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Further insight into an unnamed, medium-sized crouzeliid pliopithecoid from the Vallès-Penedès Basin (NE Iberian Peninsula)

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Abstract

Pliopithecoids are a clade of stem catarrhines represented by multiple Middle to Late Miocene genera in the Vallès-Penedès Basin (NE Iberian Peninsula). The recent description of the crouzeliid *Fanchangia* (Early Miocene, China) and the recognition that *Pliobates* (Late Miocene, Spain) is a crouzeliid enable to revisit the taxonomic affinities of some pliopithecoid remains from this basin, namely an M^2 from Trinxera del Ferrocarril-Sant Quirze (SQ-TF; ~11.6–11.2 Ma), generally interpreted as a pliopithecid, and a dP_4 from Can Feliu 2 (CF2; <11.2 Ma), previously considered a crouzeliid. We redescribe these remains based on both external morphology and enamel-dentine junction (EDJ), and compare them with those of other pliopithecoids. A cladistic analysis of dental features is performed using a dental matrix that includes the dP_4 position, while the M^2 EDJ shape is compared using landmark-based three-dimensional geometric morphometric (3DGM) analysis. Finally, body mass is estimated based on M^2 size using available allometric equations. Our qualitative comparisons show that the M^2 resembles in some regards the Asian anapithecines *Laccopithecus* and *Fanchangia* but is less derived than *Anapithecus*, while the 3DGM analysis supports its crouzeliid affinities and hints at differences from crouzeliines. In turn, the dP_4 resembles that of crouzeliids, including the anapithecine *Fanchangia* and the crouzeliines *Pliobates* and *Crouzelia*. Given size congruence and close geographic and temporal proximity, it is likely that both specimens belong to a single, medium-sized crouzeliid species. A cladistic analysis of the two specimens simultaneously supports a sister-taxon relationship with *Fanchangia* within anapithecine crouzeliids. We conclude that the remains from SQ-TF and CF2 belong to the Crouzeliidae and, likely, to a medium-sized anapithecine. Given the scarcity of the material, we refrain from erecting a new species and provisionally refer to this taxon as Anapithecinae nov.—in the hope that future fieldwork will eventually recover additional, more complete material.

Keywords Fossil primates, Pliopithecoidea, Crouzeliidae, Dental morphology, Miocene, Spain

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Introduction

Pliopithecoids are considered a clade of Early to Late Miocene stem catarrhines from Eurasia (Andrews et al., 1996; Begun, 2002, 2017; Bouchet et al., 2024a; Harrison, 2005, 2013; Harrison et al., 2020). Although their systematics differs among authors, after Ginsburg and Mein (1980), Harrison and Gu (1999), and Harrison et al. (2020), three main groups were distinguished at the family rank by Bouchet et al. (2024a): Dionysopithecidae, Pliopithecidae, and Crouzeliidae, with the latter subdivided into subfamilies Crouzeliinae and Anapithecinae.

In the Iberian Peninsula, pliopithecoids are restricted to the Vallès-Penedès Basin, which has yielded a rich record of Early to Late Miocene terrestrial vertebrates (Casanovas-Vilar et al., 2016a, 2022). The crouzeliids recorded from this basin include: *Pliobates cataloniae* Alba et al., 2015 from two coeval late Aragonian (~11.6 Ma) localities of Abocador de Can Mata (ACM; Alba et al., 2015; Bouchet et al., 2021, 2024a, 2024b; Raventós-Izard et al., 2025), originally described as a stem hominoid (Alba et al., 2015) but subsequently reinterpreted as a pliopithecoid (Gilbert et al., 2020; Nengo et al., 2017) and, more specifically, a crouzeliid (Bouchet et al., 2024a, 2024b); *Barberapithecus huerzeleri* Alba & Moyà-Solà, 2012 from Castell de Barberà (Alba & Moyà-Solà, 2012; Arias-Martorell et al., 2021), traditionally correlated to the latest Aragonian (e.g., Casanovas-Vilar et al., 2011) but currently considered earliest Vallesian (MN9, ~11.2 Ma) in age (Alba et al., 2019, 2022; Casanovas-Vilar et al., 2016a); *Egarapithecus narcisoi* Moyà-Solà et al., 2001 from Torrent de les Febulines (Moyà-Solà et al., 2001), dated to the late Vallesian (MN10, ~9.1 Ma; Casanovas-Vilar et al., 2016b); and an indeterminate crouzeliid from Can Feliu 2 (CF2),[1] currently considered roughly coeval with Castell de Barberà (Alba et al., 2022, 2025; Casanovas-Vilar et al., 2016a). The remains of these species other than *P. cataloniae* were initially assigned to *Pliopithecus* sp. (Crusafont-Pairó & Golpe-Posse, 1981, 1982; Golpe-Posse, 1982), their crouzeliid affinities being subsequently recognized by most authors (Ginsburg, 1986; Moyà-Solà et al., 1990, 2001; Andrews et al., 1996; Harrison et al., 2002, 2020; Alba & Moyà-Solà, 2012; Marigó et al., 2014), with only a few exceptions (Begun, 2002). The taxonomic identity of the CF2 crouzeliid remains enigmatic because it is only represented by a single dP_4 (initially misidentified as an M_3; Crusafont-Pairó & Golpe-Posse, 1981, 1982). As noted by Andrews et al. (1996), this specimen would be consistent in size and shape with *E. narcisoi*, but the older age of the former suggests that it probably belongs to another species.

In addition, there is an indeterminate pliopithecoid, recorded by an isolated M^2 from Trinxera del Ferrocarril-Sant Quirze (SQ-TF), which is probably latest Aragonian (MN7+8, ~11.6–11.2 Ma) in age (Alba et al., 2022, 2025). This tooth was discovered in the 1920s by amateur fossil collector Màrius Guerín but remained undescribed until Harrison et al. (2002) attributed it to *Pliopithecus* sp. These authors noted similarities with *Pliopithecus platyodon* Biedermann, 1863 from the early Middle Miocene (MN5) sites of Elgg (Switzerland; type locality) and Göriach (Austria; Andrews et al., 1996; Begun, 2002; Harrison et al., 1991; Hofmann, 1893; Hürzeler, 1954), coupled with some differences, but refrained from describing a new species given the scarcity of the material. Dentognathic remains of *Pliopithecus canmatensis* Alba et al., 2010 (see also Alba & Moyà-Solà, 2014) and *P. cataloniae* (Alba et al., 2015; Bouchet et al., 2024a) were subsequently recovered from various localities of the ACM local stratigraphic sequence (Alba et al., 2006, 2017, 2022), which are slightly older than SQ-TF. However, an attribution of the SQ-TF specimen to these species can be readily discounted based on size (Bouchet et al., 2024b; Marigó et al., 2014). In contrast, the SQ-TF specimen would be consistent in size not only with *E. narcisoi* but also with the indeterminate crouzeliid from CF2. Harrison et al. (2002) dismissed the possibility that the SQ-TF molar might represent a crouzeliid based on multiple differences from both *Anapithecus hernyaki* (Kretzoi, 1975) from Hungary (Begun, 2002; Kordos & Begun, 2001; Nargolwalla et al., 2005) and *Laccopithecus robustus* (Wu & Pan, 1984) from China (Pan et al., 1989), which at the time were the only described crouzeliid genera preserving the upper molars. Such differences, however, do not apply if *B. huerzeleri* from Castell de Barberà—assigned to *Pliopithecus* cf. *antiquus* by Harrison et al. (2002)—is considered a crouzeliid (Alba & Moyà-Solà, 2012; Bouchet et al., 2024a; Harrison et al., 2020). In addition, a recent analysis of the molar enamel-dentine junction shape of Iberian pliopithecoids (Bouchet et al., 2024b) revealed closer similarities in occlusal shape of the SQ-TF specimen with *B. huerzeleri* than with *Pl. canmatensis*.

Until recently, the main problem to adequately evaluate the potential crouzeliid affinities of the SQ-TF M^2 was the lack of upper cheek teeth of the crouzeliid genera *Crouzelia* and *Plesiopliopithecus*, coupled with the crouzeliid status of *B. huerzeleri*, disputed by some authors (Begun, 2002). The description of the more plesiomorphic crouzeliid *Fanchangia jini* Harrison et al., 2020,

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[1] Frequently referred to as just Can Feliu without number (e.g., Moyà-Solà et al., 1990; Andrews et al., 1996; Begun, 2002; Harrison et al., 2002), or else as Can Sant Feliu (e.g., Crusafont-Pairó & Golpe-Posse 1981, 1982; Ginsburg, 1986), the correct name of this locality according to Alba et al. (2025) is Can Feliu 2 (= Can Pagès) to distinguish it from Can Feliu 1, which yielded no mammal remains (Golpe-Posse, 1971, 1972).

coupled with the recognition that *P. cataloniae*—like the maxillary fragment with P^4–M^1 from Mörgen (MN9; Heißig, 1999; Seehuber, 2009)—is a crouzeliine crouzeliid closely related to *Crouzelia* and *Plesiopliopithecus* (Bouchet et al., 2024a), provide the opportunity to revisit the taxonomic affinities of both the M^2 from SQ-TF and the dP_4 from CF2. Based on the original specimens and µCT-derived enamel-dentine junction (EDJ) surface models, here we redescribe these teeth and compare them (both on qualitative and quantitative grounds) with those of other pliopithecoids, with emphasis on *Fanchangia* and *Pliobates*. The described teeth are also included for the first time in a cladistic analysis of pliopithecoids based on dental characters, so as to determine their closest phylogenetic relationships. The phenetic affinities of the M^2 are also evaluated by means of a three-dimensional geometric morphometric (3DGM) analysis of EDJ shape, which is known to embed strong phylogenetic signal (e.g., Zanolli et al., 2022) and has the potential to resolve systematic issues in stem catarrhines such as pliopithecoids (Bouchet et al., 2024b). The taxonomic and evolutionary implications of the results of these analyses are discussed from a biochronological and paleobiogeographic perspective.

Materials and methods

Studied material

The right M^2 from SQ-TF (MGSB48874; Fig. 1a–e; see also Harrison et al., 2002: fig. 1) is housed at the Museu de Geologia del Seminari de Barcelona (MGSB), Barcelona, Spain. In turn, the right dP_4 (IPS34565) from CF2 (Fig. 1f–j; see also Crusafont-Pairó & Golpe-Posse, 1981: fig. 2; Moyà Solà et al., 1990: fig. 1; Marigó et al., 2014: fig. 2c) is housed at the Institut Català de Paleontologia Miquel Crusafont (ICP), Sabadell, Spain.

Microcomputed tomography scans

The two studied specimens were scanned by X-ray microtomography at the Centro Nacional de Investigación sobre la Evolución Humana (CENIEH; Burgos, Spain) using a GE Phoenix V|Tome|X s240 mCT scanner. For MGSB48874, the following parameters were used: 0.125 mA current, 120 kV voltage, and 0.2 mm Cu filter. In turn, for IPS34565 the following parameters were used: 0.120 mA current, 115 kV voltage, 0.2 mm Cu filter, and a magnification of 16.67 (see Bouchet et al., 2024b: SOM tables S2 and S3). The final reconstructed volumes have an isometric voxel size of 12.5 µm and 12 µm, respectively.

Virtual surfaces of the two specimens were obtained through both watershed-based and semiautomatic threshold-based segmentation methods in Avizo v. 7.0 (Visualization Sciences Group, Hillsboro). The outer enamel surface model of MGSB48874 is available from MorphoSource (https://doi.org/10.17602/M2/M580826) after Bouchet et al. (2024b) or after this work in the case of IPS34565 (https://doi.org/10.17602/M2/M722341). Their enamel-dentine junction models were also deposited in MorphoSource (https://doi.org/10.17602/M2/M580823 and https://doi.org/10.17602/M2/M7223

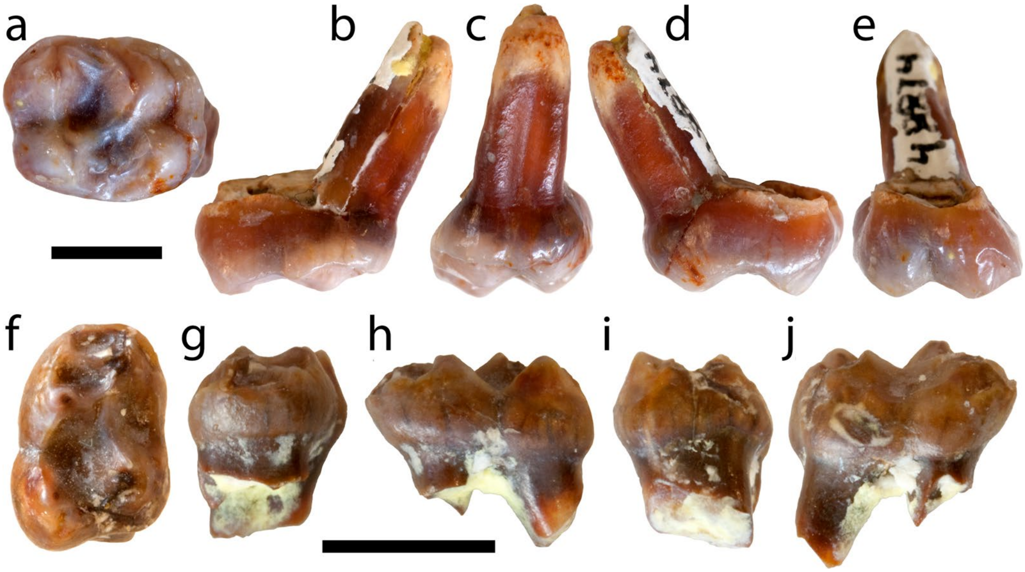

Fig. 1 Teeth of Anapithecinae nov. from the Vallès-Penedès Basin described in this paper: **a**–**e** right M^2 (MGSB48874) from SQ-TF, in occlusal (**a**), mesial (**b**), lingual (**c**), distal (**d**), and buccal (**e**) views; **f**–**j** right dP_4 (IPS34565) from CF2, in occlusal (**f**), mesial (**g**), lingual (**h**), distal (**i**), and buccal (**j**) views

39, respectively) but remain embargoed until an ongoing study of the enamel thickness is published. The µCT scan raw data are curated at the ICP and deposited in MorphoSource, being accessible upon reasonable request for research purposes to the ICP collection manager.

Measurements, dental nomenclature, and body mass estimation

Dental measurements of mesiodistal length (MD) and buccolingual breadth (BL) were taken from the original specimens to the nearest 0.1 mm with a digital caliper. A breadth/length index was computed (in %) as BLI = BL/MD × 100. Dental nomenclature follows Harrison and Gu (1999) and is further depicted for the M^2 and dP_4 in Fig. 2. Body mass (BM, in kg) was estimated for the SQ-TF M^2 based on occlusal square area (A, in mm^2) by means of anthropoid allometric equations (Egi et al., 2004); logarithmic detransformation bias was corrected using the ratio estimator (Smith, 1993); both the 50% and 95% confidence intervals (CIs) for the prediction were computed using the standard error of estimate and an inverse Student's t distribution with the degrees of freedom determined by the effective sample size (Smith, 1994).

Geometric morphometric analysis

The 3DGM analysis of EDJ shape was performed using the M^2 set of landmarks previously used in Bouchet et al. (2024b), composed of five landmarks placed at the apices of the four main dentine horns and at the mesiobuccal end of the cervix, as well as a total of 104 semilandmarks positioned along the main occlusal crests, the mesial and distal marginal ridges, and the cervical contour of the crown. Besides the M^2 from SQ-TF, only four pliopithecoid M^2s were included in this analysis, representing *B. huerzeleri* (IPS1724e), *P. cataloniae* (IPS58443.1 and IPS94888), and *Pl. canmatensis* (IPS41718). Landmark data were imported into R v. 4.1.1 (R Development Core Team, 2021) to perform Procrustes alignments using the 'ProcSym' function of the package 'Morpho' v. 2.9 (Schlager, 2021).

Similarities between the M^2 from SQ-TF and the other Iberian pliopithecoids were evaluated by means of cluster analysis based on the Euclidean distances between pairs of taxa raw landmark configurations (after Procrustes alignment). The unweighted pair group method with arithmetic mean (UPGMA) was employed, using the 'average' method of the 'hclust' function of the 'stats' package. The cophenetic correlation coefficient was calculated in both cases using the 'stats' package.

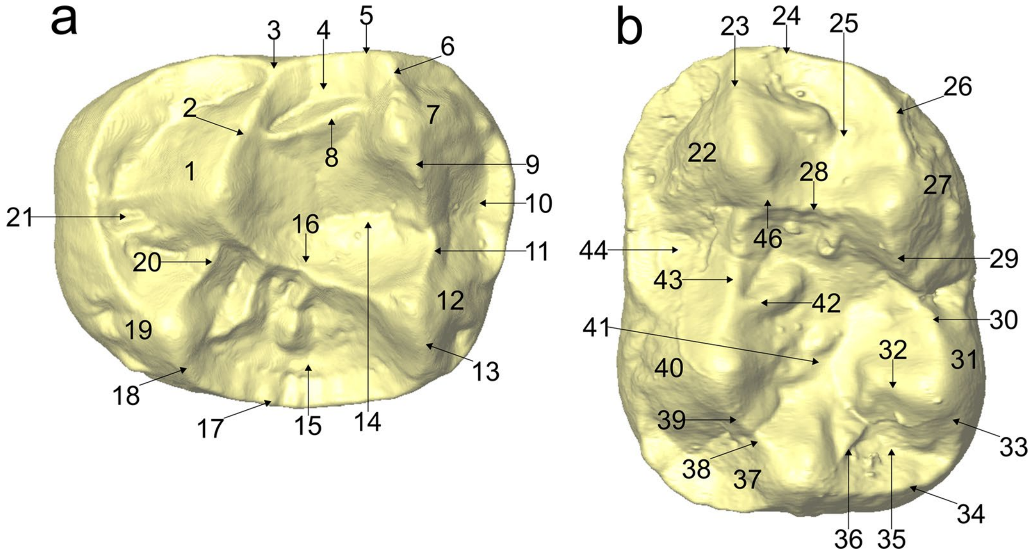

Fig. 2 Dental terminology used in this paper as exemplified by the renderings of two 3D outer enamel surface models of the crouzeliine *P. cataloniae* in occlusal view (see Bouchet et al., 2024a, 2024b): **a** left M^2 IPS94888; **b** left M_1 IPS43936. Legend: 1, protocone; 2, preprotocrista; 3, paraconule (= protoconule); 4, mesial fovea; 5, mesial marginal ridge; 6, preparacrista; 7, paracone; 8, hypoparacrista; 9, postparacrista; 10, buccal cingulum; 11, premetacrista; 12, metacone; 13, postmetacrista; 14, trigon basin (= central fovea); 15, distal fovea (= talon basin); 16, crista obliqua (= hypometacrista + postprotocrista); 17, distal marginal ridge; 18, posthypocrista; 19, hypocone; 20, prehypocrista; 21, lingual cingulum; 22, protoconid; 23, preprotocristid; 24, mesial marginal ridge; 25, mesial fovea (= trigonid basin); 26, premetacristid; 27, metaconid; 28, hypoprotocristid + hypometacristid; 29, postmetacristid; 30, pre-entocristid; 31, entoconid; 32, hypoentocristid; 33, postentocristid; 34, distal marginal ridge; 35, distal fovea; 36, postcristid; 37, hypoconulid; 38, prehypoconulid cristid; 39, posthypocristid; 40, hypoconid; 41, talonid basin; 42, distal arm of the pliopithecine triangle; 43, cristid obliqua (= prehypocristid + postprotocristid); 44, buccal cingulid

Cladistic analysis

We assessed the phylogenetic relationships of the species recorded by the M^2 from SQ-TF and the dP_4 from CF2—see the Discussion for the justification to treat them as a single species—by means of a cladistic analysis based on maximum parsimony using PAUP* v.4.0a169 for PC (Swofford, 2003). We relied primarily on the character-taxon matrix of dental features employed in Bouchet et al. (2024a), to which 12 newly defined characters for the dP_4 were added. Besides codifying the two specimens redescribed here (as a single taxon), we further coded the dP_4 from Contres (Gagnaison et al., 2006), dated to ~15.3 Ma (MN5; De Perthuis et al., 2025), which we reassign to *Crouzelia auscitanensis* Ginsburg, 1975 for the reasons explained later in this paper. The present version of the character-taxon matrix (Additional file 1: Table S1; see character statements in Additional file 1: Table S2) includes 107 dental characters, of which 24 continuous and 9 parsimony uninformative. As in Bouchet et al. (2024a), the stem catarrhine *Aegyptopithecus zeuxis* was used as outgroup, all characters were treated as unordered, variable characters were scored as multistate, and continuous characters were discretized using the gap-weighted coding method (Thiele, 1993). A heuristic search method was applied to search for most parsimonious trees, using a random stepwise addition sequence (1000 replicates) followed by a tree bisection-reconnection branch swapping process (Swofford & Bell, 2017), and a strict consensus tree was generated. The consistency index (CI) excluding uninformative characters, retention index (RI), and rescaled consistency index (RCI) were computed. Clade robusticity was assessed by means of bootstrap analysis (1000 replicates) and Bremer's support indices.

Systematic paleontology

Order **Primates** Linnaeus, 1758
Parvorder **Catarrhini** Geoffroy Saint-Hilaire, (Geoffroy Saint-Hilaire, 1812)
Superfamily **Pliopithecoidea** (Zapfe, 1961a)
Family **Crouzeliidae** (Ginsburg & Mein, 1980)
Subfamily **Anapithecinae** (Alba & Moyà-Solà, 2012)
Anapithecinae nov.
(Figs. 1a–j and 3a, g).

Description

Trinxera del Ferrocarril-Sant Quirze The M^2 from SQ-TF (MD = 7.2 mm, BL = 8.9 mm, BLI = 124%; Figs. 1a–e and 3a) yielded a BM estimate of 11.0 kg (95% CI = 10.0–11.9 kg; 50% CI = 10.7–11.3 kg). This tooth (see also detailed description in Harrison et al., 2002) preserves the moderately worn crown and the lingual root. The presence of both mesial and distal interproximal wear facets discounts an alternate attribution to an M^3. The crown displays a subrectangular occlusal contour (somewhat broader than long) that is moderately constricted at about midlength (particularly on the buccal side) and slightly tapers distally (particularly on the buccal side). There are four pyramidal and relatively low main cusps, the buccal ones slightly more mesially located and buccolingually compressed than the lingual ones. The protocone is the largest cusp, followed by the paracone; the metacone is clearly smaller than the paracone, and subequal in size to the well-developed hypocone. The latter is more peripheral than the protocone, being located close to the distolingual corner of the crown. The curved preprotocrista ends in a distinct but small protoconule, located close to the middle of the crown at the mesial marginal ridge. The mesially directed preparacrista is very short; an obliquely oriented hypoparacrista runs from the mesial end of the preparacrista to about midlength of the preprotocrista, defining a fissure-like and oblique mesial fovea that is mostly situated on the buccal half of the crown. The subtriangular trigon basin is much deeper and more extensive, being buccally delimited by the moderately long postparacrista and the very short premetacrista, as well as by a thick, continuous and slightly curved crista obliqua. The postmetacrista is only slightly longer and more obliquely oriented than the premetacrista, ending at the buccal end of the distal marginal ridge. The moderately short and rather thin prehypocrista is mesiobuccally directed toward the distal aspect of the protocone base, at about midway of the hypoprotocrista but without joining it. The similarly short posthypocrista is obliquely oriented and merges with the lingual end of the distal marginal ridge. The distal fovea is subrectangular (broader than long) and well developed (subequal in size to the trigon basin but shallower). It displays a conspicuous development of enamel wrinkling (consisting of irregular crests radiating from the center of the basin toward the surrounding cusps and crista obliqua) but there is no continuous hypocone-metacone crest. There is a distinct and continuous lingual cingulum, which is particularly well developed (ledge-like) around the protocone, and much narrower along the mesial and lingual aspects of the hypocone (not encircling the distal aspect of the latter cusp). The buccal cingulum is discontinuous and poorly developed, constituted by distinct but narrow parastyle and metastyle, as well as a very short but wider cingular development coinciding with the buccal cleft between the paracone and metacone. The lingual root is longer than broad and displays an apicobasal sulcus on its lingual aspect, whereas the buccal roots are broken away from about the cervix level.

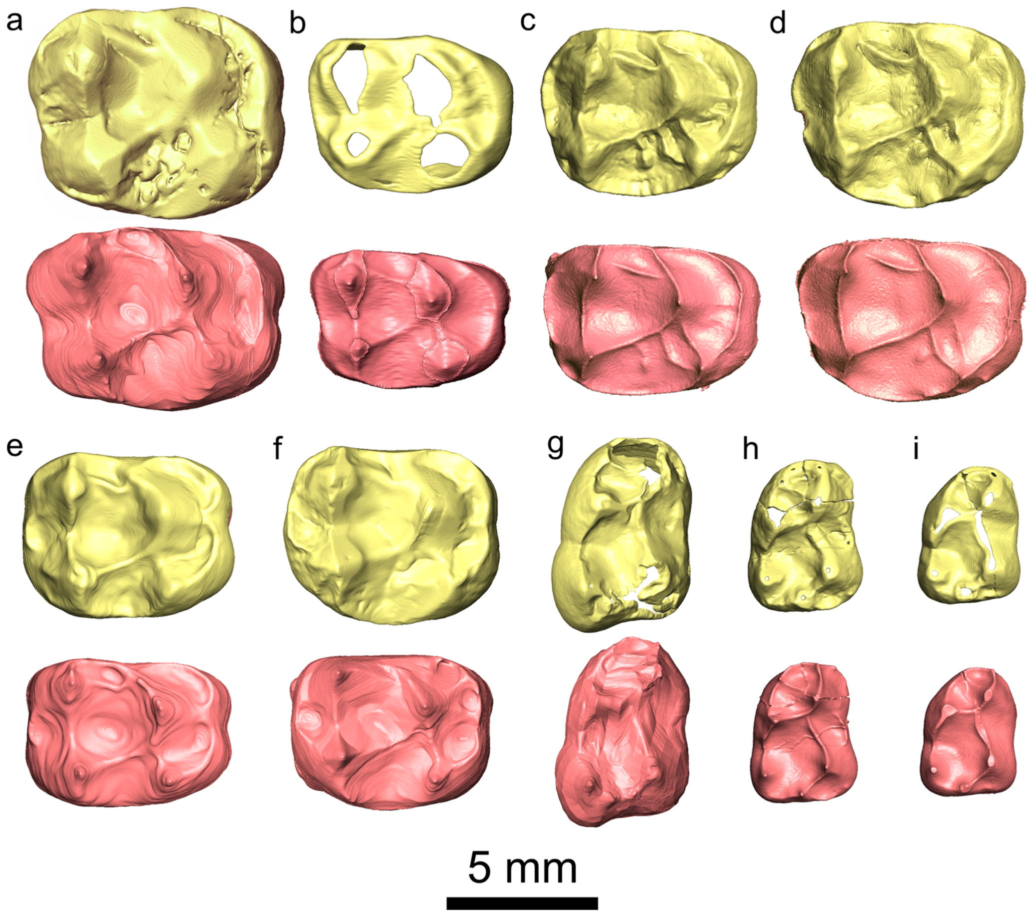

Fig. 3 Three-dimensional virtual renderings of the OES and EDJ of the anapithecine M^2 and dP_4 described in this paper and other pliopithecoid specimens of the same tooth loci from the Vallès-Penedès Basin: **a** right M^2 (MGSB48874) of Anapithecinae nov. from SQ-TF; **b**–**d** right M^2 (IPS58443.1, holotype; **b**), left M^2 (IPS94888; reversed; **c**), and left M^2 (IPS100384; reversed; **d**) of *Pliobates cataloniae* from ACM; **e** left M^2 (IPS1724e, holotype; reversed) of *Barberapithecus huerzeleri* from Castell de Barberà; **f** right M^2 (IPS41718) of *Pliopithecus canmatensis* from ACM; **g** right dP_4 (IPS34565) of Anapithecinae nov. from CF2; **h**–**i** left dP_4 (IPS43936, reversed; **h**) and left dP_4 (IPS106878, reversed; **i**) of *P. cataloniae* from ACM. The OES (in yellow) and EDJ (in rose) are depicted in occlusal view as if from the right side (indicated when reversed). Mesial is on top

Can Feliu 2 The dP_4 from CF2 (MD = 6.6 mm, BL = 4.7 mm, BLI = 71%; Figs. 1f–j and 3g) preserves the moderately worn crown as well as the basal-most portion of the mesial and distal roots. The crown only displays very slight dentine exposure at the apex of the lingual cuspids but some enamel chips are missing from the buccal cuspids, the preprotocristid, and the distolingual crown wall. The crown displays an asymmetric suboval contour that is much longer than broad and mesially tapering, with mild constrictions at about crown midlength (more marked on the lingual side) and a distolingually protruding corner. There are four main cuspids, which appear quite buccolingually compressed; the buccal ones are less peripheral and more mesially located than the corresponding lingual ones. A cuspulid-like thickening of the enamel (interpretable as a rudimentary hypoconulid) is located toward the lingual half of the crown just distobuccally from the entoconid. The crests are narrow and sharp. The short preprotocristid and the longer and curved premetacristid merge with the mesial marginal ridge. The mesial fovea is very extensive and longer than wide, being subdivided by a sharp secondary transverse cristid that connects the protoconid with a small cuspule-like thickening of the premetacristid (which might be alternatively interpreted as a vestigial paraconid). The mesial fovea is distally enclosed by the short hypometacristid and the obliquely oriented and longer hypoprotocristid, which originate distally from the protoconid. The cristid obliqua is longer and obliquely oriented (particularly the prehypocristid), with the postprotocristid originating from the hypoprotocristid rather than the protoconid apex. There is no pliopithecine triangle, although a poorly-developed secondary cristid originates midway from the hypometacristid and runs in parallel to the postprotocristid. The trigon basin is much longer and deeper than the mesial fovea, and about twice longer than broad, expanding distally to some extent because the hypoconid and entoconid are more peripherally located than the mesial cuspids. The prehypocristid is oriented toward the postprotocristid, forming a single and markedly oblique cristid obliqua. In contrast, the long postmetacristid and the pre-entocristid are not mesiodistally aligned. The morphology of the posthypocristid cannot be evaluated due to damage, but is present in the EDJ, and directed toward the central and distal parts of the crown. A very restricted (groove-like) and shallow distal fovea is located between the entoconid and the vestigial hypoconulid. There is no lingual cingulid, whereas the buccal cingulid is narrow and discontinuous, including a distinct protostylid and a broader portion at the level of the cristid obliqua, but further mildly extending around the distal aspect of the hypoconid.

Comparisons

Three-dimensional models of the OES and EDJ of the SQ-TF M^2 and CF2 dP_4 are compared with the same tooth loci from other Vallès-Penedès pliopithecoids in Fig. 3 (see also Bouchet et al., 2024a, 2024b).

Trinxera del Ferrocarril-Sant Quirze The occlusal morphology of the SQ-TF molar (Figs. 1a and 3a) clearly differs from the typical crouzeliid pattern displayed by *A. hernyaki*—characterized by very buccolingually compressed and peripheralized cusps (Begun, 2002: fig. 15.10c; Nargolwalla et al., 2005: figs. 2 and 3), as well as a buccal contour longer than the lingual (Bouchet et al., 2024a)—but it is not so different from the pattern displayed by *L. robustus* (Wu & Pan, 1984: pl. 1, fig. 2, pl. 3, fig. 2a; Pan et al., 1989: fig. 9) and *F. jini* (Harrison et al., 2020: fig. 7n–o). The SQ-TF M^2 differs from those of pliopithecids—i.e., *Pliopithecus* spp. and *Epipliopithecus vindobonensis* (Zapfe & Hürzeler, 1957; Hürzeler, 1954: figs. 2, 4, 5a, 7a; Zapfe, 1961a: figs. 5, 15, 16a; Harrison et al., 1991: figs. 7b–c, 8–9; Alba et al., 2010: fig. 10d; Fig. 3f; see also Begun, 2002: fig. 15.4b–c)—and, to a lesser extent, the European crouzeliines *B. huerzeleri* (Alba & Moyà-Solà, 2012: fig. 4i, k; Fig. 3e), *P. cataloniae* (Alba et al., 2015; Bouchet et al., 2024a: fig. 2 m–r, 2024b; Fig. 3b–d), and the Mörgen M^1 (Heißig, 1999; Seehuber, 2009: pl. 11, fig. 8; Bouchet et al., 2024a) in the following features: somewhat more constricted occlusal contour at crown midlength, especially buccally; more reduced buccal cingulum and narrower lingual cingulum around the protocone; larger hypocone; more lingually-located hypocone (except the Mörgen M^1 and most *P. cataloniae* molars); shorter distal fovea (except for the three crouzeliines); and hypocone not very distal relative to the metacone (except for the three crouzeliines). In these regards, the SQ-TF molar more closely resembles the Asian anapithecines *L. robustus* (except for the long distal fovea and the large hypocone) and *F. jini*. The SQ-TF M^2 further differs from the three crouzeliines (and *A. hernyaki*) in having less compressed cusps, blunter crests, a buccal contour similarly long to the lingual and, except for *P. cataloniae* and the Mörgen specimen, less constricted lingually. The SQ-TF specimen resembles *L. robustus* and *F. jini* in the moderate buccolingual compression of the cusps and the very lingual position of the hypocone (as in *A. hernyaki*, which similarly displays a large hypocone), but differs from both taxa in the less peripheralized buccal cusps and the somewhat less reduced lingual cingulum (with a faint extension around the lingual portion of the hypocone), and further differs from *F. jini* in the much more obliquely oriented mesial fovea. In turn, the SQ-TF molar more closely resembles the M^1 from Mörgen than other crouzeliines and pliopithecids in the moderately developed lingual cingulum around the hypocone, as well as the M^1 from Mörgen and most *P. cataloniae* M^1s and M^2s in the more lingually located hypocone. The metacone is relatively small in the SQ-TF specimen, unlike in *A. hernyaki* and *L. robustus*, but like in *B. huerzeleri*, *F. jini*, *P. cataloniae*, and the M^1 from Mörgen.

Can Feliu 2 The dP_4 from CF2 (Figs. 1f and 3g) markedly differs from those of dionysopithecids (Harrison & Gu, 1999; Bouchet et al., 2024a: supplementary fig. 3d) and in many features it more closely resembles instead those of both pliopithecids and crouzeliids. Begun (2002) noted close similarities between the CF2 specimen and the dP_4 of *Pl. platyodon* (see Hürzeler, 1954: fig. 24d; Bouchet et al., 2024a: supplementary fig. 3e), but the former differs in several features: (1) a more elongate and relatively narrower crown, with a more mesially tapering contour; (2) a longer mesial fovea, with the protoconid much more mesially situated relative to the protoconid; (3) a distally instead of transversely oriented hypoprotocristid; (4) a more oblique cristid obliqua that joins the hypoprotocristid instead of the distal aspect of the protoconid; and (5) a relatively narrower talonid basin. In these regards, the CF2 specimen more closely resembles a dP_4 from the MN5 of Contres (France), which was attributed to *Pliopithecus piveteaui* (Hürzeler, 1954) by Gagnaison et al. (2006: fig. 2.4). However, given its closer similarities with the dP_4 of *F. jini* (Harrison et al., 2020: SOM fig. S1u–w; Bouchet et al., 2024a: supplementary fig. 3f–h), *P. cataloniae* (Fig. 3h–i), and *A. hernyaki* (Nargolwalla et al., 2005: fig. 2; Bouchet et al., 2024a: supplementary fig. 3c), an attribution of the Contres specimen to the crouzeliine *C. auscitanensis* seems more likely (see Discussion). The CF2 dP_4 resembles those of *A. hernyaki*, *P. cataloniae*, the Contres specimen, and, to a lesser extent, *F.*

jini, in the configuration of the hypoprotocristid and the cristid obliqua, which is also characteristic of the M_1 of some crouzeliids such as *A. hernyaki* (including the Salmendingen specimen; Begun, 1989: fig. 1; Begun, 2002: fig. 15.10; Bouchet et al., 2024a: supplementary fig. 1f–g) and *E. narcisoi* (Moyà-Solà et al., 2001: fig. 1; Bouchet et al., 2024a: supplementary fig. 1e, 2024b: fig. 3c–d). The CF2 specimen more closely resembles the Contres dP_4 than those of *A. hernyaki*, *F. jini*, and *P. cataloniae* in the poorly developed hypoconulid, the almost indistinct distal fovea (albeit it is similarly closed in, and very small in one specimen of, *F. jini*), and the more extensive mesial fovea (despite being also quite large in *P. cataloniae*). In contrast, the CF2 dP_4 more closely resembles those of *A. hernyaki*, *F. jini*, and *P. cataloniae* rather than the Contres specimen in the much less distal location of the metaconid, the relatively wider distal lobe compared to the mesial one, and the more extensive talonid basin. The CF2 specimen shows a distolingually protruding occlusal contour (with the entoconid more distally located than the hypoconid) more similar to the Contres dP_4, that of *F. jini* and, to a lesser extent, *A. hernyaki*, and has cuspids as compressed as those of *A. hernyaki*, *P. cataloniae*, and the Contres dP_4. In dP_4 size, the CF2 taxon is most similar to *A. hernyaki*, larger than *P. cataloniae*, and smaller than *F. jini.*

Results

Geometric morphometric analysis

The UPGMA cluster based on the EDJ shape (Fig. 4a) yields a well-supported topology, with a high cophenetic correlation coefficient (0.70). It shows greater affinities between *B. huerzeleri* and *P. cataloniae*, with the SQ-TF M^2 clustering with the former instead of *Pl. canmatensis*. The SQ-TF M^2 EDJ more closely resembles that of *B. huerzeleri* and *P. cataloniae* in the narrower occlusal contour, shorter distal fovea, slightly less distally located hypocone horn, and longer and more protruding trigon basin + mesial fovea (Fig. 4b). Compared with *B. huerzeleri* and *P. cataloniae*, the SQ-TF M^2 differs by the somewhat longer lingual profile and more prominent mesial marginal ridge, which is straighter (Fig. 4b). However, the structure of the UPGMA cluster analysis supports that the SQ-TF M^2 displays derived crouzeliid rather than pliopithecid affinities.

Cladistic analysis

The cladistic analysis based on dental features (Additional file 1: Tables S1–S2) results in 144 most parsimonious trees of 340 steps. The topology of the strict consensus tree (Fig. 5) is identical to that in Bouchet et al. (2024a: Fig. 5), except for the addition of the unnamed taxon from SQ-TF + CF2. The analysis thus supports the monophyly of pliopithecoids and dendropithecids as successive lineages of stem catarrhines, as well as that of dionysopithecids and crouzeliids within the Pliopithecoidea, whereas pliopithecids appear paraphyletic but are not well resolved (Bouchet et al., 2024a). Two crouzeliid subclades are further distinguished, which we classify as subfamilies Crouzeliinae and Anapithecinae following Harrison et al. (2020) and Bouchet et al. (2024a). The unnamed species from SQ-TF + CF2 is recovered by the analysis as an anapithecine sister to *F. jini*. According to the results of the analysis, the species from SQ-TF + CF2 possesses the following unambiguous anapithecine synapomorphies (Additional file 1: Table S3): M^1–M^2 with moderate to marked buccolingual waisting (at crown midlength) and dP_4 with narrow to reduced buccal cingulid and small distal fovea (actually vestigial in SQ-TF + CF2). In turn, among anapithecines, the species from SQ-TF + CF2 shares with *F. jini* the following unambiguous synapomorphies (Additional file 1: Table S3): upper molars with rather low cusps and very narrow dP_4.

Discussion

Taxonomic attribution

The presence of a medium-sized crouzeliid in the earliest Vallesian of the Vallès-Penedès Basin was generally accepted based on the CF2 dP_4 (Ginsburg, 1986; Moyà-Solà et al., 1990, 2001; Andrews et al., 1996; Harrison et al., 2002; Alba & Moyà-Solà, 2012; Marigó et al., 2014; but see Begun, 2002). In contrast, the pliopithecid status of the M^2 from SQ-TF (Harrison et al., 2002) remained unchallenged (e.g., Marigó et al., 2014) until recently, when Bouchet et al. (2024b) left it unassigned to family but noted that its "potential crouzeliid status deserves further scrutiny". The SQ-TF molar does not display the derived pattern of the anapithecine *A. hernyaki*, but somewhat resembles the Asian anapithecines *L. robustus* and *F. jini*, and is more similar in some respects to crouzeliines (*P. cataloniae* and the Mörgen specimen). The dP_4 from CF2 similarly resembles that of crouzeliids, especially *P. cataloniae* and, to a lesser extent, *F. jini* as well as the dP_4 from Contres, here attributed to *C. auscitanensis*. Begun (2002) noted similarities between the CF2 dP_4 and that of *Pl. platyodon* and suggested that the former might belong to the same taxon recorded at Castell de Barberà, later described as a crouzeliid (*B. huerzeleri*) by Alba and Moyà-Solà (2012). However, this is most unlikely on the basis of size, with the CF2 dP_4 belonging to a taxon larger than *B. huerzeleri* and more similar in size to that represented at SQ-TF, *A. hernyaki*, and—as already noted by Andrews et al. (1996)—*E. narcisoi*. It is very likely that the CF2 and the SQ-TF specimens, given their crouzeliid affinities as well as close

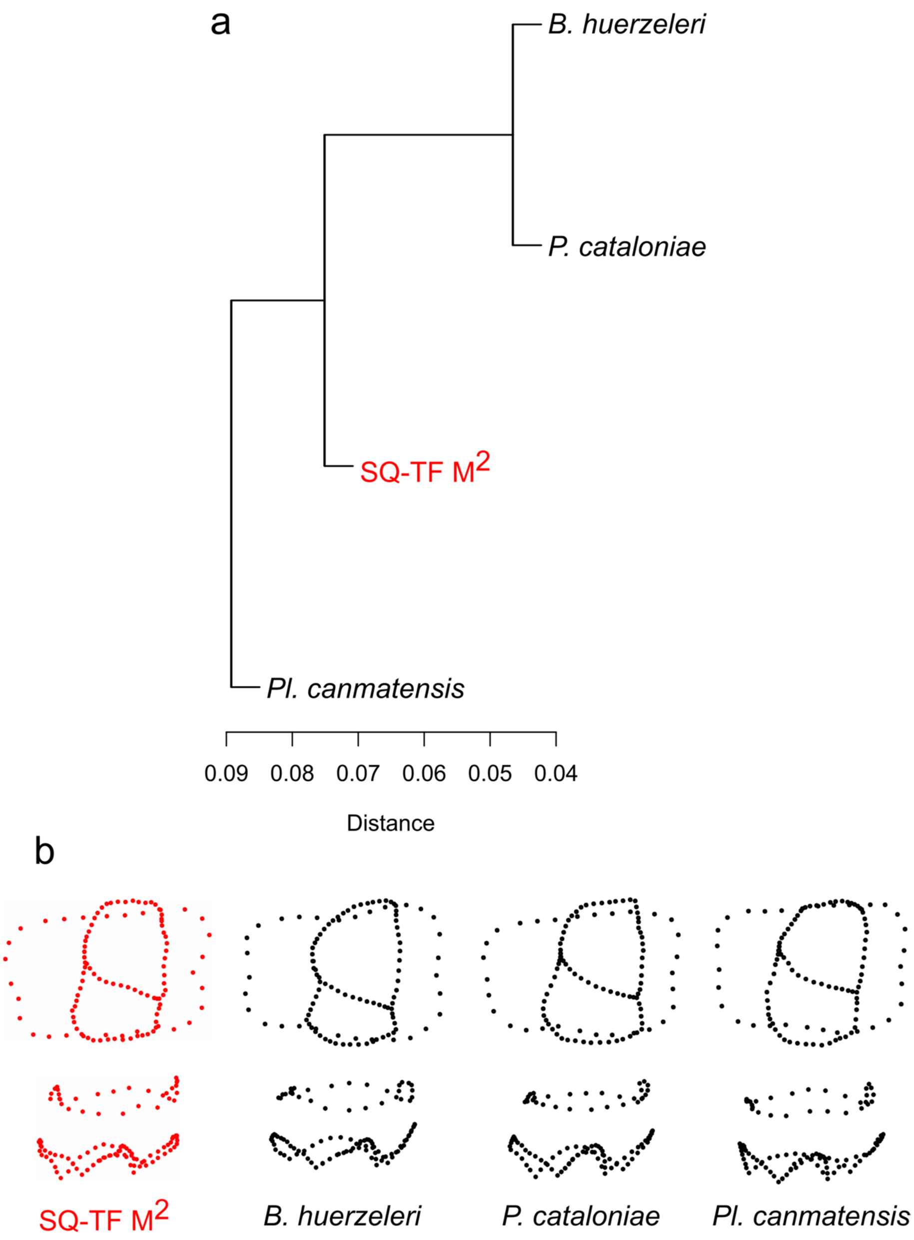

Fig. 4 Results of the three-dimensional geometric morphometric analysis of EDJ shape for the anapithecine crouzeliid M^2 from SQ-TF and those of other pliopithecoids from the Vallès-Penedès Basin: **a** Cluster using the unweighted pair group method with arithmetic mean based on the Euclidean distances calculated from raw coordinates of EDJ landmark configurations (cophenetic correlation = 0.70); **b** EDJ shapes illustrated both in occlusal (top, with mesial on top) and buccal (bottom, with mesial on left) views

geographic and temporal proximity, belong to a single, medium-sized crouzeliid species.

The scarcity of the available remains and the lack of more diagnostic material (such as the lower molars) makes it difficult to determine, based on qualitive comparisons, whether this species would be more closely related to similarly-sized anapithecines (such as *Anapithecus* and *Egarapithecus*) or to small-bodied crouzeliines (such as *Crouzelia*, *Pliobates*, and the Mörgen specimen). However, assuming that both specimens belong to a single species, our cladistic analysis supports closest affinities with anapithecines and, in particular, with the basal-most species of this clade (*F. jini* from the Early Miocene of China), instead of crouzeliines or other anapithecines recorded in the Vallès-Penedès Basin. Although the inclusion of the species from SQ-TF + CF2 in *Fanchangia* can be discounted based on multiple occlusal differences, our results tentatively suggest that

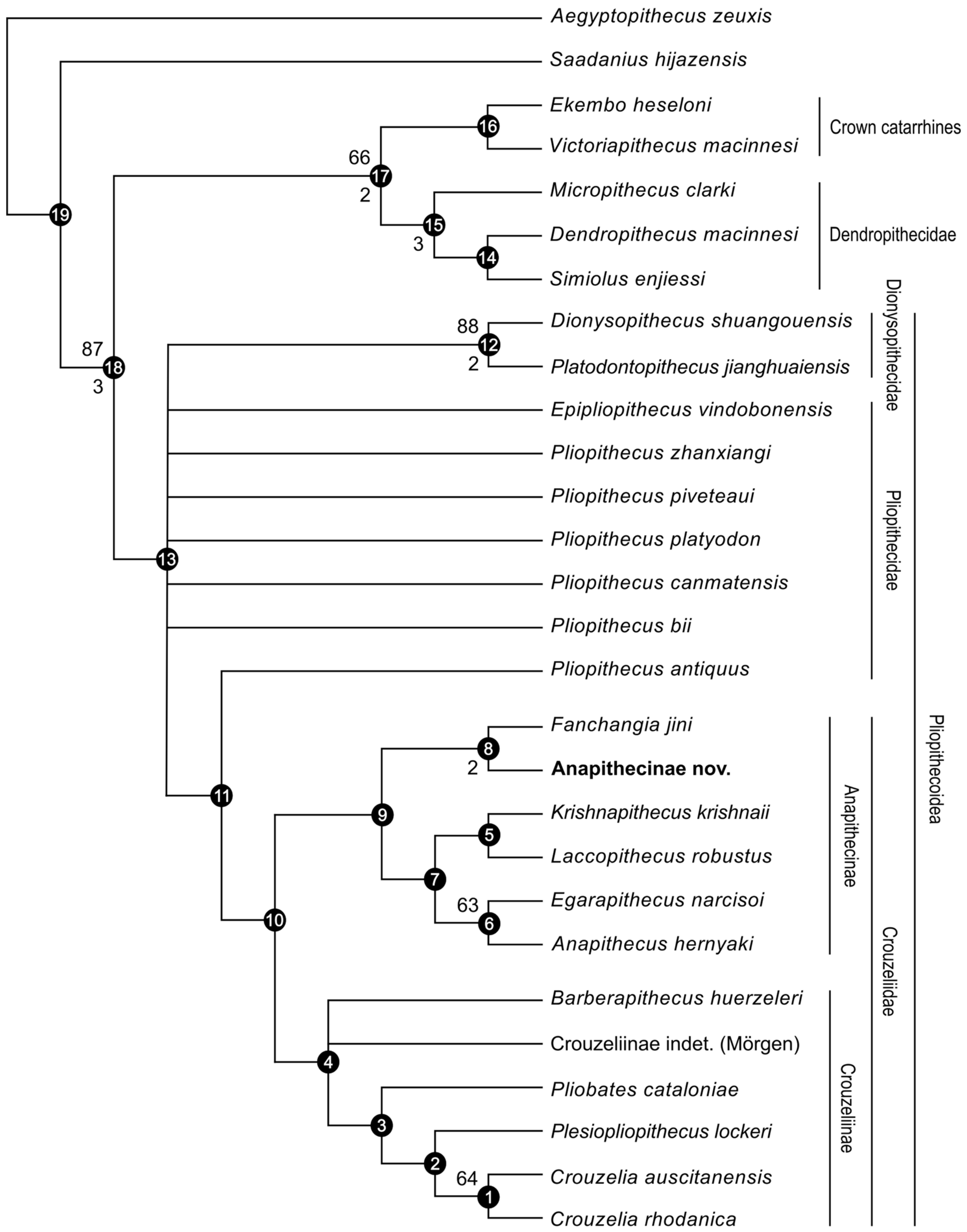

Fig. 5 Strict consensus cladogram derived from the 144 most parsimonious trees based on a taxon-character data matrix for 28 taxa and 107 dental characters. Tree length = 340 steps; CI (excluding uninformative characters) = 0.409; RI = 0.512; RCI = 0.209. Bootstrap percentages (only shown when ≥ 50%) and Bremer's indices (only shown when > 1) are reported above and below the nodes, respectively. The list of characters and the taxon-character matrix can be found in Additional file 1: Tables S1–S2, respectively. Node numbers refer to the apomorphy list in Additional file 1: Table S3. The systematic position of the SQ-TF pliopithecoid is highlighted in bold

the studied remains belong to a genus different from *Egarapithecus*. On the other hand, additional material would be required to (1) confirm that the remains from SQ-TF and CF2 belong to the same species, and (2) to discount that the sister-taxon relationship with *F. jini* recovered by the analysis is not merely an artifact caused by the large number of missing data. In the light of such uncertainties, and pending the recovery of additional material, we refrain from erecting a new taxon and refer the pliopithecoid specimens from SQ-TF and CF2 to Anapithecinae nov.

Paleobiogeographic implications

The attribution of the SQ-TF and CF2 material to a medium-sized anapithecine crouzeliid has some paleobiogeographic implications for the evolutionary history of this clade. Although pliopithecoids probably originated in Afro-Arabia by the end of the Oligocene (Harrison, 1987; Bernor, 1988; Harrison et al., 1991; Andrews, 1996; Harrison & Gu, 1999), their fossil record is restricted to Eurasia. They seemingly dispersed after the closure of the Tethys seaway ~19 Ma (Fig. 6a), which enabled multiple intercontinental faunal dispersals (Harzhauser et al., 2007; Rögl, 1998, 1999). Soon thereafter (~19–18 Ma), dionysopithecid pliopithecoids are recorded in Asia (Harrison & Gu, 1999), closely followed by the crouzeliid *Fanchangia* from China ~18–17 Ma (Harrison et al., 2020; Fig. 6a). The latter predates the earliest record of crouzeliids from Europe, which is customarily dated to ~14 Ma (MN6; Fig. 6b), corresponding to the crouzeliines *Crouzelia* from France (Bergounioux & Crouzel, 1965; Ginsburg & Mein, 1980) and *Plesiopliopithecus* from Austria (Alba & Berning, 2013; Ginsburg, 1975; Zapfe, 1960, 1961b). The first occurrence of pliopithecids (*Pl. piveteaui*) is dated to early MN5 (Ginsburg, 1986; Ginsburg & Mein, 1980), i.e., ~16–15 Ma (Hilgen et al., 2012). However, the first occurence of crouzeliids in Europe might be older than customarily assumed, and roughly coeval with that of pliopithecids, if the Contres specimen belongs to *C. auscitanensis* instead of *Pl. piveteaui* (as proposed here), given that this site is correlated to late MN5 (Castillo et al., 2006; Gaignaison et al., 2006), ~15–14 Ma (Hilgen et al., 2012). This would support the view that crouzeliids diverged from pliopithecids in Asia and that both clades dispersed

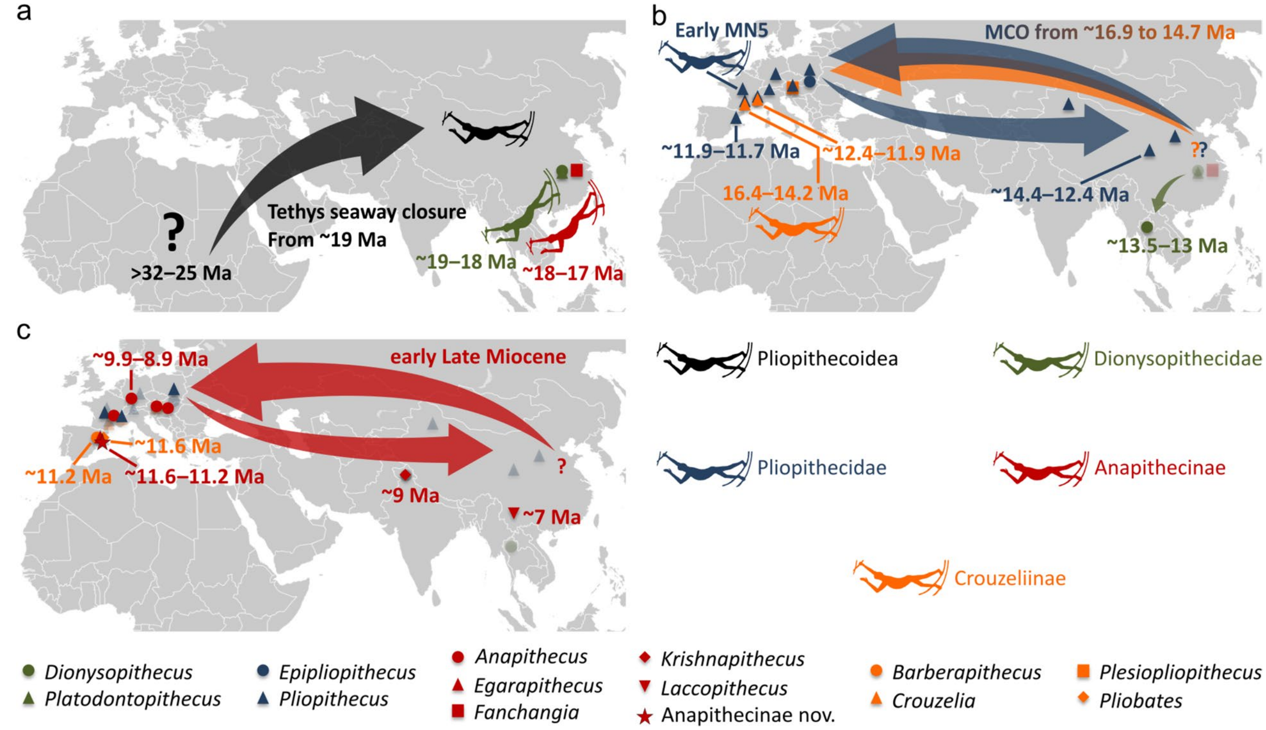

Fig. 6 Pliopithecoid geographic distribution and dispersal event hypotheses from Early to Late Miocene. **a** Early Miocene (23.0–16.0 Ma); **b** Middle Miocene (16.0–11.6 Ma); **c** Late Miocene (11.6–5.3 Ma). Colored arrows (with colors corresponding to the various clades) indicate dispersal events. In each panel, the first and last occurrences for each pliopithecoid (sub)family (in Europe and Asia separately) are detailed by specifying the ages. Question marks denote the likely place of origin for the various clades. MN5 spans from ~16.4 to 14.4 Ma (Casanovas-Vilar et al., 2016a; Hilgen et al., 2012; McKenzie et al., 2022), while the Miocene Climatic Optimum (MCO) spans between ~16.9 and 14.7 Ma (Steinthorsdottir et al., 2021). Except for the anapithecine from SQ-TF and CF2, only formally described pliopithecoid taxa are represented

into Europe (Harrison, 2005) during the Miocene Climatic Optimum (MCO, ~16.9–14.7 Ma; Steinthorsdottir et al., 2021)—given that both clades are first recorded in Europe during MN5, postdating the first appearance datum of crouzeliids (i.e., *Fanchangia*) in Asia. Crouzeliids subsequently experienced an evolutionary radiation during the late Middle and early Late Miocene of Europe—where they are last recorded by the anapithecine *Egarapithecus* at ~9.1 Ma (Casanovas-Vilar et al., 2016a; Moyà-Solà et al., 2001)—whereas in contrast they survived until later in Asia, being last recorded by *Laccopithecus* ~7 Ma (Begun, 2017; Harrison, 2013; Harrison et al., 2020; Fig. 6c).

Given the close phylogenetic relationships between *Laccopithecus* from China and the European anapithecines *Anapithecus* and *Egarapithecus* (Bouchet et al., 2024a), it has been hypothesized that this crouzeliid subclade (i.e., Anapithecinae) originated in Europe (presumably from crouzeliine ancestor) not later than MN9 and subsequently dispersed back into Asia (Harrison et al., 2020; Fig. 6c). Alternatively, European anapithecines might have originated from a dispersal event of crouzeliids from Asia different from the one that gave rise to crouzeliines. This second possibility would be most reasonable from a biochronological and paleobiogeographic viewpoint, given that the beginning of the Vallesian land mammal age (MN7+8/MN9 boundary) is characterized by the arrival of eastern immigrants (hipparionin equids, machairodontine felids, giraffids, and suines) into Europe at ~11.2 Ma (Alba et al., 2022). The strong faunal similarities between Europe and China by this time (Begun & Kelley, 2016) have led to consider the possibity that primates such as hominoids where also involved in intercontinental dispersal events around the MN7+8/MN9 boundary (Alba et al., 2022)—particularly in the light of the possible dryopithecine affinities of *Sinopithecus* spp. (formerly considered a pongine and included in *Lufengpithecus*; see discussion in Urciuoli & Alba, 2023).

The fact that a medium-sized anapithecine crouzeliid is recorded both before and after the beginning of the Vallesian in the Vallès-Penedès Basin argues against a synchronous dispersal event with hipparionins and other eastern immigrants at this time. However, the closest phylogenetic relationships with the basal crouzeliid *Fanchangia*, recovered as an anapithecine by our analyses (see also Bouchet et al., 2024a), does indeed support the possibility that two dispersal events of crouzeliids from Asia into Europe took place: one during the early Middle Miocene, giving rise to crouzeliines; and another during the early Late Miocene, involving anapithecines.

Conclusions

The redescription and comparisons of the pliopithecoid M^2 from SQ-TF (~11.6–11.2 Ma) and dP_4 from CF2 (<11.2 Ma) with other pliopithecoids support their crouzeliid status as well as closer affinities with anapithecines. Based on size congruence and close geographic and temporal proximity, the two specimens most likely belong to a single medium-sized species, which our cladistic analysis recovers as the sister taxon of *Fanchangia*, within anapithecines. It was previously considered that anapithecines locally evolved in Europe after the dispersal of the earliest crouzeliids from Asia during the early Middle Miocene. However, the record from the Vallès-Penedès Basin of a European anapithecine that is older than other known anapithecines from Europe and appears most closely related to the oldest crouzeliid (and anapithecine) *Fanchangia* rather supports a separate dispersal event for anapithecines (not later than the earliest Late Miocene), independent from the oldest dispersal of crouzeliines during the MCO. In conclusion, our results support that crouzeliines might have locally arisen in Europe after the first dispersal event of crouzeliids from Asia, but did not give rise to anapithecines, which would have dispersed from Asia at a later time.

Abbreviations

D/d	Deciduous
EDJ	Enamel-dentine junction
M/m	Molar
OES	Outer enamel surface
P/p	Premolar
BL	Maximum buccolingual breadth
BLI	Breadth/length index
MD	Mesiodistal length
CI	Consistency index
RCI	Rescaled consistency index
RI	Retention index
CF2	Can Feliu 2 (=Can Pagès, Can Sant Feliu)
SQ-TF	Sant Quirze–Trinxera del Ferrocarril
ICP	Institut Català de Paleontologia Miquel Crusafont, Sabadell, Barcelona, Spain
IPS	Acronym of the ICP collections (following the former informal name of this institution, 'Institut de Paleontologia de Sabadell')
MGSB	Museu Geològic del Seminari de Barcelona, Barcelona, Spain

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13358-025-00404-2.

Additional file 1.

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Author contributions

FB and DMA designed research; FB, SMS, and DMA assembled the cladistic data matrix; FB and DMA performed the descriptions and comparisons; FB performed the analyses; JF supervised microCTscanning and segmentation; CZ contributed to the segmentation and reconstruction of MGSB48874; CZ, SMS, and DMA contributed to the interpretation of the results; FB and DMA wrote the paper with input from all other authors.

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Data availability

All data supporting the findings of this study are available within the paper and its additional file. The described original fossils are available for study from the ICP and MGSB, which are registered museums recognized by the Generalitat de Catalunya.

Declarations

Ethics approval and consent to participate

Not applicable.

Competing interests

The authors declare no competing interests.

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