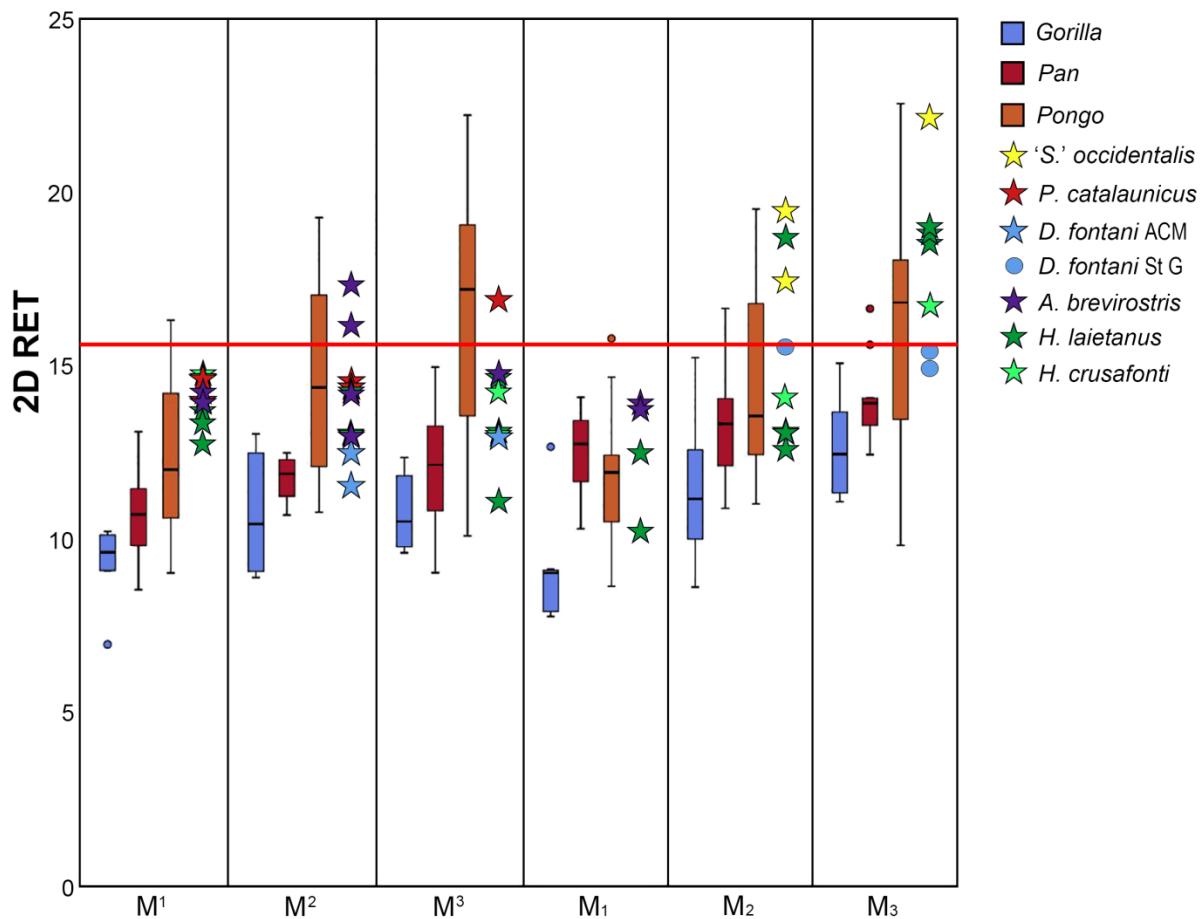


**SOM Figure S5.** Bivariate plots of buccolingual breadth (BL) vs. mesiodistal length (MD) in the male C<sup>1</sup> (a), the P<sup>4</sup> (b), and the M<sup>1</sup> c) of *Anoiapithecus brevirostris* from ACM/C4-Cp as compared with other Middle Miocene dryopithecines from the Vallès-Penedès Basin.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

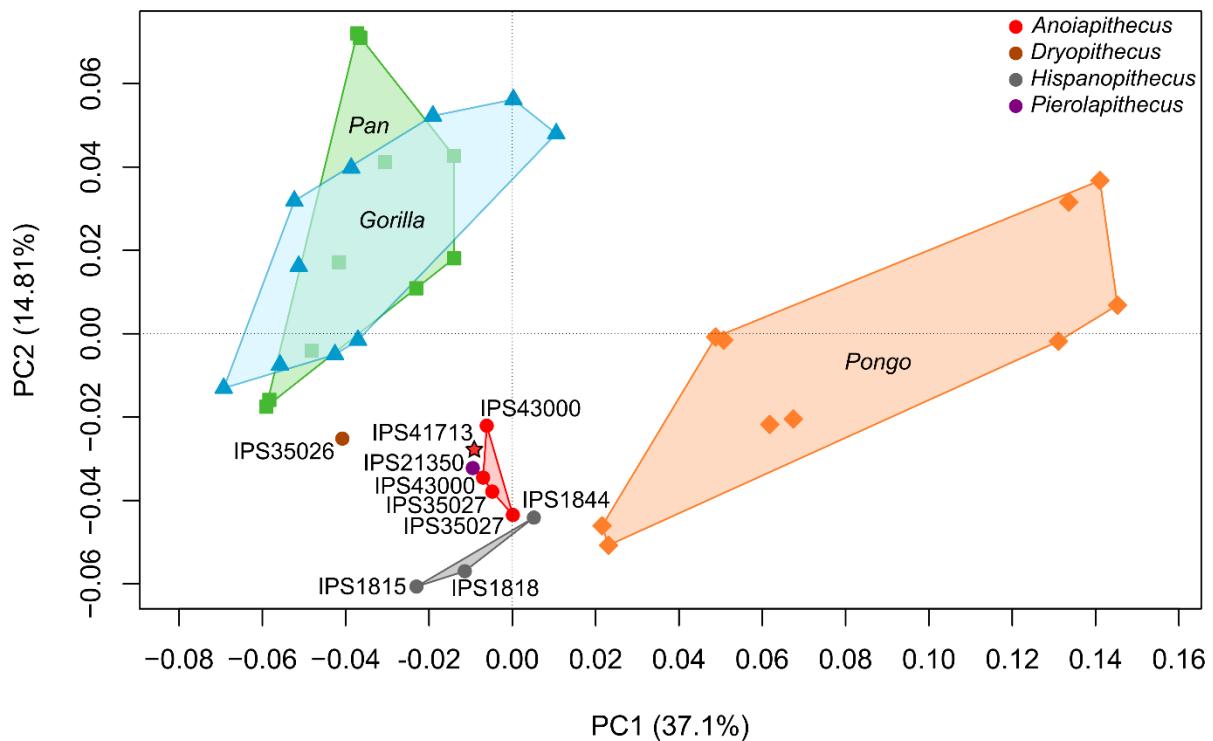


**SOM Figure S6.** Outer enamel surface (OES, in green) and enamel-dentine junction (EDJ, in red) three-dimensional surface renders of the  $M^1$  of *Anoiapithecus brevirostris* described in this paper as compared with homologous teeth of Middle Miocene dryopithecines from the same area (reproduced from Fortuny et al., 2021: Fig. 4 and Supplementary Fig. 9): a) IPS41713d, left  $M^1$  of *A. brevirostris* from ACM/C4-Cp; b–c) IPS43000 (holotype), left (b) and right (c, reversed)  $M^1$  of *A. brevirostris* from ACM/C3-Aj; d) IPS35027, left  $M^1$  of *A. brevirostris* from ACM/C1-E\*; e) IPS35026, left  $M^1$  of *Dryopithecus fontani* from ACM/C3-

Ae; f) IPS21350 (holotype), left  $M^1$  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 M<sup>1</sup> (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  $M^1$  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<sup>a</sup> 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 <sup>b</sup>
<i>Anoiapithecus brevirostris</i>	ACM/C4-Cp	IPS41713a	C <sup>1</sup>	L	12.6	8.0	63.5	This study
<i>Anoiapithecus brevirostris</i>	ACM/C3-Aj	IPS43000	C <sup>1</sup>	R	14.3	9.7	67.8	Moyà-Solà et al. (2009a)
<i>Pierolapithecus catalaunicus</i>	ACM/BCV1	IPS21350	C <sup>1</sup>	R	15.5	11.3	72.9	Moyà-Solà et al. (2004)
<i>Pierolapithecus catalaunicus</i>	ACM/BCV1	IPS21350	C <sup>1</sup>	L	15.8	11.0	69.6	Moyà-Solà et al. (2004)
<i>Dryopithecus fontani</i>	ACM/C3-Ae	IPS35026	C <sup>1</sup>	R	18.0	13.0	72.2	Moyà-Solà et al. (2009b)
<i>Dryopithecus fontani</i>	ACM/C3-Ae	IPS35026	C <sup>1</sup>	L	17.6	13.2	75.0	Moyà-Solà et al. (2009b)
<i>Dryopithecus fontani</i>	ACM/C4-Ap	IPS41714	C <sup>1</sup>	L	>13.8	12.4	—	Alba and Moyà-Solà (2012) <sup>c</sup>
<i>Anoiapithecus brevirostris</i>	ACM/C4-Cp	IPS41713c	P <sup>3</sup>	L	>7.3	>9.9	—	This study
<i>Anoiapithecus brevirostris</i>	ACM/C3-Aj	IPS43000	P <sup>3</sup>	L	7.0	11.7	167.1	Moyà-Solà et al. (2009a)
<i>Anoiapithecus brevirostris</i>	ACM/C3-Aj	IPS41712	P <sup>3</sup>	L	6.4	9.4	146.9	Alba et al. (2013)
<i>Pierolapithecus catalaunicus</i>	ACM/BCV1	IPS21350	P <sup>3</sup>	R	7.9	11.9	150.6	Moyà-Solà et al. (2004)
<i>Pierolapithecus catalaunicus</i>	ACM/BCV1	IPS21350	P <sup>3</sup>	L	7.4	11.5	155.4	Moyà-Solà et al. (2004)
<i>Dryopithecus fontani</i>	ACM/C3-Ae	IPS35026	P <sup>3</sup>	R	7.5	12.0	160.0	Moyà-Solà et al. (2009b)

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

<i>Pierolapithecus catalaunicus</i>	ACM/BCV1	IPS21350	M <sup>1</sup>	L	10.0	11.3	113.0	Moyà-Solà et al. (2004)
<i>Dryopithecus fontani</i>	ACM/C3-Ae	IPS35026	M <sup>1</sup>	R	10.1	12.0	118.8	Moyà-Solà et al. (2009b)
<i>Dryopithecus fontani</i>	ACM/C3-Ae	IPS35026	M <sup>1</sup>	L	9.8	11.9	119.0	Moyà-Solà et al. (2009b)
<i>Anoiapithecus brevirostris</i>	ACM/C4-Cp	IPS41713e	M <sup>2</sup>	L	>10.3	—	—	This study
<i>Anoiapithecus brevirostris</i>	ACM/C3-Aj	IPS43000	M <sup>2</sup>	R	11.3	12.2	109.0	Moyà-Solà et al. (2009a)
<i>Anoiapithecus brevirostris</i>	ACM/C3-Aj	IPS43000	M <sup>2</sup>	L	10.9	12.2	111.9	Moyà-Solà et al. (2009a)
<i>Anoiapithecus brevirostris</i>	ACM/C1-E*	IPS35027	M <sup>2</sup>	R	9.3	11.7	125.8	Alba et al. (2013)
<i>Anoiapithecus brevirostris</i>	ACM/C1-E*	IPS35027	M <sup>2</sup>	L	9.5	11.6	122.1	Alba et al. (2013)
<i>Pierolapithecus catalaunicus</i>	ACM/BCV1	IPS21350	M <sup>2</sup>	R	11.3	12.4	109.7	Moyà-Solà et al. (2004)
<i>Pierolapithecus catalaunicus</i>	ACM/BCV1	IPS21350	M <sup>2</sup>	L	11.3	12.5	110.6	Moyà-Solà et al. (2004)
<i>Dryopithecus fontani</i>	ACM/C3-Ae	IPS35026	M <sup>2</sup>	L	12.7	13.8	108.7	Moyà-Solà et al. (2009b)
<i>Dryopithecus fontani</i>	Can Mata s.l.	MGSB48486	M <sup>2</sup>	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 × 100; ACM = Abocador de Can Mata; BCV1 = Barranc de Can Vila 1; C1 = Cell 1; C3 = Cell 3; C4 = Cell 4.

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

<sup>b</sup> 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.

<sup>c</sup> 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 <sup>3</sup>	OES	<a href="https://doi.org/10.17602/M2/M575286">https://doi.org/10.17602/M2/M575286</a>
IPS41713c	P <sup>3</sup>	EDJ	<a href="https://doi.org/10.17602/M2/M575289">https://doi.org/10.17602/M2/M575289</a>
IPS41713b	P <sup>4</sup>	OES	<a href="https://doi.org/10.17602/M2/M575272">https://doi.org/10.17602/M2/M575272</a>
IPS41713b	P <sup>4</sup>	EDJ	<a href="https://doi.org/10.17602/M2/M575283">https://doi.org/10.17602/M2/M575283</a>
IPS41713d	M <sup>1</sup>	OES	<a href="https://doi.org/10.17602/M2/M575292">https://doi.org/10.17602/M2/M575292</a>
IPS41713d	M <sup>1</sup>	EDJ	<a href="https://doi.org/10.17602/M2/M575295">https://doi.org/10.17602/M2/M575295</a>
IPS41713e	M <sup>2</sup>	OES	<a href="https://doi.org/10.17602/M2/M575299">https://doi.org/10.17602/M2/M575299</a>
IPS41713e	M <sup>2</sup>	EDJ	<a href="https://doi.org/10.17602/M2/M575302">https://doi.org/10.17602/M2/M575302</a>

### SOM Table S3

Comparative sample of Miocene dryopithecine M<sup>1</sup>s 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	<a href="https://doi.org/10.17602/M2/M166408">https://doi.org/10.17602/M2/M166408</a>
<i>A. brevirostris</i>	IPS43000	L	ACM/C3-Aj	12.0 Ma	<a href="https://doi.org/10.17602/M2/M166414">https://doi.org/10.17602/M2/M166414</a>
<i>A. brevirostris</i>	IPS35027	R	ACM/C1-E*	12.4–12.3 Ma	<a href="https://doi.org/10.17602/M2/M166403">https://doi.org/10.17602/M2/M166403</a>
<i>A. brevirostris</i>	IPS35027	L	ACM/C1-E*	12.4–12.3 Ma	<a href="https://doi.org/10.17602/M2/M166405">https://doi.org/10.17602/M2/M166405</a>
<i>D. fontani</i>	IPS35026	L	ACM/C3-Ae	11.9 Ma	<a href="https://doi.org/10.17602/M2/M166397">https://doi.org/10.17602/M2/M166397</a>
<i>P. catalaunicus</i>	IPS21350	L	ACM/BCV1	12.0 Ma	<a href="https://doi.org/10.17602/M2/M166321">https://doi.org/10.17602/M2/M166321</a>
<i>H. crusafonti</i>	IPS1815	L	CP1	10.4–10.0 Ma	<a href="https://doi.org/10.17602/M2/M166372">https://doi.org/10.17602/M2/M166372</a>
<i>H. crusafonti</i>	IPS1818	L	CP1	10.4–10.0 Ma	<a href="https://doi.org/10.17602/M2/M166229">https://doi.org/10.17602/M2/M166229</a>
<i>H. laietanus</i>	IPS1844	R	CLL1	9.8 Ma	<a href="https://doi.org/10.17602/M2/M166318">https://doi.org/10.17602/M2/M166318</a>

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  $M^1$  of *Anoiapithecus brevirostris* from ACM/C4-Cp (IPS41713d) to compute enamel thickness.<sup>a</sup>

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

<sup>a</sup> 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  $M^1$  enamel-dentine junction shape in extant great ape genera ( $n = 30$ ).<sup>a</sup>

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%)	<b>29 (96.7%)</b>

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%)	<b>28 (93.3%)</b>

<sup>a</sup> Percentage classification results are given within parentheses.

<sup>b</sup> 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  $M^1$  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 M<sup>1</sup> enamel-dentine junction shape in extant great ape genera, including typicality probabilities<sup>a</sup> 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. brevirostris</i>	<0.01	<0.01	<0.01
IPS35027 (left)	<i>A. brevirostris</i>	<0.01	<0.01	0.03
IPS35027 (right)	<i>A. brevirostris</i>	<0.01	<0.01	<0.01
IPS43000 (left)	<i>A. brevirostris</i>	<0.01	<0.01	<0.01
IPS43000 (right)	<i>A. brevirostris</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. brevirostris</i>	5.93	6.26	7.10
IPS35027 (left)	<i>A. brevirostris</i>	9.83	9.85	3.21
IPS35027 (right)	<i>A. brevirostris</i>	7.55	7.75	5.47
IPS43000 (left)	<i>A. brevirostris</i>	7.12	7.50	5.87
IPS43000 (right)	<i>A. brevirostris</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

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Abbreviations: R = right; L = left.

<sup>a</sup> 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  $M^1$  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

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