



Short Communications

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)

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1. Introduction

The Miocene vertebrate record from the Vallès-Penedès Basin (NE Iberian Peninsula; Casanovas-Vilar et al., 2016a) differs from that of inner Iberian basins by the presence of fossil hominoids (Alba, 2012; Marigó et al., 2014) as a result of moister and more forested environments during the late Aragonian and Vallesian (ca. 12.6–8.9 Ma; Casanovas-Vilar et al., 2008, 2016a, b; Marmi et al.,

2012; Alba et al., 2018). However, until a couple of decades ago, the Aragonian hominoid remains from this basin were very scarce,¹ including a molar crown fragment from Trinxera del Ferrocarril-Sant Quirze, an M² from Can Mata s.l., a C₁ of a female individual from Can Mata 1, and a left mandibular fragment with M₂–M₃ and a lower molar germ fragment from Can Vila (Supplementary Online Material [SOM] Table S1 and references therein). Villalta Comella and Crusafont Pairó (1941) first attributed the Can Vila specimen to *Dryopithecus fontani* Lartet, 1856. However, soon thereafter the same authors erected *Sivapithecus occidentalis* Villalta Comella and Crusafont Pairó, 1944 based on distinctive features such as “the buccolingual convergence of the cusps,” the “elongate and narrow lower molars,” and the presence of “secondary cusps on the lingual crest [= postmetacristid]” (Villalta Comella and Crusafont Pairó, 1944: 115 and 118, our translation from the original in Spanish). This species has been considered a junior subjective synonym of *Hispanopithecus laietanus* Villalta Comella and Crusafont Pairó, 1944 (formerly also in *Dryopithecus*) by many authors, or most recently a nomen dubium (e.g., Moyà-Solà et al., 2004, 2009a; Alba, 2012), only with few exceptions (Begun, 2009; Pickford, 2012; see SOM Table S1 for further details).

The huge sampling effort at the middle to late Miocene stratigraphic section of Abocador de Can Mata (ACM), at els Hostalets de Pierola (Alba et al., 2006, 2017), has uncovered a previously unsuspected diversity of primates from 12.4 to 11.6 Ma (Alba et al.,

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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).

2017). They include small-bodied catarrhines (Alba et al., 2010a, 2012a, 2015; Alba and Moyà-Solà, 2014; Urciuoli et al., 2018) and three species of dryopithecine great apes (Moyà-Solà et al., 2004, 2009a, b; Almécija et al., 2009; Casanovas-Vilar et al., 2011; Alba, 2012; Alba and Moyà-Solà, 2012; Pérez de los Ríos et al., 2012; Alba et al., 2013, 2017; Hammond et al., 2013; Marigó et al., 2014; Pina et al., 2014): *Pierolapithecus catalaunicus* Moyà-Solà et al., 2004 at 12.0 Ma; *Anoiapithecus brevirostris* Moyà-Solà et al., 2009b at 12.4–12.0 Ma; and *D. fontani* at 11.9 Ma. Their distinction at the genus rank—initially questioned by Begun and colleagues (Begun, 2009, 2010, 2015; Begun et al., 2012), but subsequently accepted by others (e.g., Pickford, 2012; Fleagle, 2013; Böhme et al., 2019; Andrews, 2020)—is mostly based on cranial differences (Moyà-Solà et al., 2004, 2009a, b; Alba, 2012; Pérez de los Ríos et al., 2012) but further supported by dental morphology (Alba et al., 2010b, 2013; Alba and Moyà-Solà, 2012; Alba et al., 2013; Pérez de los Ríos et al., 2013; Fortuny et al., 2014).

Moyà-Solà et al. (2004) first proposed to consider ‘S.’ *occidentalis* as a nomen dubium owing to its previous synonymization with *H. laietanus* and uncertainties about its exact provenance (and age)—given the vague indications provided by Villalta Comella and Crusafont Pairó (1941)—which contrast with the accurate dating of ACM localities (Casanovas-Vilar et al., 2011, 2016b; Alba et al., 2017). Subsequently, it has been noted (Jordi Martinell, pers. comm. in Alba et al., 2013 and Marigó et al., 2014) that Can Vila would have been located within the same ravine as ACM/BCV1 (the type locality of *P. catalaunicus*, dated to 12.0 Ma with an interpolated age of 11.96 Ma; Alba et al., 2017), albeit in somewhat lower stratigraphic levels, implying an age of ca. 12.0 Ma. However, deciphering the taxonomic status of ‘S.’ *occidentalis* is still hindered by the distinction of multiple roughly coeval genera at ACM (see above). To shed new light on this question, we describe a hominoid mandibular fragment with M₂ from yet another locality from the same ravine (ACM/BCV4), which is located 5 m above ACM/BCV1 (interpolated age of 11.94 Ma; Alba et al., 2017). Although previously mentioned in some papers—either as unassigned to the genus (Casanovas-Vilar et al., 2011; Alba, 2012; Marigó et al., 2014) or tentatively attributed to cf. *P. catalaunicus* (Alba et al., 2017)—the ACM/BCV4 specimen is first described and figured here (for a preliminary report in abstract form, see Alba et al., 2019b). Based on the outer enamel surface (OES) and enamel-dentine junction (EDJ) morphology, together with 2D relative enamel thickness (RET), we compare this specimen with the holotype of ‘S.’ *occidentalis*, other ACM dryopithecines, and *D. fontani* from its type locality to evaluate the taxonomic affinities of the former and revisit the taxonomic status of ‘S.’ *occidentalis*.

2. Materials and methods

The newly described specimen (IPS41734), the ‘S.’ *occidentalis* holotype (IPS1826 + 1827), and the comparative sample from ACM (Moyà-Solà et al., 2004, 2009a, b; Alba et al., 2013) are housed at the Institut Català de Paleontologia Miquel Crusafont. Comparative material further includes a right M² (MGSB48486) of *D. fontani* from Can Mata s.l. (van der Made and Ribot, 1999; Alba et al., 2013; Fig. 3V), housed at the Museu de Geologia del Seminari de Barcelona (MGSB), Spain, and all of the available lower molars of *D. fontani* from Saint-Gaudens (type locality). These include the holotype mandible HGP2 (Lartet, 1856; Begun, 2002; Fig. 20.3B, D) and the Gaudry mandible HGP1 (Gaudry, 1890; Begun, 2002; Fig. 20.3A, C), housed at the Muséum National d’Histoire Naturelle (MNHN), Paris, France, as well as a partial mandible (Harlé 44) and two isolated molars (Harlé 46 and 47; Harlé, 1898, 1899; Pl. VI; Begun, 2002; Fig. 20.3F), housed at the Muséum d’Histoire Naturelle de Bordeaux (MHNB), France. Extant comparative

material was measured by D.M.A. at the American Museum of Natural History (AMNH), New York, USA. Mesiodistal length (MD) and buccolingual breadth (BL) were measured to the nearest 0.1 mm by D.M.A., M.P.R., and C.Z., and a breadth/length index (BLI, in %) was computed (see SOM Table S1). Dental terminology (SOM Fig. S1) follows Harrison and Gu (1999).

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

3. Results

3.1. Morphology of the outer enamel surface

Description IPS41734 is a right mandibular fragment that preserves the M₁ roots (broken at the cervix, 8.4 × 8.2 mm), the socketed M₂, and the mesial root of the M₃ (Fig. 1a–c). Mandibular corpus depth cannot be reliably measured (>19 mm), while corpus width increases laterally from the mesial M₁ level (13 mm) to M₂–M₃ level (17 mm).

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

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

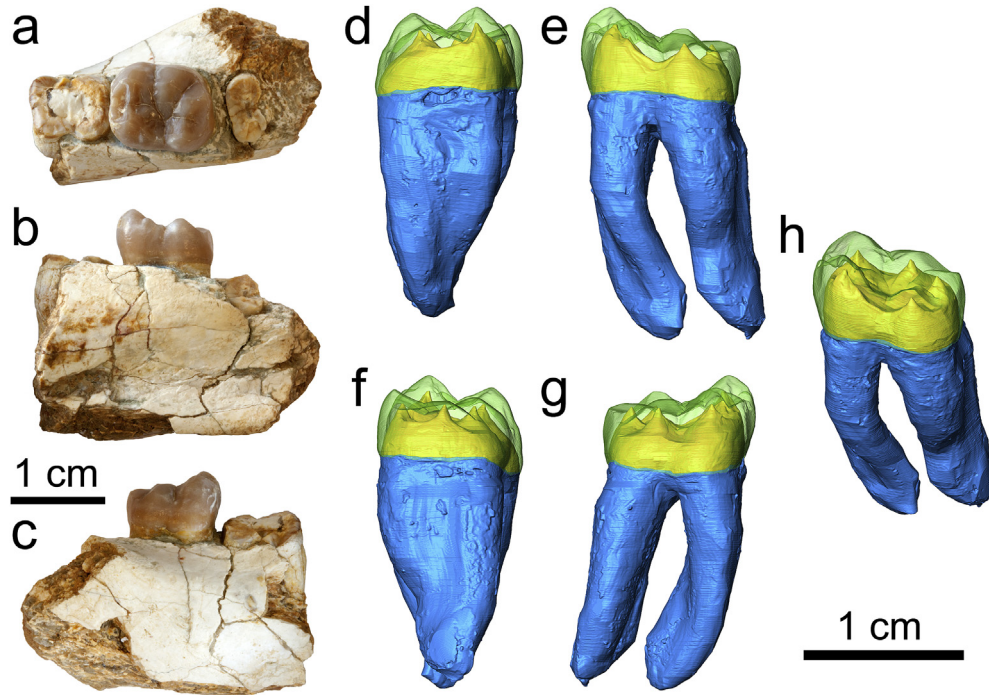


Figure 1. Right mandibular fragment with M₂ (IPS41734) of the dryopithecine from ACM/BCV4, assigned to '*Sivapithecus*' *occidentalis*. a–c) Photographs of the whole specimen in occlusal (a), lingual (b), and buccal (c) views. d–h) Renderings of the digitally extracted 3D model of the M₂ to show the morphology of the roots and the EDJ, in mesial (d), lingual (e), distal (f), buccal (g), and linguo-occlusal oblique (h) views; the roots are depicted in blue, the EDJ is depicted in yellow, and the enamel is depicted in semitransparent green (see Fig. 3a, b for separate views of the OES and EDJ). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

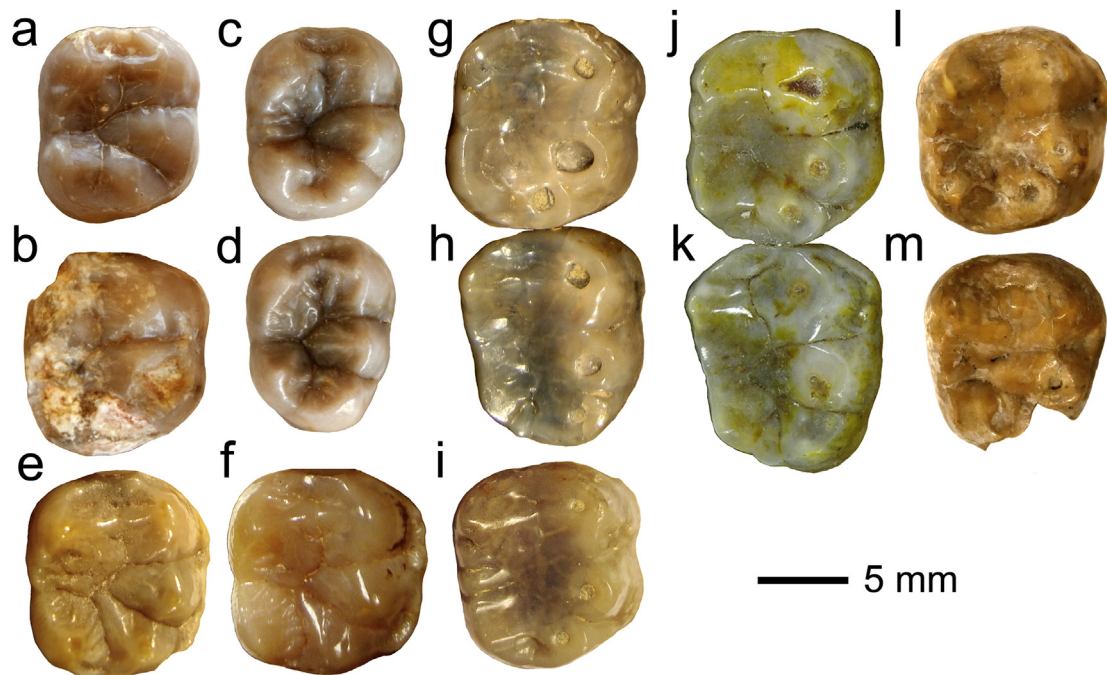


Figure 2. Occlusal views of the IPS41734 molar compared with the M₂ and M₃ of other middle Miocene dryopithecines from ACM and southern France (left specimens mirrored as right for comparison): a) IPS41734, right M₂ of '*Sivapithecus*' *occidentalis* from ACM/BCV4; b) IPS43000, left M₂ (damaged) of the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

including two obliquely aligned short secondary crests distal to the hypoprotocristid and hypometacristid. There are two (mesial and distal) roots almost twice as high as the crown, both displaying two

(buccal and lingual) lobes demarcated by longitudinal grooves in the middle of the mesial and distal aspects (Fig. 1d–h; SOM File S1). They bifurcate close to the cervix; the mesial one is straight in the

first half below the cervix and twists in distolingual direction on its apical half, while the distal root is straighter and only slightly tilted distalward. Each root has a buccolingually elongated pulp canal (SOM Fig. S2).

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

The *D. fontani* M₂ (Figs. 2e–g, i, j, l, and 3i) displays additional differences compared with IPS41734 and IPS1826+1827 (SOM Table S3): more peripheral cusps, especially the lingual ones (resulting in a broader trigonid basin and a less oblique postmetacristid); better developed buccal cingulid (also compared with *A. brevisrostris*), extending also to the distobuccal aspect of the hypoconid, even if discontinuous and variable to some extent among individuals; and a relatively much broader crown (SOM Table S2; SOM Fig. S2) that does not protrude distolingually, with the entoconid situated more distally and transversely aligned with the hypoconulid, and a more restricted or inconspicuous distal fovea. In some (Figs. 2e, f, l, and 3d) but not all (Fig. 2g, j) M₂s of *D. fontani* (see also SOM Fig. S4), the hypoconid base does not reach the entoconid (so that the hypoconulid base contacts the metaconid). Also variable is the development of the distal fovea—which

is indistinct in some specimens (Fig. 2e, f; SOM Fig. S4d, e) and small in the remaining ones (Fig. 2g, i, j, l; SOM Fig. S4a–c)—but in all cases more restricted than in IPS41734 and IPS1826+1827. The various *D. fontani* M₂s from Saint-Gaudens similarly display a variably developed tuberculum intermedium behind the metaconid, although more peripheral than in the ACM specimens. Similar differences apply to the *D. fontani* M₃ (Fig. 2h, k, m; SOM Fig. S4) compared with that of ‘S.’ *occidentalis* (Figs. 2d and 3c), particularly regarding the more peripheral lingual cusps, the more distal entoconid, and the more restricted distal fovea in the former.

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

3.2. Morphology of the enamel-dentine junction

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

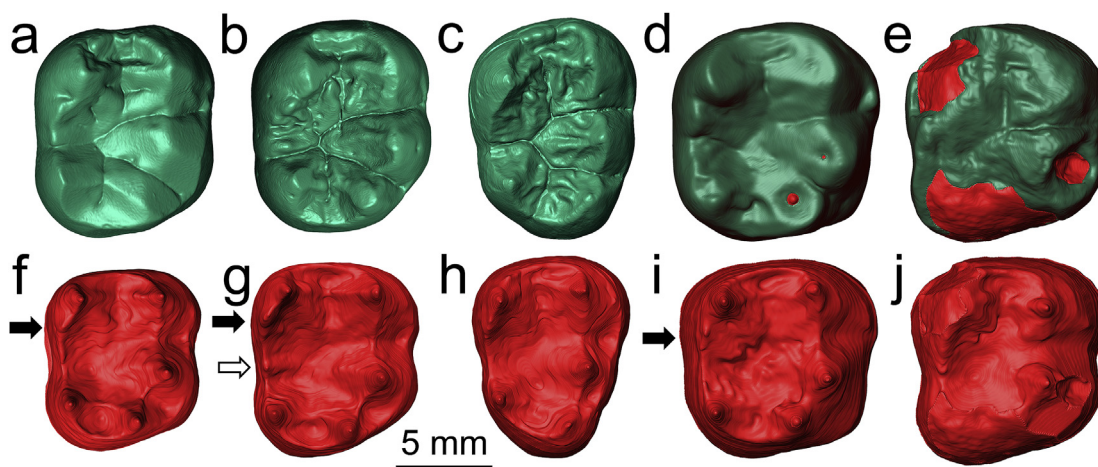


Figure 3. Morphology of the outer enamel surface (a–e) and enamel dentine junction (f–j): a, f) IPS41734, right M₂ from ACM/BCV4; b, c, g, h) IPS1826+1827, holotype of ‘Sivapithecus’ *occidentalis* from Can Vila (mirrored for comparison), including the left M₂ (b, g) and M₃ (c, h); d, i) Harlé 46, right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

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

3.3. Relative enamel thickness

The RET results based on the new coronal sections of dryopithecines from els Hostalets de Pierola (Fig. 4) and *D. fontani* from Saint-Gaudens are reported in SOM S4 and SOM Table S4. Based on the enlarged sample sizes compared with Alba et al. (2013), irrespective of whether all molar positions are analyzed simultaneously or whether comparisons are restricted to second and third molars (SOM Table S5; SOM Fig. S6), *D. fontani* displays slightly lower mean and median values than both *A. brevisrostris* and *P. catalaunicus*, although with considerable overlap, whereas IPS41734 and the 'S.' *occidentalis* holotype display somewhat higher RET values. Statistical comparisons do not show significant differences between *Dryopithecus* and either *Pierolapithecus* or *Anoiapithecus* and only substantiate significantly thicker enamel in 'S.' *occidentalis* (including IPS41734) compared with *Dryopithecus* (SOM S4; SOM Table S7). The comparison of RET values for the inspected dryopithecines with those of extant great apes separately for each tooth locus (SOM Fig. S7; SOM Table S6) further suggests that *Dryopithecus* displays lower values, while those of 'S.' *occidentalis* might match the variation of both *Pierolapithecus* and *Anoiapithecus* when comparing the upper molars available for these taxa (SOM S4).

4. Discussion and conclusions

Similarities in OES and EDJ morphology, and to a lesser extent also in RET values, support the conspecificity between IPS41734 and the 'S.' *occidentalis* holotype. Although most previous authors synonymized 'S.' *occidentalis* with *H. laietanus*, we consider more likely that this taxon is a senior synonym of one of the three other species recorded at ACM (Alba, 2012; Alba et al., 2017). There is also the possibility that 'S.' *occidentalis* represents a fourth distinct species, as suggested by its somewhat higher RET values. However, we consider this very unlikely because its RET values could be accommodated within the intraspecific variation of *P. catalaunicus* or *A. brevisrostris*. Furthermore, it would be unparsimonious to advocate for an additional species before being able to discount a synonymy with the two latter species on morphological grounds. Begun (2009) favored the view that *P. catalaunicus* and *A. brevisrostris* are junior synonyms of *D. fontani* and noted similarities in M₃ morphology between 'S.' *occidentalis* and *D. fontani* from Saint-Gaudens. However, our comparisons above for the external and internal morphology of the M₂ show greatest similarities between IPS41734 and IPS1826+1827, as well as multiple differences (metaconid and entoconid position, crown proportions, distal fovea and buccal cingulid development), which, in our opinion, do not support their assignment to *D. fontani*. Pickford (2012) reached the same conclusion for IPS1826+1827 based on M₃ entoconid position and root morphology and suggested an attribution to *Neopithecus brancoi* (Schlosser, 1901), whose holotype is an isolated M₃ from Salmendingen, Germany (Begun and Kordos, 1993: Fig. 1; Begun, 2002: Fig. 20.4E, 2009; Pickford,

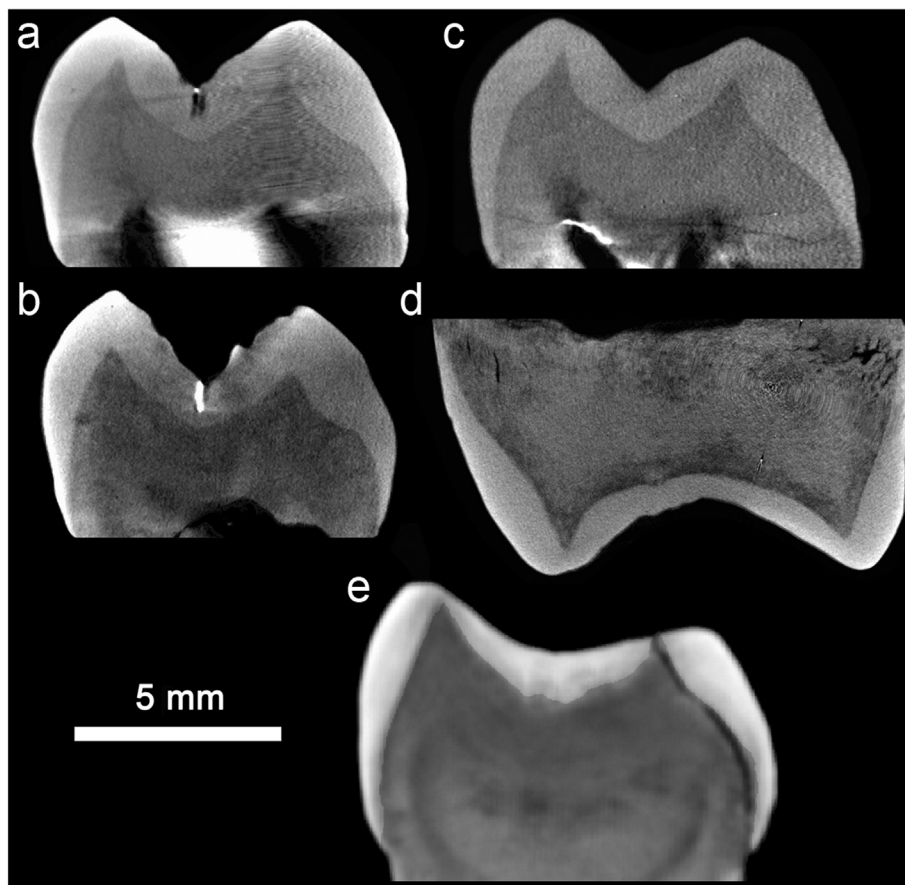


Figure 4. Selected coronal crown μ CT slices used to compute 2D RET: a, b) IPS1826+1827, holotype of 'Sivapithecus' *occidentalis* from Can Vila, including the left M₂ (a) and M₃ (b); c) IPS41734, right M₂ of 'S.' *occidentalis* from ACM/BCV4; d) MGSB48486, right M₂ of *Dryopithecus fontani*; e) Harlé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

2012: Fig. 21F). However, as recognized by Pickford (2012), the latter specimen differs from IPS1826+1827 by the more extensive mesial fovea and also shows similarities with some specimens from Can Llobateres, currently assigned to *H. laietanus* by most authors (e.g., Alba et al., 2012). Indeed, for many years, the Salmendingen molar was considered conspecific (as *Dryopithecus brancoi*) with the sample from Rudabánya, Hungary (Begun and Kordos, 1993; Begun, 2002). However, the latter is currently distinguished as *Rudapithecus hungaricus* (Begun, 2009, 2010, 2015; Begun et al., 2012) because *N. brancoi* is generally considered a nomen dubium (Moyà-Solà et al., 2009a; Casanovas-Vilar et al., 2011; Begun, 2015).

Begun (2009) asserted that all the Miocene apes from the Vallès-Penedès Basin displayed thin enamel, which was subsequently challenged for *Anoiapithecus* and *Pierolapithecus* (Moyà-Solà et al., 2009b; Alba et al., 2010b, 2013; Fortuny et al., 2014). The larger samples analyzed in this study indicate considerable overlap between *Dryopithecus* and the two other ACM dryopithecines but substantiate the view that '*S. occidentalis*' displays thicker enamel than at least *D. fontani*—particularly when different tooth loci are considered separately, with the latter more closely resembling African apes instead of orangutans, as it is the case for both *Anoiapithecus* and *Pierolapithecus*—thus supporting the taxonomic distinction between the two former species. Coupled with additional differences in upper tooth morphology (Alba et al., 2013; Pérez de los Ríos et al., 2013), our results are consistent with the view that *D. fontani* is not the only dryopithecine recorded at ACM. Based on the data reported in this paper, we formally assign IPS41734 to '*S. occidentalis*', but due to the lack of directly comparable evidence for the lower molars, we cannot favor a synonymy of the latter with either *P. catalaunicus* or *A. brevisrostris*. This is unfortunate because—as previously noted (Alba, 2012; Marigó et al., 2014)—the nominal species '*S. occidentalis*' is potentially a senior synonym of either *P. catalaunicus* or *A. brevisrostris*, in which case the trivial name of the former would take priority.

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

Conflict of interest

There is no conflict of interests.

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Supplementary Online Material

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