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1 Short Communication

2 A new dryopithecine mandibular fragment from the middle Miocene of Abocador de Can
3 Mata and the taxonomic status of ‘*Sivapithecus*’ *occidentalis* from Can Vila (Vallès-Penedès
4 Basin, NE Iberian Peninsula)

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29

30 **Keywords:** Hominoidea; Dryopithecinae; Fossil apes; Relative enamel thickness; Dentine-
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32

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7 enamel junction; *Dryopithecus fontani*

8

9 1. Introduction

10 The Miocene vertebrate record from the Vallès-Penedes Basin (NE Iberian Peninsula;
11 Casanovas-Vilar et al., 2016a) differs from that of inner Iberian basins by the presence of
12 fossil hominoids (Alba, 2012; Marigó et al., 2014) as a result of moister and more forested
13 environments during the late Aragonian and Vallesian (ca. 12.6–8.9 Ma; Casanovas-Vilar et
14 al., 2008, 2016a, b; Marmi et al., 2012; Alba et al., 2018). However, until a couple of decades
15 ago the Aragonian hominoid remains from this basin were very scarce¹, including a molar
16 crown fragment from Trinxera del Ferrocarril-Sant Quirze, an M² from Can Mata s.l., a C₁ of
17 a female individual from Can Mata 1, and a left mandibular fragment with M₂–M₃ and lower
18 molar germ fragment from Can Vila (Supplementary Online Material [SOM] Table S1 and
19 references therein). Villalta Comella and Crusafont Pairó (1941) first attributed the Can Vila
20 specimen to *Dryopithecus fontani* Lartet, 1856. However, soon thereafter the same authors
21 erected *Sivapithecus occidentalis* Villalta Comella and Crusafont Pairó, 1944 based on
22 distinctive features such as “the buccolingual convergence of the cusps”, the “elongate and
23 narrow lower molars”, and the presence of “secondary cusps on the lingual crest

¹ The postcranial hominoid remains from Castell de Barberà (Alba et al., 2011; Almécija et al., 2012) are not counted here because they are currently dated to the earliest Vallesian (11.2 Ma; Alba et al., 2019a).

24 [=postmetacristid]” (Villalta Comella and Crusafont Pairó, 1944: 115 and 118, our translation
25 from the original in Spanish). This species has been considered a junior subjective synonym
26 of *Hispanopithecus laietanus* Villalta Comella and Crusafont Pairó, 1944 (formerly also in
27 *Dryopithecus*) by many authors, or most recently a nomen dubium (e.g., Moyà-Solà et al.,
28 2004, 2009a; Alba, 2012), only with few exceptions (Begun, 2009; Pickford, 2012; see SOM
29 Table S1 for further details).

30 The huge sampling effort at the middle to late Miocene stratigraphic section of Abocador
31 de Can Mata (ACM), at els Hostalets de Pierola (Alba et al., 2006, 2017) has uncovered a
32 previously unsuspected diversity of primates from 12.4 to 11.6 Ma (Alba et al., 2017). They
33 include small-bodied catarrhines (Alba et al., 2010a, 2012a, 2015; Alba and Moyà-Solà,
34 2014; Urciuoli et al., 2018) as well as three species of dryopithecine great apes (Moyà-Solà et
35 al., 2004, 2009a, b; Almécija et al., 2009; Casanovas-Vilar et al., 2011; Alba, 2012; Alba and
36 Moyà-Solà, 2012; Pérez de los Ríos et al., 2012; Alba et al., 2013, 2017; Hammond et al.,
37 2013; Marigó et al., 2014; Pina et al., 2014): *Pierolapithecus catalaunicus* Moyà-Solà et al.,
38 2004 at 12.0 Ma; *Anoiapithecus brevirostris* Moyà-Solà et al., 2009b at 12.4–12.0 Ma; and *D.*
39 *fontani* at 11.9 Ma. Their distinction at the genus rank—initially questioned by Begun and
40 colleagues (Begun 2009, 2010, 2015; Begun et al. 2012), but subsequently accepted by others
41 (e.g., Pickford, 2012; Fleagle, 2013; Böhme et al., 2019; Andrews, 2020)—is mostly based on
42 cranial differences (Moyà-Solà et al., 2004, 2009a,b; Alba, 2012; Pérez de los Ríos et al.,
43 2012) but further supported by dental morphology (Alba et al., 2010b, 2013; Alba and Moyà-
44 Solà 2012; Alba et al., 2013; Pérez de los Ríos et al., 2013; Fortuny et al., 2014).

45 Moyà-Solà et al. (2004) first proposed to consider ‘*S.*’ *occidentalis* as a nomen dubium due
46 to its previous synonymization with *H. laietanus* and uncertainties about its exact provenance
47 (and age)—given the vague indications provided by Villalta Comella and Crusafont Pairó
48 (1941)—which contrast with the accurate dating of ACM localities (Casanovas-Vilar et al.,

49 2011, 2016b; Alba et al., 2017). Subsequently it has been noted (Jordi Martinell, pers. comm.
50 in Alba et al., 2013 and Marigó et al., 2014) that Can Vila would have been located within the
51 same ravine as ACM/BCV1 (the type locality of *P. catalaunicus*, dated to 12.0 Ma with an
52 interpolated age of 11.96 Ma; Alba et al., 2017), albeit in somewhat lower stratigraphic levels,
53 implying an age of ca. 12.0 Ma. However, deciphering the taxonomic status of ‘*S.*’
54 *occidentalis* is still hindered by the distinction of multiple roughly coeval genera at ACM (see
55 above). To shed new light on this question, we describe a hominoid mandibular fragment with
56 M₂ from yet another locality from the same ravine (ACM/BCV4), which is located 5 m above
57 ACM/BCV1 (interpolated age of 11.94 Ma; Alba et al., 2017). Although previously
58 mentioned in some papers—either as unassigned to genus (Casanovas-Vilar et al., 2011;
59 Alba, 2012; Marigó et al., 2014) or tentatively attributed to cf. *P. catalaunicus* (Alba et al.,
60 2017)—the ACM/BCV4 specimen is first described and figured here (for a preliminary report
61 in abstract form, see Alba et al., 2019b). Based on outer enamel surface (OES) and enamel-
62 dentine junction (EDJ) morphology, together with 2D relative enamel thickness (RET), we
63 compare this specimen with the holotype of ‘*S.*’ *occidentalis*, other ACM dryopithecines, and
64 *D. fontani* from its type locality in order to evaluate the taxonomic affinities of the former and
65 revisit the taxonomic status of ‘*S.*’ *occidentalis*.

66

67 **2. Materials and methods**

68 The newly described specimen (IPS41734), the ‘*S.*’ *occidentalis* holotype
69 (IPS1826+1827), and the comparative sample from ACM (Moyà-Solà et al., 2004, 2009a, b;
70 Alba et al., 2013) are housed at the Institut Català de Paleontologia Miquel Crusafont.
71 Comparative material further includes a right M² (MGSB48486) of *D. fontani* from Can Mata
72 s.l. (van der Made and Ribot, 1999; Alba et al., 2013: Fig. 3V), housed at the Museu de
73 Geologia del Seminari de Barcelona (MGSB), Spain, and all of the available lower molars of

74 *D. fontani* from Saint-Gaudens (type locality). These include the holotype mandible HGP2
75 (Lartet, 1856; Begun, 2002: Fig. 20.3B, D) and the Gaudry mandible HGP1 (Gaudry, 1890;
76 Begun, 2002: Fig. 20.3A, C), housed at the Muséum National d'Histoire Naturelle (MNHN),
77 Paris, France, as well as a partial mandible (Harlé 44) and two isolated molars (Harlé 46 and
78 47; Harlé, 1898, 1899: Pl. VI; Begun, 2002: Fig. 20.3F), housed at the Muséum d'Histoire
79 Naturelle de Bordeaux (MHNB), France. Extant comparative material was measured by
80 D.M.A. at the American Museum of Natural History (AMNH), New York, USA. Mesiodistal
81 length (MD) and buccolingual breadth (BL) were measured to the nearest 0.1 mm by D.M.A.,
82 M.P.R., and C.Z, and a breadth/length index (BLI, in %) was computed (see SOM Table S1).
83 Dental terminology (SOM Fig. S1) follows Harrison and Gu (1999).

84 To inspect the EDJ morphology and measure RET, IPS41734 and IPS1826+1827, the
85 holotype of *A. brevirostris* (IPS43000), MGSB48486, and the Harlé specimens of *D. fontani*
86 were imaged by microfocus X-ray μ CT (see SOM S1 for further details). 2D RET was
87 computed from mesial coronal virtual sections following Martin (1983, 1985; see also Smith
88 et al., 2005 and SOM S1). RET values for the studied specimens were compared with data
89 previously reported for ACM dryopithecines (Alba et al., 2013) as well as extant great apes
90 and other Miocene great apes (Smith et al., 2019, and references therein; Böhme et al., 2019).
91 Differences were tested by means of analysis of variance (ANOVA) and Kruskal-Wallis test
92 for equality of medians (a non-parametric alternative that does not assume normality), with
93 post hoc pairwise comparisons based on Tukey's and Dunn's tests, respectively. Statistical
94 computations and box plots (interpolation method) were made with PAST v. 3.24 (Hammer et
95 al., 2001).

96

97 **3. Results**

98 *3.1. Morphology of the OES*

99 Description IPS41734 is a right mandibular fragment that preserves the M₁ roots (broken at
100 the cervix, 8.4 × 8.2 mm), the socketed M₂, and the mesial root of the M₃ (Fig. 1a–c).

101 Mandibular corpus depth cannot be reliably measured (>19 mm), while corpus width
102 increases laterally from mesial M₁ level (13 mm) to M₂–M₃ level (17 mm).

103 The M₂ (Figs. 1d–h and 2a; SOM File S1) is only slightly worn. It displays a Y5 occlusal
104 pattern, with five main cuspids and a conspicuous groove pattern in which the hypoconid base
105 contacts the bases of the remaining cuspids (including the entoconid). The crown displays a
106 subrectangular (longer than broad) occlusal contour (BLI = 84%; see measurements in SOM
107 Table S2), with slight buccal waisting and minimal distal tapering (except for the protruding
108 distolingual corner, so that the crown is longer on the lingual than on the buccal side). The
109 protoconid and the metaconid are transversely aligned and not very peripherally situated. The
110 entoconid is not very peripheral and more distally located than the hypoconid, although
111 clearly less so than the hypoconulid. Along the postmetacristid, which is longer than the
112 postprotocristid and obliquely aligned, there is a distinct tuberculum intermedium² just distal
113 to the metaconid and a lesser developed enamel thickening toward its terminus. The mesial
114 fovea is much shorter mesiodistally than broad buccolingually, being distally delimited by a
115 short transverse cristid formed by the hypoprotocristid and hypometacristid, whose juncture is
116 interrupted by a mesiodistal groove. The talonid basin is much more extensive and deeper
117 than the mesial fovea. There is a distal fovea delimited by the hypoentocristid and postcristid
118 (also interrupted by a mesiodistal groove), and mostly located on the protruding distolingual
119 corner of the crown. There are no patent cingulids except for very small remnants on the
120 mesio Buccal wall of the protoconid and the talonid notch. On the talonid basin there is some
121 development of secondary enamel wrinkling, only partially obliterated by wear, including two

² Swindler (2002: 276) defined the ‘tuberculum intermedium’ or ‘postmetaconulid’ as “a tubercle on the distal surface of the metaconid or in the groove between the metaconid and endoconid on lower molars”.

122 obliquely aligned short secondary crests distal to the hypoprotocristid and hypometacristid.
123 There are two (mesial and distal) roots almost twice as high as the crown, both displaying two
124 (buccal and lingual) lobes demarcated by longitudinal grooves in the middle of the mesial and
125 distal aspects (Fig. 1d–h; SOM File S1). They bifurcate close to the cervix; the mesial one is
126 straight in the first half below the cervix and twists in distolingual direction on its apical half,
127 while the distal root is straighter and only slightly tilted distalward. Each root has a
128 buccolingually elongated pulp canal (SOM Fig. S2).

129 Comparisons The main differences among IPS41734, other ACM dryopithecines, and *D.*
130 *fontani* from Saint-Gaudens have been summarized in SOM Table S3. In occlusal
131 morphology, IPS41734 (Figs. 2a and 3a) closely resembles the M₂ of the '*S.* *occidentalis*
132 holotype (Figs. 2c and 3b; SOM File S2), although the latter is even less worn and, as a result,
133 it displays more conspicuous enamel wrinkling (similarly including two secondary crests
134 behind the hypoprotocristid and hypometacristid, albeit more mesiodistally aligned).
135 Similarities include the non-peripheral metaconid with a tuberculum intermedium behind, the
136 distolingually protruding crown with a distinct distal fovea, the entoconid less distal than the
137 hypoconulid, and the elongated crown proportions (SOM Table S2). The M₂ of
138 IPS1826+1827 only differs from IPS41734 in the slightly more marked buccal waisting, the
139 better-developed tuberculum intermedium, and the presence of additional enamel thickenings
140 along the postmetacristid. Comparisons with *A. brevirostris* are restricted due to the poor
141 preservation of the single available M₂ (IPS43000, holotype; Fig. 2b and 3e), so that most of
142 the main features noted above cannot be adequately ascertained (but see SOM Table S3),
143 except for the slightly less elongated crown proportions of IPS43000 (SOM Table S2; SOM
144 Fig. S3).

145 The *D. fontani* M₂ (Figs. 2e–g, i, j, l and 3i) displays additional differences compared to
146 IPS41734 and IPS1826+1827 (SOM Table S3): more peripheral cusps, especially the lingual

147 ones (resulting in a broader trigonid basin and a less oblique postmetacristid); better
148 developed buccal cingulid (also compared to *A. brevirostris*), extending also to the
149 distobuccal aspect of the hypoconid, even if discontinuous and variable to some extent among
150 individuals; and relatively much broader crown (SOM Table S2; SOM Fig. S2) that does not
151 protrude distolingually, with the entoconid situated more distally and transversely aligned
152 with the hypoconulid, and a more restricted or inconspicuous distal fovea. In some (Figs. 2e,
153 f, l and 3d) but not all (Fig. 2g, j) M₂s of *D. fontani* (see also SOM Fig. S4), the hypoconid
154 base does not reach the entoconid (so that the hypoconulid base contacts the metaconid). Also
155 variable is the development of the distal fovea—which is indistinct in some specimens (Fig.
156 2e, f; SOM Fig. S4d, e) and small in the remaining ones (Fig. 2g, i, j, l; SOM Fig. S4a–c)—
157 but in all cases more restricted than in IPS41734 and IPS1826+1827. The various *D. fontani*
158 M₂'s from Saint-Gaudens similarly display a variably developed tuberculum intermedium
159 behind the metaconid, although more peripheral than in the ACM specimens. Similar
160 differences apply to the *D. fontani* M₃ (Fig. 2h, k, m; SOM Fig. S4) compared to that of '*S.*'
161 *occidentalis* (Figs. 2d and 3c), particularly regarding the more peripheral lingual cuspids, the
162 more distal entoconid, and the more restricted distal fovea in the former.

163 A randomization test based on extant apes (e.g., see Alba et al., 2012b) shows that the
164 probability that the variation in BLI displayed by the M₂ sample including the '*S.*'
165 *occidentalis* holotype, IPS41734, and *D. fontani* individuals comes from a single species is
166 very low ($p = 0.060$) compared with hoolock gibbons and can be rejected ($p = 0.024$)
167 compared with chimpanzees (SOM S2), supporting the presence of more than a single
168 species.

169

170 *3.2. Morphology of the enamel-dentine junction*

171 EDJ morphology confirms the close similarities between the M₂ of IPS41734 (Fig. 3f) and
172 the '*S.*' *occidentalis* holotype (Fig 3g) noted above in relation to OES morphology. The
173 dentine horns corresponding to the five main cuspids are vertically set except for that of the
174 metaconid, which in both specimens is centrally tilted and mesiodistally elongated (with a
175 distinct secondary horn corresponding to the tuberculum intermedium). Buccal waisting is
176 better expressed than at the OES, but still not very marked, and the buccal cingulid also
177 appears more conspicuous (even if discontinuous) at the EDJ level. The only appreciable
178 difference between IPS41734 and the IPS1826+1827 M₂ at the EDJ level is that only the
179 latter displays yet another secondary dentine horn toward the end of the postmetacristid (Fig.
180 3g), in agreement with the more evident enamel thickening appreciable toward the end of the
181 postmetacristid at the OES. *Dryopithecus fontani* (Fig. 3i) displays a more vertically set
182 metaconid horn and a twinned secondary horn corresponding to the single tuberculum sextum
183 at the EDJ morphology (Fig. 3d), while the *A. brevirostris* specimen (Fig. 3j) is too damaged
184 to make reliable comparisons. The secondary cristids present behind the hypoprotocristid and
185 hypometacristid in the ACM specimens and *D. fontani* are only faintly expressed at the EDJ.

186 A 2D geometric morphometric analysis of EDJ contour through the mesial cusp apices of
187 lower molars in ACM dryopithecines, *D. fontani* and extant great apes shows greatest
188 similarities between IPS41734 and the M₂ of the '*S.*' *occidentalis* holotype (SOM S3; SOM
189 Fig. S5), supporting their assignment to the same species.

190

191 3.3. Relative enamel thickness

192 The RET results based on the new coronal sections of dryopithecines from els Hostalets de
193 Pierola (Fig. 4) and *D. fontani* from Saint-Gaudens are reported in SOM S4 and SOM Table
194 S4. Based on the enlarged sample sizes compared to Alba et al. (2013), irrespective of
195 whether all molar positions are analyzed simultaneously or whether comparisons are

196 restricted to second and third molars (SOM Table S5; SOM Fig. S6), *D. fontani* displays
197 slightly lower mean and median values than both *A. brevirostris* and *P. catalaunicus*, although
198 with considerable overlap, whereas IPS41734 and the ‘*S.*’ *occidentalis* holotype display
199 somewhat higher RET values. Statistical comparisons do not show significant differences
200 between *Dryopithecus* and either *Pierolapithecus* or *Anoiapithecus*, and only substantiate
201 significantly thicker enamel in ‘*S.*’ *occidentalis* (including IPS41734) as compared to
202 *Dryopithecus* (SOM S4; SOM Table S7). The comparison of RET values for the inspected
203 dryopithecines with those of extant great apes separately for each tooth locus (SOM Fig. S7;
204 SOM Table S6) further suggest that *Dryopithecus* displays lower values, while those of ‘*S.*’
205 *occidentalis* might match the variation of both *Pierolapithecus* and *Anoiapithecus* when
206 comparing the upper molars available for these taxa (SOM S4).

207

208 **4. Discussion and conclusions**

209 Similarities in OES and EDJ morphology, and to a lesser extent also in RET values,
210 support the conspecificity between IPS41734 and the ‘*S.*’ *occidentalis* holotype. Although
211 most previous authors synonymized ‘*S.*’ *occidentalis* with *H. laietanus*, we consider more
212 likely that this taxon is a senior synonym of one of the three other species recorded at ACM
213 (Alba, 2012; Alba et al., 2017). There is also the possibility that ‘*S.*’ *occidentalis* represents a
214 fourth distinct species, as suggested by its somewhat higher RET values. However, we
215 consider this very unlikely, since its RET values could be accommodated within the
216 intraspecific variation of *P. catalaunicus* or *A. brevirostris*. Furthermore, it would be
217 unparsimonious to advocate for an additional species before being able to discount a
218 synonymy with the two latter species on morphological grounds. Begun (2009) favored the
219 view that *P. catalaunicus* and *A. brevirostris* are junior synonyms of *D. fontani*, and noted
220 similarities in M₃ morphology between ‘*S.*’ *occidentalis* and *D. fontani* from Saint-Gaudens.

221 However, our comparisons above for the external and internal morphology of the M₂ show
222 greatest similarities between IPS41734 or IPS1826+1827, as well as multiple differences
223 (metaconid and entoconid position, crown proportions, distal fovea and buccal cingulid
224 development) that, in our opinion, do not support their assignment to *D. fontani*. Pickford
225 (2012) reached the same conclusion for IPS1826+1827 based on M₃ entoconid position and
226 root morphology, and suggested an attribution to *Neopithecus brancoi* (Schlosser, 1901),
227 whose holotype is an isolated M₃ from Salmendingen, Germany (Begun and Kordos, 1993:
228 Fig. 1; Begun, 2002: Fig. 20.4E, 2009; Pickford, 2012: Fig. 21F). However, as recognized by
229 Pickford (2012), the latter specimen differs from IPS1826+1827 by the more extensive mesial
230 fovea and also shows similarities with some specimens from Can Llobateres, currently
231 assigned to *H. laietanus* by most authors (e.g., Alba et al., 2012). Indeed, for many years the
232 Salmendingen molar was considered conspecific (as *Dryopithecus brancoi*) with the sample
233 from Rudabánya, Hungary (Begun and Kordos, 1993; Begun, 2002). However, the latter is
234 currently distinguished as *Rudapithecus hungaricus* (Begun, 2009, 2010, 2015; Begun et al.,
235 2012) because *Neopithecus brancoi* is generally considered a nomen dubium (Moyà-Solà et
236 al., 2009a; Casanovas-Vilar et al., 2011; Begun, 2015).

237 Begun (2009) asserted that all the Miocene apes from the Vallès-Penedes Basin displayed
238 thin enamel, which was subsequently challenged for *Anoiapithecus* and *Pierolapithecus*
239 (Moyà-Solà et al., 2009b; Alba et al., 2010b, 2013; Fortuny et al., 2014). The larger samples
240 analyzed in this study indicate considerable overlap between *Dryopithecus* and the two other
241 ACM dryopithecines, but substantiate the view that '*S.*' *occidentalis* displays thicker enamel
242 than at least *D. fontani*—particularly when different tooth loci are considered separately, with
243 the latter more closely resembling African apes instead of orangutans, as it is the case for both
244 *Anoiapithecus* and *Pierolapithecus*—thus supporting the taxonomic distinction between the
245 two former species. Coupled with additional differences in upper tooth morphology (Alba et

246 al., 2013; Pérez de los Ríos et al., 2013), our results are consistent with the view that *D.*
247 *fontani* is not the only dryopithecine recorded at ACM. Based on the data reported in this
248 paper, we formally assign IPS41734 to ‘*S.*’ *occidentalis*, but due to the lack of directly
249 comparable evidence for the lower molars, we cannot favor a synonymy of the latter with
250 either *P. catalaunicus* or *A. brevisrostris*. This is unfortunate, because—as previously noted
251 (Alba, 2012; Marigó et al. 2014)—the nominal species ‘*S.*’ *occidentalis* is potentially a senior
252 synonym of either *P. catalaunicus* or *A. brevisrostris*, in which case the trivial name of the
253 former would take priority.

254 Based on less detailed comparisons, some previous authors (Moyà-Solà et al., 2004,
255 2009a; Casanovas-Vilar et al., 2011; Alba, 2012; Marigó et al., 2014) considered ‘*S.*’
256 *occidentalis* a nomen dubium—i.e., “a name of unknown or doubtful application” (ICZN,
257 1999: Glossary). Within this general concept, some authors (Mones, 1989: 233) further
258 distinguish between ‘nomina vana’ (taxon names based on inadequate types for definitive
259 diagnosis, and hence unlikely to become taxonomically valid) and ‘nomina dubia’ (currently
260 of doubtful application, but which “may regain standing in zoology through the study of type
261 specimens or new material”). Given our assignment of IPS41734 to ‘*S.*’ *occidentalis*, rather
262 than a nomen dubium it seems preferable to consider this taxon a ‘species inquirenda’ (i.e., “a
263 species of doubtful identity needing further investigation”; ICZN, 1999: Glossary) within the
264 Dryopithecini sensu Alba (2012). This term applies to species correctly diagnosed (and hence
265 both nomenclaturally and taxonomically valid), but whose identity cannot be demonstrated at
266 present because their remains are not comparable with those available closely related taxa
267 (Mones, 1989)—as it is the case of ‘*S.*’ *occidentalis* as compared to *A. brevisrostris* and
268 especially *P. catalaunicus*. Ongoing analyses on 3D RET and EDJ morphology in these and
269 other Vallès-Penedès hominoids might shed additional light on this issue, although additional

270 dentognathic hominoid material from ACM (ideally combining upper and lower molars)
271 would ultimately be required.

272

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446

447 **Figure legends**

448

449 **Figure 1.** Right mandibular fragment with M₂ (IPS41734) of the dryopithecine from
450 ACM/BCV4, assigned to '*Sivapithecus*' *occidentalis*. a–c) Photographs of the whole
451 specimen in occlusal (a), lingual (b), and buccal (c) views. d–h) Renderings of the digitally
452 extracted 3D model of the M₂ to show the morphology of the roots and the EDJ, in mesial (d),
453 lingual (e), distal (f), buccal (g), and linguo-occlusal oblique (h) views; the roots are depicted
454 in blue, the EDJ in yellow, and the enamel in semitransparent green (see Fig. 3a, b for
455 separate views of the OES and EDJ).

456

457 **Figure 2.** Occlusal views of the IPS41734 molar compared to M₂ and M₃ of other middle
458 Miocene dryopithecines from ACM and southern France (left specimens mirrored as right for
459 comparison): a) IPS41734, right M₂ of '*Sivapithecus*' *occidentalis* from ACM/BCV4; b)
460 IPS43000, left M₂ (damaged) of the holotype of *Anoiapithecus brevirostris* from ACM/C3-
461 Aj; c, d) IPS1826+1827, left M₂ (c) and M₃ (d) of the holotype of '*S.*' *occidentalis* from Can
462 Vila; e, f) HGP2, left (e) and right (f) M₂ of the holotype of *Dryopithecus fontani* from Saint-
463 Gaudens; g–i) HGP1, left M₂ (g), left M₃ (h) and right M₂ (i) of *D. fontani* from Saint-
464 Gaudens; j, k) Harlé 44, left M₂ (j) and M₃ (k) of *D. fontani* from Saint-Gaudens from a
465 picture kindly provided by the MHNB); l) Harlé 46, right M₂ of *D. fontani* from Saint-
466 Gaudens; m) Harlé 47, right M₃ (damaged) of *D. fontani* from Saint-Gaudens.

467

468 **Figure 3.** Morphology of the OES (a–e) and EDJ (f–j): a, f) IPS41734, right M₂ from
469 ACM/BCV4; b, c, g, h) IPS1826+1827, holotype of ‘*Sivapithecus*’ *occidentalis* from CV
470 (mirrored for comparison), including the left M₂ (b, g) and M₃ (c, h); d, i) Harlé 46, right M₂
471 *Dryopithecus fontani* from Saint-Gaudens; e, j) IPS43000, left M₂ (damaged) of the holotype
472 of *Anoiapithecus brevirostris* from ACM/C3-A (mirrored for comparison). Black arrows
473 denote the secondary dentine horns of the tuberculum intermedium, while the white arrow
474 denotes the secondary dentine horn of the enamel thickening present toward the end of the
475 postmetacristid in the ‘*S.*’ *occidentalis* M₂.

476

477 **Figure 4.** Selected coronal crown μ CT slices employed to compute 2DRET: a, b)
478 IPS1826+1827, holotype of ‘*Sivapithecus*’ *occidentalis* from Can Vila, including the left M₂
479 (a) and M₃ (b); c) IPS41734, right M₂ of ‘*S.*’ *occidentalis* from ACM/BCV4; d) MGSB48486,
480 right M₂ of *Dryopithecus fontani*; e) Harlé 47, right M₃ of *D. fontani* from Saint-Gaudens.

481







