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Late Miocene Tapiridae from Vallès-Penedès Basin (NE Iberian Peninsula): taxonomic and paleoenvironmental implications

Luca Pandolfi[1*], Sara G. Arranz[4], Sergio Almécija[2,3,4], Jordi Galindo[4], Àngel H. Luján[4], Marta Pina[4], Alessandro Urciuoli[4,5,6], Isaac Casanovas-Vilar[4] and David M. Alba[4]

Abstract

European Miocene tapirs (Perissodactyla, Tapiridae) are mainly documented by isolated and fragmentary remains, and little is known about the morphological variability of the various recognized species, in particular concerning the deciduous dentition. Here, we describe new material from three Vallesian (Late Miocene) sites of the Vallès-Penedès Basin (NE Iberian Peninsula): Creu de Conill 20 (CCN20; earliest MN9, 11.2 Ma), Can Llobateres 1 (CLL1; earliest MN10, 9.8 Ma), and Can Gambús-Illeta 5 (CGS-I5; MN10, 9.7–9.1 Ma). The described material, including previously reported specimens from CLL1, consists of a juvenile cranium as well as deciduous and permanent teeth, which are compared with those of Late Miocene tapirid species from Europe (*Tapirus priscus*, *Tapirus antiquus*, *Tapiriscus pannonicus*, *Tapiriscus balkanicus*, and *Tapirus arvernensis*), supporting an attribution to *T. priscus*. The Vallès-Penedès specimens provide further insight into the morphological variability of *T. priscus*, particularly regarding its deciduous dentition, as well as its distinction from *T. arvernensis*. *Tapirus priscus* occurred in Western Europe during the early and late Vallesian (MN9–MN10) and became extinct in Central Europe during the early Turolian (MN11), leaving a gap in the fossil record of *Tapirus* until the arrival of *T. arvernensis* at the MN13–MN14 transition. From a paleoecological perspective, the presence of *Tapirus* agrees with paleoenvironmental reconstructions of CLL1 as a humid and densely forested wetland/riparian forest with more open areas nearby, while the CGS-I5 material attests to the persistence of such kind of environments in the Vallès-Penedès Basin sometime into the late Vallesian. In contrast, the occurrence of *Tapirus* is at odds with previous paleoenvironmental inferences for CCN20, which indicated a more open and arid environment, suggesting that the earliest Vallesian in this basin was characterized by more humid and forested conditions than previously assumed (in further agreement with the roughly coeval site of Castell de Barberà).

Keywords *Tapirus*, Deciduous dentition, Dental morphology, Vallesian, Spain

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*Correspondence:
Luca Pandolfi
luca.pandolfi1@unipi.it
Full list of author information is available at the end of the article

Introduction

Tapirids are currently represented by the single genus *Tapirus* Brisson, 1762, which is nowadays restricted to Southeast Asia (Traeholt et al., 2016) and some areas of Central (García et al., 2016) and South America (Lizcano et al., 2016; Varela et al., 2019). However, during the Neogene tapirids were widespread in Europe (Eisenmann & Guérin, 1992; Guérin & Eisenmann, 1994; Heissig, 1999; Tsoukala, 2022; Pandolfi et al., 2023), where they apparently reached a diversity peak during the Late Miocene, being represented by several species of the genera *Tapirus* and *Tapiriscus* Kretzoi, 1951; these include *Tapirus antiquus* Kaup, 1833, *Tapirus priscus* Kaup, 1833, and, possibly, *Tapirus arvernensis* Croizet & Jobert, 1828, as well as the smaller *Tapiriscus pannonicus* Kretzoi, 1951 and *Tapiriscus balkanicus* (Spassov & Ginsburg, 1999). Although *Tapirus* has a long chronostratigraphic range (being first recorded by *Tapirus telleri* Hofmann, 1893 from the Middle Miocene) and geographic distribution (from Iberia to Georgia and from England to Greece) in Europe, the Miocene remains of this genus are scarce, and usually fragmentary, being mostly represented by isolated teeth or partial tooth series of adult individuals.

Tapirus antiquus is known only by two isolated teeth (Kaup, 1833, 1861; Guérin & Eisenmann, 1994): the M2 holotype from Eppelsheim (MN9, Germany), which is currently lost, and an M3 from Bermersheim (MN9, Germany). Meyer (1867) considered *T. antiquus* to be a junior synonym of *T. priscus*, but Haupt (1935) disagreed based on the larger dimensions of the M3, which Guérin and Eisenmann (1994) designated as the neotype of the species. More recently, Pandolfi et al. (2023) considered *T. antiquus* as a nomen dubium, because without additional specimens it is not possible to determine whether the M3 represents a distinct species or just a large individual of *T. priscus*. In contrast, *T. priscus* is documented by more complete material, including a partial skull and mandibles from Eppelsheim, together with isolated dental remains from several Central European localities spanning from MN9 to early MN11 (Eisenmann & Guérin, 1992; Franzen, 2013; Guérin & Eisenmann, 1994). In turn, *T. arvernensis* is well known during the Pliocene (Capellini, 1881; Croizet & Jobert, 1828; Del Campana, 1910; Fejfar et al., 2012; Guérin & Tsoukala, 2013; Janštová, 2004; Michaux et al., 1976; Pandolfi & Kotsakis, 2017; Pandolfi et al., 2023; Rustioni, 1992; Sala et al., 1990), whereas its latest Miocene record, based on two fragmentary teeth from Baccinello V3 (MN13, Italy, *T.* cf. *arvernensis* in Rook & Rustioni, 1991), has been disputed (Franzen, 2013). However, in Eastern Europe, *T. arvernensis* has been reported from the Turolian of the Beli Breg Basin (Bulgaria), together with *Tetralophodon longirostris*, by Maisch (2014). *Tapiriscus pannonicus* was described based on small-sized isolated lower premolars from Hungary, but it is also recorded from other Central and Eastern European sites from MN9 to MN12 (Azanza et al., 1993; Franzen, 2013; Guérin & Eisenmann, 1994; Schlosser, 1902). Finally, *Ta. balkanicus*—closely related to *Ta. pannonicus* according to Pandolfi et al. (2023)—is only known from the Turolian (MN12–MN13) in Bulgaria.

In the Iberian Peninsula, Late Miocene tapirids are particularly scarce, being restricted to two sites from Catalonia in NE Spain (Arranz et al., 2023; Golpe-Posse & Crusafont-Pairó, 1982): Teuleria del Firal (=El Firal; Seu d'Urgell Basin), including a P2 and an upper molar fragment (Almera, 1898; Bataller, 1918, 1924; Chevalier, 1909), and Can Llobateres 1 (Vallès-Penedès Basin), including by a DP2–M1 series, a lower molar, and a pyramidal. These remains, which are Vallesian in age (Casanovas-Vilar et al., 2011, 2016a), were assigned to *T. priscus* by previous authors (Bataller, 1918, 1924; Chevalier, 1909; Golpe-Posse & Crusafont-Pairó, 1982). Other reports from Catalonia, including the sites of Can Poncic (Vallès-Penedès Basin) and Ballestar (Seu d'Urgell Basin; Crusafont-Pairó & Golpe-Posse, 1974), must be considered erroneous (Golpe-Posse & Crusafont-Pairó, 1982). However, in recent years, new tapirid specimens have been collected from the Vallès-Penedès Basin, enriching the scanty Iberian record of the genus *Tapirus*. Here, we describe these new specimens and compare them with those previously published to justify their taxonomic attribution. Overall, the tapirid record from the Vallès-Penedès Basin includes eight specimens, mainly belonging to young individuals. The newly described specimens enable, for the first time, to describe in detail and investigate the morphological variability of craniodental features among juvenile individuals in a Miocene tapirid species.

Age and geological background

The tapirid material described herein comes from the fossil sites of Can Llobateres 1 (CLL1), Creu de Conill 20 (CCN20), and Can Gambús-Illeta 5 (CGS-I5), which are located in the Vallès Sector of the Vallès-Penedès Basin (NE Iberian Peninsula; Fig. 1). From a geological viewpoint, this basin is an elongate half-graben located near the coast of Barcelona (Spain), between the Littoral and Prelittoral Ranges. Thanks to considerable sampling efforts for about a century, the Vallès-Penedès Basin has yielded a rich record of fossil vertebrates that ranges from the Early to the Late Miocene (Casanovas-Vilar et al., 2016a, 2022). The three aforementioned sites belong to a continental lithostratigraphic formation termed the Upper Continental Units, which spans from the Middle

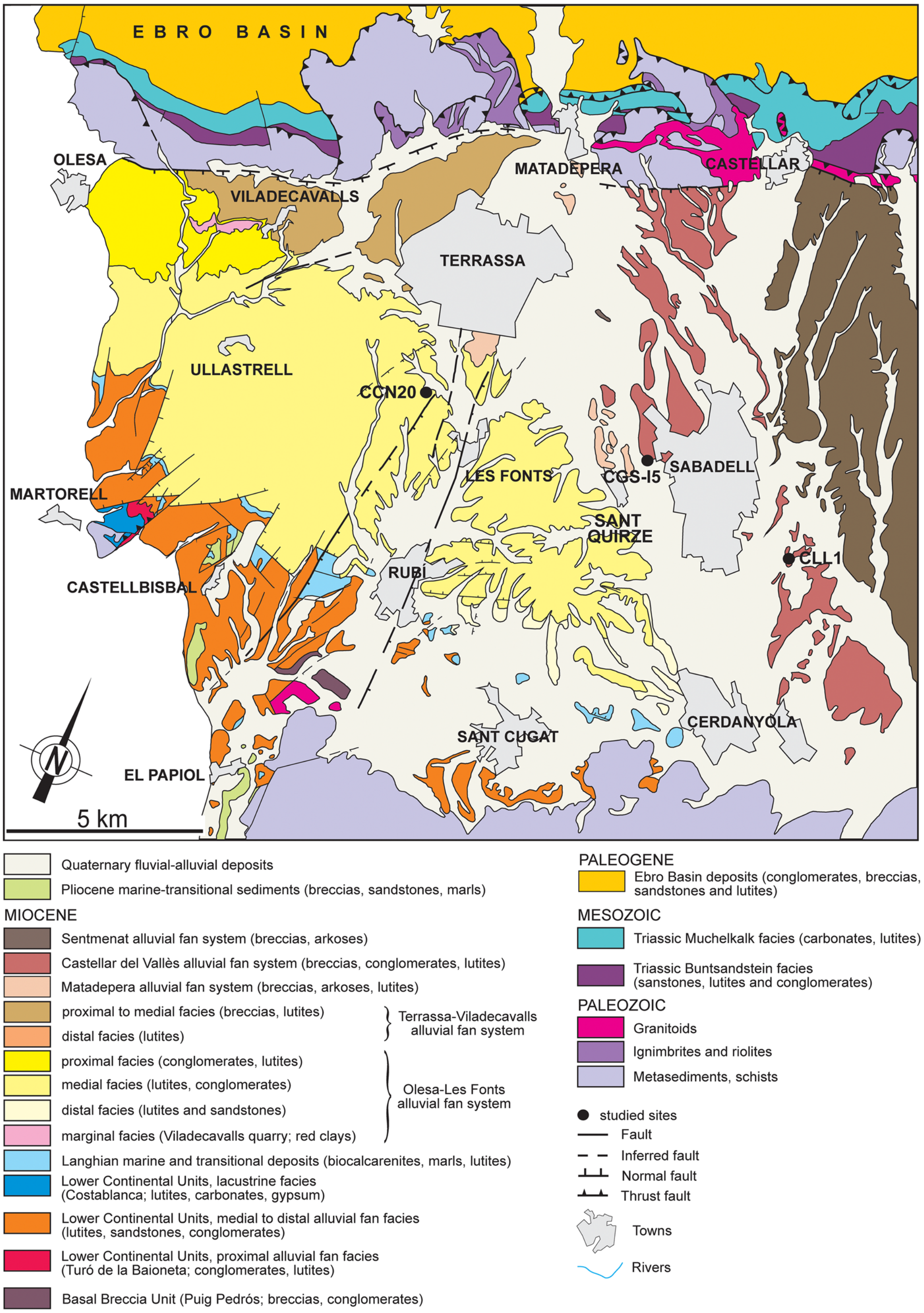

Fig. 1 Schematic geological map of the Vallès Sector of the Vallès-Penedès Basin (NE Iberian Peninsula) indicating the location of the sites from which the described tapirid material comes from. CCN20, Creu de Conill 20; CLL1, Can Llobateres 1, CGS-I5; Can Gambús-Illeta 5. Modified from Casanovas-Vilar et al., (2016a: Fig. 2). The UTM coordinates (31N/ETRS89) of each site are the following: CCN20 (418105, 4598340); CLL1 (428000, 4598250); CGS-I5 (423824, 4599134)

to the Late Miocene (Agustí et al., 1985; Casanovas-Vilar et al., 2016a, 2022).

Most of the material from CLL1 (Sabadell) was described by Golpe-Posse and Crusafont-Pairó (1982), who referred to the site without a number (i.e., CLL), although, in all probability, they come from the lower levels subsequently labeled as CLL1—as the upper levels (CLL2) were not systematically excavated until the 1990s (Moyà-Solà & Köhler, 1993, 1996; Fig. 2). However, we further describe here an isolated molar that was previously attributed by Golpe-Posse (1971) to a suid, as well as a previously unpublished deciduous premolar that, following the reopening of the site in 2010 (Alba et al., 2012a; Marmi et al., 2012), was recovered in 2012 from a sandstone layer corresponding to the paleochannel deposits termed CLL1.4a by Alba et al. (2012a). From a biostratigraphic viewpoint, CLL1 belongs to the *Cricetulodon hartenbergeri—Progonomys hispanicus* interval subzone of the Vallès-Penedès Basin, which spans from 9.98 Ma to 9.73 Ma (Casanovas-Vilar et al., 2016b), while based on magnetostratigraphic data (Agustí et al., 1996, 1997) an interpolated age of 9.76 Ma has been estimated for the locality (Casanovas-Vilar et al., 2016b; Fig. 2). Note, however, that while CLL1 was chosen as reference locality for MN9 (De Bruijn et al., 1992; Fahlbusch, 1976), based on a stratigraphic concept of MN zones (Hilgen et al., 2012), it should be correlated to MN10 because the MN9/MN10 boundary is placed at 10.0 Ma (Alba et al., 2018; Casanovas-Vilar et al., 2016a).

In turn, the material from CCN20 (Terrassa) was recently recovered in 2023 during systematic excavations of the site performed by the Institut Català de Paleontologia Miquel Crusafont (ICP). The site of CCN20 is correlated to the *Hippotherium—Cricetulodon hartenbergeri*

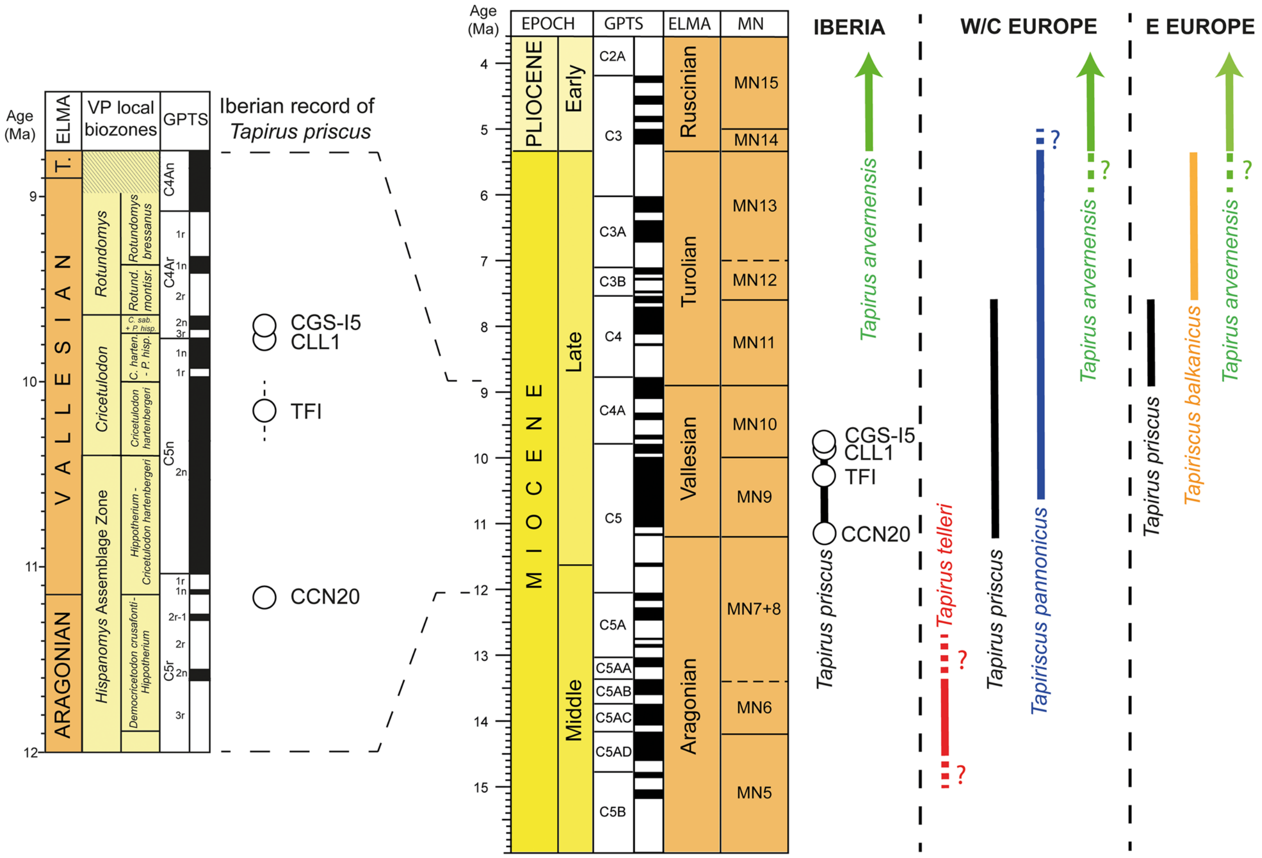

Fig. 2 Stratigraphic ranges of Miocene European tapirids and correlation of the studied sites. The different tapirid species are represented with different colors and their ranges are indicated in three distinct regions: Iberia, Western/Central Europe and Eastern Europe. Neogene timescale follows Hilgen et al. (2012). In the case of MN (Mammal Neogene) zones, their boundaries are indicated as defined by selected first appearance events (after Hilgen et al., 2012). The left panel indicates the Vallès-Penedès (VP) Basin local biozones after Casanovas-Vilar et al. (2016b). Teuleria del Firal, in the Seu d'Urgell Basin (Catalonia), is correlated to the VP biozones following Casanovas-Vilar et al. (2011). Dashed lines indicate uncertainties in the range of a given taxon or the correlation of a particular site. Locality abbreviations: CCN20, Creu de Conill 20; CLL1, Can Llobateres 1; CGS-I5, Can Gambús-Illeta 5; TFI, Teuleria del Firal. Other abbreviations: ELMA, European Land Mammal Ages; GPTS, Geomagnetic Polarity Timescale; MN, European Mammal Neogene zones

interval subzone of the Vallès-Penedès Basin (11.18–10.3 Ma; Casanovas-Vilar et al., 2016b; Fig. 2) but, indeed, it represents the first accurately dated appearance datum of hipparionin equids in Western Europe (2016b; Agustí et al., 1997; Alba et al., 2022; Casanovas-Vilar et al., 2006; Garcés et al., 1996; McKenzie et al., 2023). It is thus dated to the earliest Vallesian (MN9), with an interpolated age of 11.18 Ma corresponding to the base of chron C5r.1n (Casanovas-Vilar et al., 2016b), based on magnetostratigraphic correlation (Agustí et al., 1997; Garcés et al., 1996). Systematic excavations since 2016 have shown that, along the outcropping section, several successive mudstone fossiliferous layers, with a total thickness of ~5 m, can be distinguished between the conglomeratic layer CCN20H at the bottom and the capping layer of sandstone and conglomerates CCN20A at the top of the sequence (authors' unpublished data). The tapirid fossil reported here was recovered from CCN20E, approximately located at the middle of the sequence (~2.4–3.0 m above the bottom of the sequence), while the paleomagnetic samples used to estimate the interpolated age of the site, despite belonging to the same magnetozone, would presumably correspond to levels CCN20B (~4.5–5.5 m from the bottom). Based on the intrachron sedimentation rate of 69 cm/ky than can be computed for C5r.1n from the Can Guitart 1 section (Garcés et al., 1996), which is higher than the average sedimentation rate of ~20 cm/kyr for the Vallesian of the Vallès-Penedès Basin (Garcés et al., 1996), the fossiliferous sequence from CCN20 might represent a time span of ~8 kyr, implying a negligible age difference of just ~4 kyr between CCN20E and CCN20B. Furthermore, except for the lowermost fossiliferous layer CCN20G (which thus far has only yielded micromammal remains and a few remains of macromammals), all the other fossiliferous layers (including CCN20E) have yielded remains of *Hippotherium* sp. and are thus Vallesian by definition.

Finally, the tapirid cranium was recovered from CGS-I5 during a rescue excavation performed by the ICP between late 2022 and early 2023 in the area of Can Gambús (Sabadell). Previous fossil vertebrate finds from the above-mentioned area correspond to the site of Can Feu (Sant Quirze del Vallès) and were found in 1987 during an archeological excavation—being variously referred to the literature as Serrat de Can Feu (Santafé-Llopis et al., 1990) and in the ICP collections as Bòbila Madurell, due to the proximity to the archaeological site of Bòbila Madurell–Serrat de Can Feu. Subsequent finds were already referred to Can Feu (Alba et al., 2012b; Casanovas-Vilar et al., 2012; Méndez & Garcia-Fernández, 2001), including a hominoid partial skeleton recovered from the locality of Can Feu 1 as a result of construction works (Alba et al., 2012b). Based on rodent biostratigraphy of the almost coeval locality of Can Feu 2 (Casanovas-Vilar et al., 2012), both localities are correlated to the same local subzone as CLL1 (9.98–9.73 Ma; Casanovas-Vilar et al., 2016b). Subsequent isolated finds from Can Feu and the neighboring area of Can Gambús during the 2010s motivated the declaration of a paleontological protection area. Thanks to this fact, construction works recently performed since 2019 at Can Gambús required paleontological surveillance, leading to the recovery of additional fossil vertebrate remains. The outcropping section at CGS-I5 has a thickness of 27 m, and the tapirid cranium was recovered about 4 m above the bottom. The recovery of an M2 of *Rotundomys* cf. *freiriensis* 7 m above the tapirid cranium (i.e., 11 m above the bottom of the series) enables a correlation with the *Cricetulodon sabadellensis* + *Progonomys hispanicus* concurrent range subzone of the Vallès-Penedès Basin (9.73–9.65 Ma), which covers the entire range of *R. freiriensis* in the basin (Casanovas-Vilar et al., 2016b). Therefore, CGS-I5 would be slightly younger than CLL1, despite being also correlated to the earliest MN10.

Materials and methods

The described material is currently housed in the Institut Català de Paleontologia Miquel Crusafont (ICP). Comparisons are based on direct observation of Neogene and extant tapirid material housed in various institutions (HNHM, IGF, MCZR, MGG, NHMUK, NMB; see abbreviations below), as well as on measurements, iconography, and descriptions available from the published literature (Boeuf, 1991; Ferrero et al., 2014; Franzen, 2013; Guérin & Eisenmann, 1994; Perini et al., 2011; Rustioni, 1992)—see Table S1 for comparative measurements of Neogene and extant tapirids. The dental terminology and measurements follow Franzen (2013) and Pandolfi et al. (2023), with some additions (Fig. 3). The studied specimens were measured using a digital caliper. The scanty sample of deciduous teeth from extinct species does not allow any kind of statistical comparisons. The pyramidal from CLL1 described by Golpe-Posse and Crusafont-Pairó (1982) is not included here. The specimen has been exhaustively described and figured by the two authors (Golpe-Posse & Crusafont-Pairó, 1982: Fig. 3a–f) and there are no additional measurements or morphological characters to question the previous attribution. Further, the DP2 from Teuleria del Firal is not figured here, being illustrated by Bataller (1924: pl. 2, fig. 7) and currently housed at Museu de Ciències Naturals de Barcelona with the catalog number MCNB 4384–1 (Gómez-Alba, 1997).

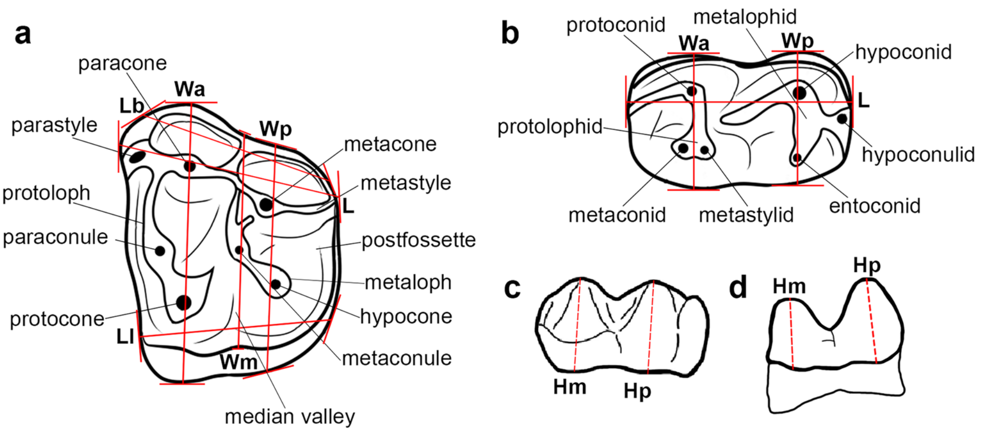

Fig. 3 Nomenclature of teeth and measurement protocol used in the text. **a**, upper left molar in occlusal view; **b**, lower right molar in occlusal view; **c**, upper left molar in labial view; **d**, lower right molar in labial view. H, maximal height of the crown measured from the base of the crown to its heighest point on the labial side; Hp, height of the paracone/protoconid; Hm, height of the metacone/hypoconid; Hpr, height of the protocone/metaconid; Hhy, height of the hypocone/entoconid; L, maximal mesiodistal length; Lb, labial length; Ll, lingual length; l, left; m, lower molar; M, upper molar; W, maximal labiolingual width; Wa, mesial (anterior) width; Wm, minimal width at the mid of the tooth; Wp, distal (posterior) width. Hpr and Hhy are not showed in figure; they are measured on the lingual side of the tooth following the same procedure used for Hp and Hm

Abbreviations

Institutional abbreviations. HNHM, Hungarian Natural History Museum, Budapest, Hungary; ICP, Institut Català de Paleontologia Miquel Crusafont, Sabadell, Barcelona, Spain; IGF, Museo di Storia Naturale dell'Università di Firenze, Sezione di Geologia e Paleontologia, Florence, Italy; IPS, Acronym of the ICP collections (for the former 'Institut de Paleontologia de Sabadell'); MCZR, Museo Civico di Zoologia di Roma, Rome, Italy; MGG, Museo di Geologia e Paleontologia G. Capellini, Bologna, Italy; NHMUK, Natural History Museum, London, UK; NMB, Naturhistorisches Museum, Basel, Switzerland.

Locality abbreviations. CCN20, Creu de Conill 20; CGS-I5, Can Gambús-Illeta 5; CLL1, Can Llobateres 1.

Anatomical and measurement abbreviations. DI, upper deciduous incisor; DP, upper deciduous premolar; r, right; H, maximal height of the crown measured from the base of the crown to its highest point on the labial side; Hp, height of the paracone/protoconid; Hm, height of the metacone/hypoconid; Hpr, height of the protocone/metaconid; Hhy, height of the hypocone/entoconid; L, maximal mesiodistal length; Lb, labial length; Ll, lingual length; l, left; m, lower molar; M, upper molar; W, maximal labiolingual width; Wa, mesial (anterior) width; Wm, minimal width at the mid of the tooth; Wp, distal (posterior) width.

Systematic paleontology

Class **Mammalia** Linnaeus, 1758
Order **Perissodactyla** Owen, 1848
Family **Tapiridae** Gray, 1821
Genus ***Tapirus*** Brisson, 1762
Tapirus priscus Kaup, 1833
Figures 4 and 5

Referred material: IPS11264, left maxillary fragment with DP2–M1 from CLL1 (Golpe-Posse & Crusafont-Pairó, 1982: Fig. 1); IPS11265, left M2 from CLL1 (figured as an M1 by Golpe-Posse & Crusafont-Pairó, 1982: fig. 2); IPS11266, partial right lower molar, probably m1 (reported, but not figured, as an m1? or dp4? by Golpe-Posse & Crusafont-Pairó, 1982); IPS11335, worn-out right DP2 from CLL1 (reported but not figured by Golpe-Posse & Crusafont-Pairó, 1982); IPS70116, right DP4 from CCL1W.S; IPS28172, worn-out lower right molar, probably m2 (identified as a left m1 of the suid *Listriodon splendens* with old catalog number [IPS1061] by Golpe-Posse, 1971, 1972); IPS136651, right mandibular fragment with m2–m3 from CCN20 (m3 is detached from the mandible); IPS133767, partial skull from CGS-I5 preserving the maxillary and premaxillary bones and bearing DI1, DI2, DP1, DP2, DP4 and M1 on the right side, and DI1, DI2, DI3, DP3–M1 on the left. See measurements in Table 1.

Description: The partial skull IPS133767 (Fig. 4) preserves the maxillary and premaxillary bones and bears the right DP1–DP2, DP4, and M1 and the left DP3–M1 (Fig. 4a), indicating that it belongs to a juvenile individual. The premaxillary bone is not connected with the main cranial fragment (Fig. 4b–c), the two parts being separated along the premaxillary-maxillary suture, which in lateral view terminates just in front of the canine alveolus (Fig. 4b–c). The premaxilla bears the left DI1–DI3 and the right DI1–DI2, although the alveolus of the

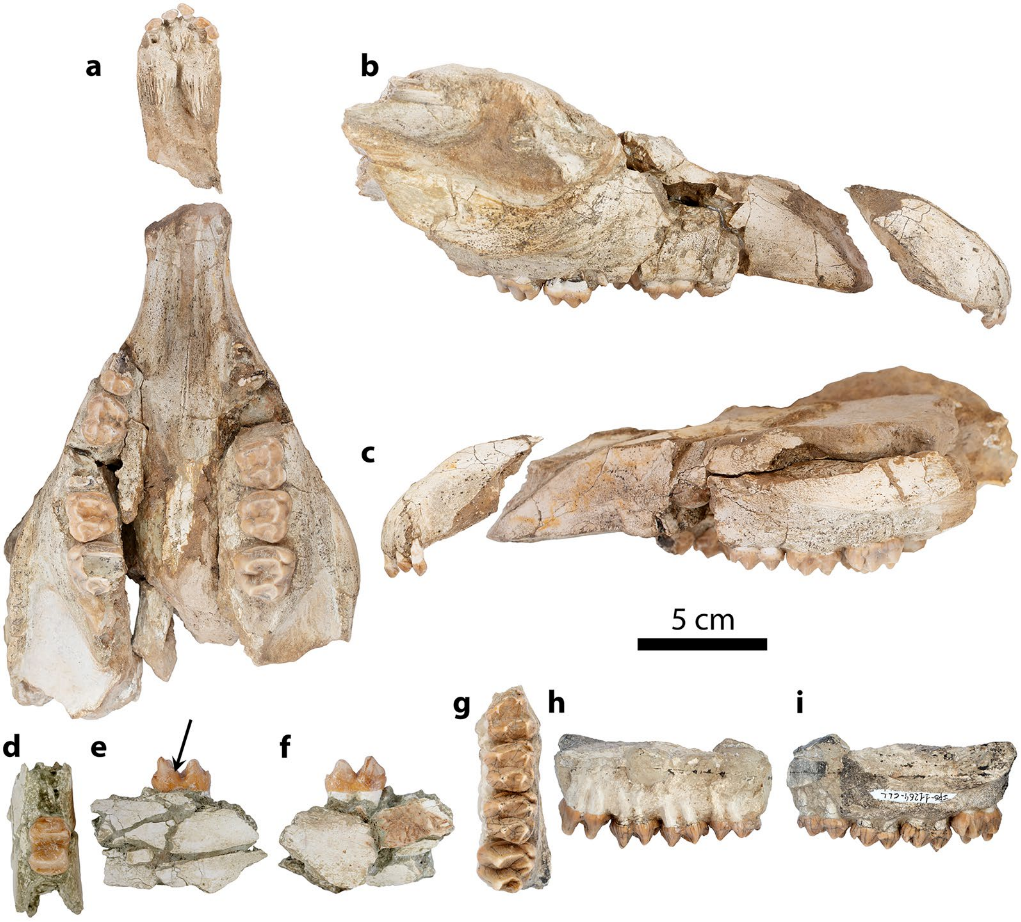

Fig. 4 Craniomandibular remains of *Tapirus priscus* from the Vallès-Penedès Basin: **a–c** IPS133767, cranium with I1–I2 and DP1–M1 from CGS-I5, in ventral (**a**), right lateral (**b**), and left lateral (**c**) views; **d–f** IPS136651, R mandibular fragment with m2 from CCN20E, in occlusal (**d**), lingual (**e**), and labial (**f**) views; **g–i** IPS11264, L maxillary fragment with DP2–M1 from CLL1, in occlusal (**g**), lingual (**h**), and labial (**i**) views. The arrow indicates the metastylid on the lingual view of m2 IPS136651

right DI3 is also present. Contrary to permanent incisors, DI1 and DI2 are longer than wide on extant *Tapirus* species, and display a less developed lingual cusp, similarly to IPS133767. DI3 is smaller than I3 and proportionally similar to DI2, while I3 is normally big and caniniform. In turn, the maxillary bone bears the alveoli of the right and left deciduous canines. The postcanine diastema is ~40 mm in length, and the most posterior part of the premaxilla terminates anteriorly to the DP1 (Fig. 4b–c). The DI1 bears a lingual cusp, and its occlusal surface is labiolingually concave. The DI2 is more asymmetric than the DI1 and displays a lingual cingulum. Both deciduous incisors display a triangular occlusal contour that is wider labially than lingually. The DI3 is slightly caniniform and displays a labial sulcus. The DI2 is larger than the DI1 and DI3. The DP1 bears a distal cingulum and an elongated lingual cusp not connected with the ectoloph (Fig. 5a). The DP2 (Fig. 5b) shows a labial cingulum below the metacone, and distal and mesial cingula. On this tooth, the parastyle is developed and connected to the protoloph by a short ridge. The protoloph is oblique and connected with the ectoloph anteriorly to the paracone, while the metaloph is transverse and connected with the metacone just at mid-height of the latter cusp. The protocone is less developed than the hypocone, and a lingual cusp is present at the entrance of the median valley. The DP3, DP4, and M1 bear a large parastyle, well-separated from the paracone. On the DP3 (Fig. 5e), the paracone is larger than the metacone, unlike in the DP4 (Fig. 5g–h) and M1 (Fig. 5k). The protocone and hypocone are similar in size in the DP3 and DP4, but the protocone is larger in the M1. Mesial, distal, and labial (below the metacone) cingula are present on the DP3, DP4, and M1. A small lingual cusp is present on the DP3 at the entrance of the median valley. The metaloph is shorter than the protoloph on all these teeth. On the DP3 and DP4, the metaloph is taller than the protoloph, and the hypocone is taller than the protocone, while on the M1 the two

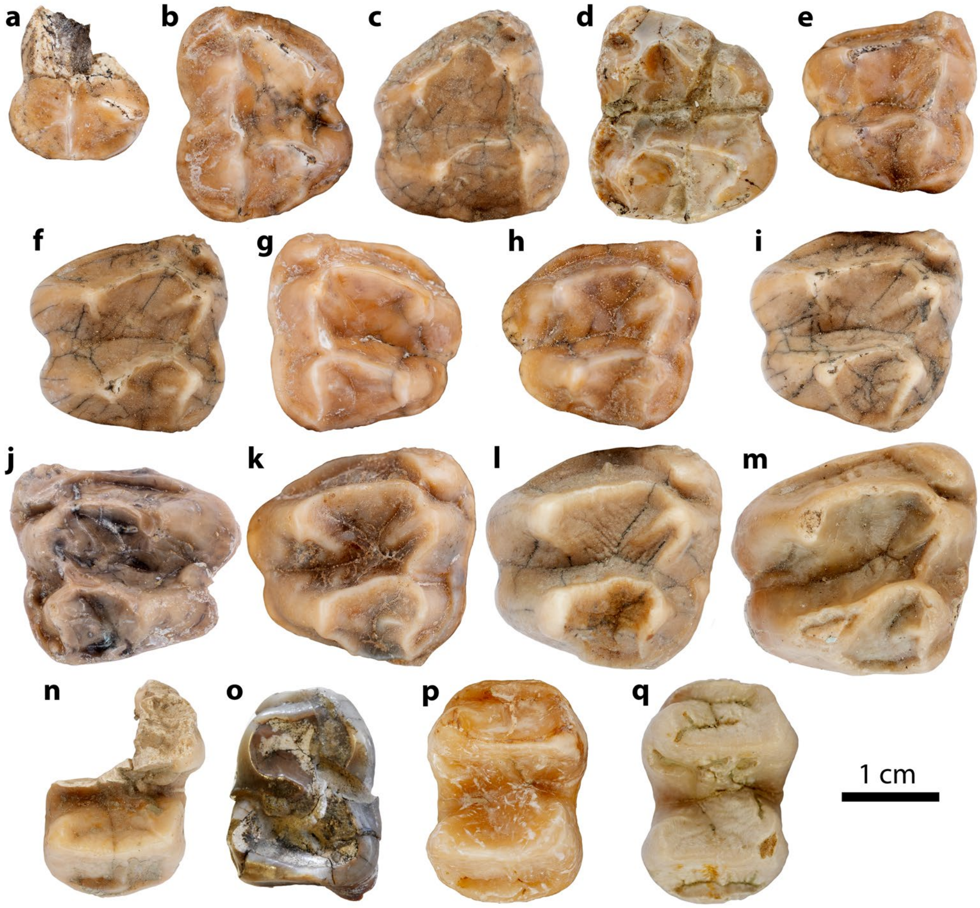

Fig. 5 Deciduous and permanent cheek teeth of *Tapirus priscus* from the Vallès-Penedès Basin, in occlusal view: **a** IPS133767, r DP1 from CGS-I5; **b** IPS133767, r DP2 from CGS-I5; **c** IPS11264, l DP2 from CLL1; **d** IPS11335, r DP2 from CLL1; **e** IPS133767, l DP3 from CGS-I5; **f** IPS11264, l DP3 from CLL1; **g** IPS133767, r DP4 from CGS-I5; **h** IPS133767, l DP4 from CGS-I5; **i** IPS11264, l DP4 from CLL1; **j** IPS70116, r DP4 from CLL1W.S; **k** IPS133767, l M1 from CGS-I5; **l** IPS11264, l M1 from CLL1; **m** IPS11265, l M2 from CLL1; **n** IPS11266, partial r m1? from CLL1; **o** IPS28172, r m2? from CLL1; **p** IPS136651, r m2 from CCN20E; **q** IPS136651, r m3 germ from CCN20E. Upper and lower teeth are depicted in anatomical position (i.e., with their occlusal side facing downward and upward, respectively) except for occlusal views (where mesial is toward the top)

latter lingual cusps are similar in height. In labial view, the paracone is similar in height to the metacone on the DP2 and DP3, but taller than the metacone on the DP4 and M1.

All the teeth in the maxillary fragment IPS11264 (Fig. 4g–i), which preserves the DP2–M1 series, bear a continuous mesial cingulum. The labial cingulum is present below the metacone and is connected with the distal cingulum (Fig. 4i). A faint lingual pillar is present on the DP2 (Fig. 5c) at the entrance of the median valley. On the DP4 (Fig. 5i) and M1 (Fig. 5l), the distal cingulum turns toward the apex of the hypocone, while it is low on the DP2 (Fig. 5c) and DP3 (Fig. 5f). The protocone and hypocone are well separated and the median valley is wide on all the teeth (Fig. 4g). The DP3–M1 have a fully developed protoloph and metaloph, joined with the ectoloph in front of the paracone and the metacone respectively (Fig. 5f, i, l). On the DP2 (Fig. 5c), the protoloph is more obliquely oriented than the metaloph, while it is transverse on the other teeth; the metaloph is weakly connected with the ectoloph. The parastyle is present and distinguished from the paracone, but on DP2–DP4 it is smaller than on the M1 and separated from the paracone by a deeper groove. The hypocone is slightly taller than the protocone on all the teeth. The paracone is taller than the metacone on DP3–M1 but not on DP2. The labial occlusal contour of the DP2 is markedly concave; this feature is less marked on the other teeth and basically absent from the M1 (Fig. 5l), where the minimal width of the crown almost equals its posterior width.

In the worn-out DP2 IPS11335 (Fig. 5d), most of the characters described above cannot be observed due to the advanced wear. The tooth displays a subtrapezoidal occlusal contour, concave on the labial side. The tooth

Table 1 Measurements in mm of the tapirid specimens from the Vallès-Penedès Basin. For abbreviations see Material and methods

Site	Specimen number	Tooth	Side	L	Lb	Ll	Wa	Wp	Wm	Hp/H	Hm	Hpr	Hhy
Can Gambús-Illeta 5	IPS133767	DP1	r		15.12			13.89			8.7		
Can Gambús-Illeta 5	IPS133767	DP2	r	21.87	21.85	14.08	16.81	18.06	14.69	9.2	9.1	9.4	6.4
Can Gambús-Illeta 5	IPS133767	M1	r		21.8		22.41						
Can Gambús-Illeta 5	IPS133767	DP4	r	20.43	20.13	15.4	20.0	18.75	18.62	9.3	8.1		12.4
Can Gambús-Illeta 5	IPS133767	DP3	l	20.57	20.57	14.99	19.36	18.11	16.24	8.8	8.6	9.4	10.6
Can Gambús-Illeta 5	IPS133767	DP4	l	20.42	20.42	14.5	22.08	18.25	18.22	9.4	8.0	11.7	12.0
Can Gambús-Illeta 5	IPS133767	M1	l	22.61	22.1	15.4	24.5	20.95	21.28	11.2	10.0	13.5	14.1
Can Gambús-Illeta 5	IPS133767	DI1	r	4.37			7.13			5.8			
Can Gambús-Illeta 5	IPS133767	DI2	r	4.86			7.5			5.3			
Can Gambús-Illeta 5	IPS133767	DI1	l	4.54			7.08			5.9			
Can Gambús-Illeta 5	IPS133767	DI2	l	4.81			7.5			5.0			
Can Gambús-Illeta 5	IPS133767	DI3	l	4.21			6.4			6.0			
Can Llobateres 1	IPS11265	M2	l	24.42			19.34	26.07	22.68	23.17			
Can Llobateres 1	IPS11266	m1	r	22.0				14.14					
Can Llobateres 1	IPS11335	DP2	r	22.13			17.68	18.2	19.82	17.05			
Can Llobateres 1	IPS11264	DP2	l	21.68			16.19	18.24	20.37	16.86	9.4	9.7	8.6
Can Llobateres 1	IPS11264	DP3	l	20.66			16.49	20.79	19.33	17.8	9.0	8.7	10.5
Can Llobateres 1	IPS11264	DP4	l	21.67			16.56	22.15	19.41	19.32	10.0	8.8	12.0
Can Llobateres 1	IPS11264	M1	l	22.48			17.36	24.2	21.09	21.34	10.7	9.8	14.8
Can Llobateres 1	IPS28172	m2	r	21.5			14.9	16.5					
Can Llobateres 1	IPS70116	DP4	r	20.7	20.9	16.8	23.6	20.2	19.3				
Creu de Conill 20	IPS136651	m2	r	22.5			16.32	15.45				13.2	12.8
Creu de Conill 20	IPS136651	m3	r	24.04				16.47	15.56				13.9

preserves part of the mesial cingulum and a distolabial cingulum. The parastyle appears well separated from the paracone by a deep groove. The protoloph is oblique and the metaloph is straight but weakly connected with the ectoloph. In labial view, the paracone and metacone are separated and look similar in height.

The DP4 IPS70116 is a right DP4 (Fig. 5j), published as M1 by Golpe-Posse and Crusafont-Pairó (1982). Similarly to the other DP4s described previously, the tooth, in occlusal view, has a slightly concave labial side and a strongly concave lingual side. The minimal width in the middle of the tooth is smaller than the posterior width. These characters suggest the tooth is deciduous. The parastyle is large and separated from the paracone by a deep groove. The mesial cingulum is continuous, and the labial-distal cingulum is strong. A large cusp is present at the entrance of the median valley, below the hypocone. Protoloph and metaloph are continuous and joined with the ectoloph. Between the paracone and the parastyle, on the labial side, there is an additional small cusp similar to DP4 IPS133767. The hypocone is slightly taller than the protocone.

The M2 IPS11265 (Fig. 5m) bears a mesial and distal cingula, as well as a labial cingulum below the metacone. In labial view, the metacone and paracone are similar in height, while in lingual view the protocone is slightly taller than the hypocone. The parastyle is large and well separated from the paracone. The protoloph and the metaloph are high and connected with the paracone and the metacone, respectively.

The partial lower molar (probably m1) IPS11266 (Fig. 5n) displays a distal cingulum. The protolophid and metalophid are separated, and the protolophid is taller than the metalophid in labial view.

In the m2–m3 of the mandibular fragment IPS136651 (Figs. 4d–f, 5p), the labial cingulid is absent. In labial view, the protoconid is taller than the hypoconid. The metalophid is not well developed and does not reach the protolophid. A metastylid is present and the hypoconulid is reduced to a cingulum (Fig. 5p–q).

In the worn-out lower molar (probably m2) IPS28172 (Fig. 5o), the protolophid is wider than the metalophid, the distal cingulid is still visible, and a mesial cingulid is barely visible on the mesiolabial corner of the crown. No further features can be discerned.

Comparisons

Comparisons among the studied material and with the tapirid from Teuleria del Firal

The isolated DP2 IPS11335 (Fig. 5d) resembles those of IPS133767 (Fig. 5b) and IPS11264 (Fig. 5c) in the general subtrapezoidal occlusal contour of the crown and the strong labiolingual constriction between the mesial and distal cusps. On all the described DP2s, the protoloph bends distolingually and is curved at the level of the connection with the paracone. The parastyle is well developed and barely connected with the mesiolabial side of the protoloph (not clearly visible on IPS11264 because of damage). On the described DP2s, the labial cingulum is strong, continuous below the metacone, and connected with the distal cingulum. The latter terminates close to the mid-lingual side of the hypocone. The entrance of the median valley bears a large cusp on IPS133767 and a faint pillar on IPS11264. Additional enamel folds develop from the protocone and the hypocone toward the median valley on all these teeth; the metaloph is barely connected with the ectoloph, and the hypocone is larger than the protocone. On the DP2s of IPS11264 and IPS133767, an enamel fold on the ectoloph, mesially to the metacone, is also present. On the IPS11264 DP2, the mesial cingulum is slightly stronger than on that of IPS11264 and the median valley looks narrower on its inner portion. Dimensionally, the DP2 of IPS11264 and IPS11335 are very similar in size and proportion, while that of IPS133767 is somewhat narrower in Wm. Similar metrical differences can be detected between the DP3s of IPS133767 and IPS11264 (Table S1). However, this dimension is also slightly variable in the comparative samples of *Tapirus indicus* (Wm varies from 20.5 mm to18.68 mm on the DP2) and *Tapirus terrestris*, even within a single individual. In terms of occlusal shape, the DP3s of IPS133767 and IPS11264 are similar regarding the development of cusps and cingula. Only the labial cingulum looks somewhat stronger on IPS133767. The DP4s of IPS133767 and IPS11264 are morphologically identical, but those of IPS133767 are a little bit smaller. The length of DP2–DP4 in IPS133767 (60.5 mm) is like that in IPS11264 (63.0 mm). The M1 of IPS133767 (Fig. 5k) differs from that of IPS11264 (Fig. 5l) in the possession of an additional fold within the postfossette, additional enamel folding on the median valley and the mesial side of the metaloph, and a slightly smaller size. However, these differences fall within the intraspecific variability of *T. indicus*. The metrical differences between the two described M1s are smaller than those reported for this tooth locus in *Ta. pannonicus* from Dorn-Dürkneim and *T. arvernensis* from Camp dels Ninots (Table S1), and those displayed by *T. terrestris* and *T. indicus*. The m2 IPS28172 and that of IPS136651 are very similar in size, but the advanced stage of wear of the former precludes an exhaustive comparison. All the lower molars (except IPS28172) have the metalophid separated from the protolophid, a protoconid taller than the hypoconid, a strong metastylid, and a strong distal cingulid.

The material from Teuleria del Firal was previously identified as a P2 or P3 and a fragment of M1 (Chevalier, 1909; Bataller, 1918, 1924: pl. 2, figs. 7, 8; Golpe-Posse & Crusafont-Pairó, 1982). However, the upper premolar figured by Bataller (1924: pl. 2, fig. 7) is actually a DP2, morphologically comparable with that of IPS133767. The length and posterior width of the DP2 from Teuleria del Firal (estimated from the Bataller's figure) are 21.6 and 19.6 mm, respectively, thus falling within the DP2 variability from the Vallès-Penedès specimens (Table S1). The length of the partial M1 from Teuleria del Firal (Bataller, 1924: pl. 2, fig. 8) was reported as 28 mm by Bataller (1924: p. 11), which exceeds the M1 lengths for all Late Miocene and Pliocene tapirid species from Europe. In fact, this tooth does not fit well with the morphology of a tapir upper molar and thus possibly represents a deciduous premolar of a rhinocerotid. Based on the comparisons above, all the studied specimens, as well as the DP2 from Teuleria del Firal, can be assigned to the same species.

Comparisons with Late Miocene tapirids from Europe

Late Miocene tapirid species are almost exclusively documented by permanent teeth. However, due to the strong similarity between deciduous and permanent teeth, as well as between premolars and molars, we cannot exclude that some determinations need to be re-evaluated. This is the case of the Asian species *Tapirus teilhardi* Zdansky, 1935, supposedly based on a mandibular fragment with (p2)–p3–p4–m1, but de facto belonging to a juvenile individual with (dp2)–dp3–dp4–m1 (Ji et al., 2015: fig. 6), or as in the case of the DP2 from Teuleria del Firal (see above). Accordingly, the comparisons are here based only on directly observed or figured specimens.

No juveniles of *T. priscus* had been described so far or reported in literature—except for the CLL1 specimens described by Golpe-Posse and Crusafont-Pairó (1982)—and previous works thus only focused on permanent teeth (Eisenmann & Guérin, 1992; Guérin & Eisenmann, 1994). Therefore, the comparison with *T. priscus* must be limited to the permanent molars (M1–M2 and m1–m3; list of specimens reported in Table S1). In the M1 (IPS133767) from CGS-I5 and M1 (IPS11264) and M2 (IPS11265) from CLL1, like in those of *T. priscus*, the parastyle is large and well separated from the paracone by a deep groove, the mesial and distolabial cingula are strong, and the protocone protrudes a little bit more lingually than the hypocone. Thus, no significant occlusal

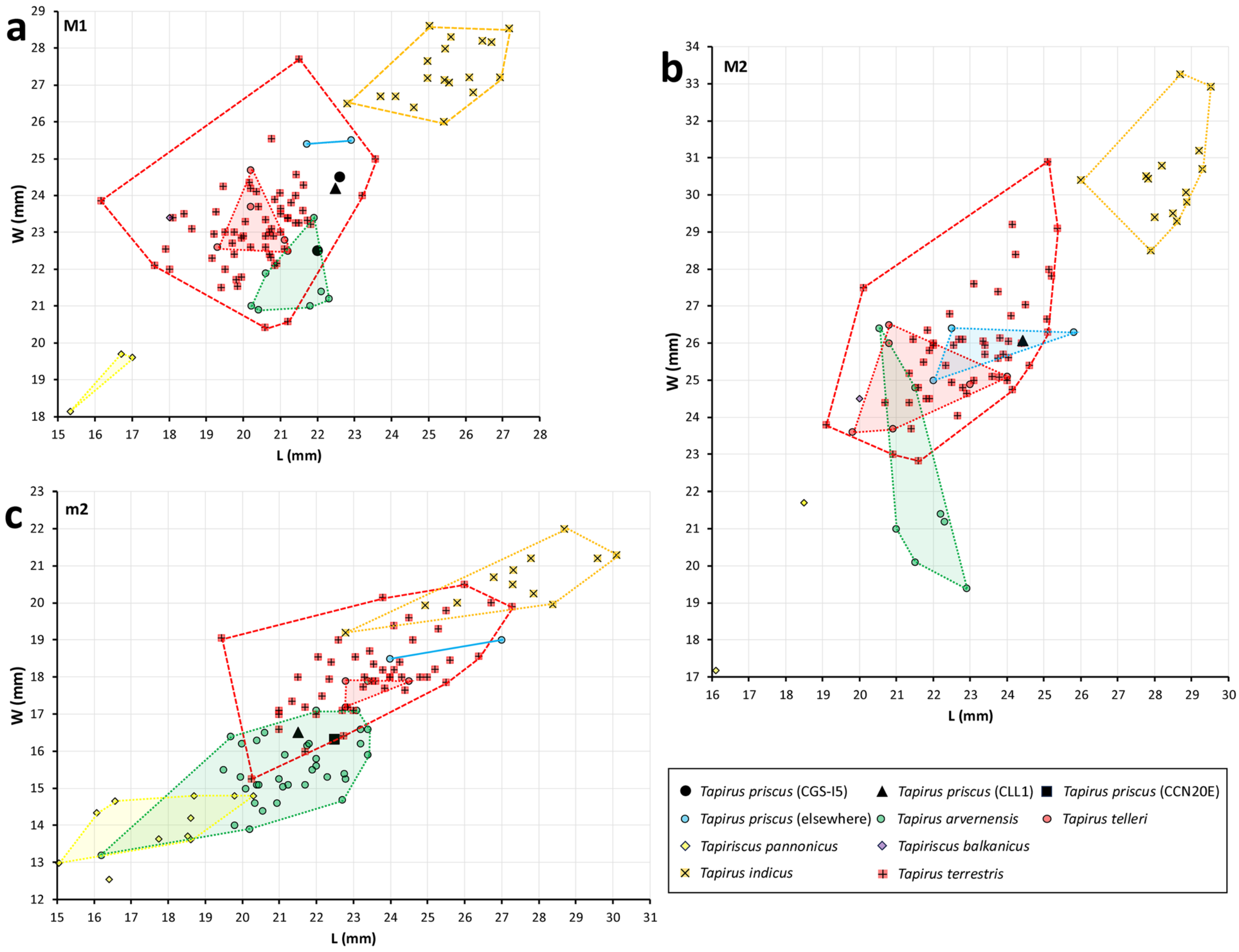

Fig. 6 Bivariate plots of maximum labiolingual width (W) vs. mesiodistal length (L), in mm, for the most representative molars among the studied material of *Tapirus priscus* from the Vallès-Penedès Basin as compared with extant and fossil tapirids: **a** M1; **b** M2; **c** m2. For measurements and data sources, see Table S1. The variation of each species is illustrated by means of convex hulls (empty for extant species and colored in semitransparency for extinct ones). Note that the Vallès-Penedès specimens overlap with the metrical variation of extant *Tapirus indicus* and fall close or within the variation of *T. priscus* from Eppelsheim (more clearly falling within the maximum and minimum ranges reported by Guérin & Eisenmann, 1994)

differences can be detected between the described upper molars and those of *T. priscus*. Dimensionally, the upper molars from the Vallès-Penedès Basin fall within the mean and maximum ranges of *T. priscus* (Fig. 6; Table S1). In contrast, the described lower molars are close to the minimal values of *T. priscus* reported by Guérin and Eisenmann (1994) (Fig. 6; Table S1). In terms of occlusal shape, the lower molars from the Vallès-Penedès Basin are characterized by a strong metastylid and well-separated metalophid and protolophid, as in the case of *T. priscus*. Given all these similarities, together with the differences described below relative to other species, the specimens from the Vallès-Penedès Basin are assigned to *T. priscus*.

In the case of *T. antiquus*, the only possible comparison refers to the dimensions of the M2 from Eppelsheim, which exceeds those of the described specimen from CLL1 (Table S1). However, the proportions of the Eppelsheim specimen (Kaup, 1833: p. 4) differ from those of all the other Neogene and extant species included in the comparative sample (Table S1) by having the Wp greater than the L and the Wa. On all the other observed or reported specimens, the Wp is always lower than the Wa and the L. In contrast, the proportions of the M3 from Bermersheim (Kaup, 1861: p. 32) resemble those of the other Neogene and extant species, and its dimensions are within the mean and maximum values of *T. indicus*. It is difficult to assert if the M3 from Bermersheim belongs to the same species recorded at Eppelsheim by the M2, but the former probably just represents a large individual of *T. priscus*. Nothing can be said about the M2 from Eppelsheim, being the specimen lost and not figured nor described in detail by Kaup (1833; p. 4), but we cannot exclude that the tooth belonged to another taxon and was misidentified as *Tapirus*.

The described material further displays multiple differences relative to *T. arvernensis*. Thus, on the M1 and M2 of the latter species, the groove separating the parastyle and the paracone is less marked than in the Vallès-Penedès specimens and, unlike in the latter, the accessory folds can be present on the protoloph, and the labial cingulum is not strongly developed or even reduced. On the lower molars of *T. arvernensis* (list of observed specimens reported in Table S1), the protoconid and the hypoconid are similar in height, and the metastylid is less developed, unlike in the studied specimens. The DP2–DP4 of *T. arvernensis* differ from those of the Vallès-Penedès material by having a more subsquare outline, a less marked groove between the parastyle and the paracone, a less developed labial cingulum, a stronger connection between metaloph and metacone, and a taller connection between the paracone and the metacone. The deciduous teeth of *T. arvernensis* are dimensionally similar to those of the studied specimens (Table S1), being generally larger than *T. terrestris* and smaller than *T. indicus*. The length of DP2–DP4 on IPS133767 (60.5 mm) and on IPS11264 (63.0 mm) is shorter than in *T. indicus* (72.1 and 71.8 mm). The length of DP1–DP4 on IPS133767 (76.6 mm) equals the minimal values of *T. arvernensis* from Camp dels Ninots (ranging 78.5–76.7 mm), is shorter than in *T. indicus* (90.7 and 90.9 mm), and is slightly longer than in *T. terrestris* (72.4 and 73.5 mm).

Finally, the described material further differs from the two species of *Tapiriscus* (list of observed specimens reported in Table S1). In particular, *Ta. pannonicus* displays smaller permanent and deciduous teeth (Fig. 6; Table S1). Unlike in the studied specimens, the DP2 of *Ta. pannonicus* has a subtriangular occlusal outline, a small parastyle, paracone and metacone closely appressed, and a weak labial cingulum. On the upper molars, the parastyle is more compressed against the paracone, and the mesial and labial cingula are weaker than in the studied material. Regarding *Ta. balkanicus*, its upper and lower permanent teeth are shorter than those of the studied material (Table S1). On the M1 and M2, the labial cingulum is strongly developed and present also under the paracone, unlike in the described specimens. Unlike in the Vallès-Penedès material, the lower molars of *Ta. balkanicus* have a less developed metastylid, and the metaconid and entoconid are more closely placed.

Discussion

Taxonomic attribution and evolutionary implications

The tapirid material from the Vallès-Penedès described here includes six specimens from CLL1, a juvenile cranium with deciduous premolars from CGS-I5, and a lower mandibular fragment from CCN20. No significant morphological differences are observed for the DP2–DP4 and M1 among the studied material. Dimensionally, the studied permanent upper teeth fall within the variability of *T. priscus* reported by Eisenmann and Guérin (1992) and Guérin and Eisenmann (1994) and are slightly larger than those of *T. arvernensis*, while the lower permanent teeth fall within the minimal and mean values of *T. priscus* and the maximal and mean values of *T. arvernensis*. However, it is important to underline that the size and proportions of the lower molars have been considered insufficient to identify fossil *Tapirus* species (Perini et al., 2011). The deciduous teeth are similar in size to those of *T. arvernensis*, larger than in *Tapiriscus*, slightly larger than in *T. terrestris*, and slightly smaller than in *T. indicus*. The deciduous teeth display a few diagnostic characters useful to discriminate among the late Neogene species and, in particular, between *T. priscus* and *T. arvernensis*. These characters mainly refer to the development of the cingula (stronger in *T. priscus*), the separation between paracone and parastyle (marked by a deep groove in *T. priscus*), and the connection between metaloph and metacone (stronger in *T. arvernensis*).

Based on the comparison with remains of other tapirid species, all the described specimens are here assigned to *T. priscus*. The scarcity of the described material reflects the rarity of tapirids in the Miocene of Europe. Indeed, they were previously known from only two sites in the Iberian Peninsula, Teuleria del Firal in the Seu d'Urgell Basin (Chevalier, 1909; Bataller, 1918, 1924), correlated to the early Vallesian (~10.3–10.0 Ma; Casanovas-Vilar et al., 2011), and CLL1 (Golpe-Posse and Crusafont-Pairó, 1982), with an estimated age of 9.8 Ma, in both cases being also attributed to *T. priscus*. Accordingly, the additional material from CLL1 and two other sites from the Vallès-Penedès Basin provides further insight into the dental morphology of this poorly known group of mammals and extends the chronological range of *T. priscus* in Western Europe, from the earliest Vallesian (11.2 Ma, MN9; CCN20) to the late Vallesian (9.7–9.1 Ma, MN10; CGS-I5) (Fig. 2).

Guérin and Eisenmann (1994) suggested a phyletic link from the Middle Miocene *T. telleri* to the Late Miocene *T. priscus* and then to *T. arvernensis*, while Pandolfi et al. (2023) recognized *T. indicus* as sister taxon to *T. arvernensis*, but without resolving the relationships with other Eurasian fossil tapirs. *Tapirus telleri* first occurs in Europe at Göriach (Hofmann, 1893), late MN5 or MN6, and it was possibly an Asian immigrant after the so-called "tapir vacuum" during the Early-Middle Miocene transition (Van der Made & Stefanovic, 2006). The species is also documented by scantly remains at Opole 2, Neudorf Sandberg and possibly Klopići (Laskarev, 1950; Thenius, 1952; Ryziewicz, 1961; Van der Made & Stefanovic, 2006; Sabol et al., 2021). The age of these localities is matter of debate: Opole 2 has been considered ranging from MN6 to MN7 and possibly of the same age as Opole 1 (Kowalski, 1990) or MN7 (Kowalski, 1997; Heissig, 1999); Neudorf Sandberg has been recently referred to MN6 (Sabol et al., 2021), and Klopići is of indeterminate age (Van der Made & Stefanovic, 2006). Accordingly, the presence of *T. telleri* during MN7+8 is not strongly supported, suggesting a second vacuum in the Miocene European record of the family, until the occurrence of *T. priscus* at the early Vallesian (MN9) (Fig. 2). The latter species might be a new Asian immigrant in Europe (Heissig, 1999) rather than a European descendant of *T. telleri*. This possibility is further supported by the occurrence of *T. priscus* in the earliest Vallesian of CCN20, which represents the first appearance datum of hipparionin horses in Western Europe at ~11.2 Ma (Garcés et al., 1996; Agustí et al., 1997; Casanovas-Vilar et al., 2016b). Although it was formerly considered that the beginning of the Vallesian only implied the dispersal of hipparionin horses in the Vallès-Penedès Basin, it has subsequently been shown that this contention mostly resulted from the misdating of some sites and the mixture of faunas of different ages (Alba et al., 2019, 2022). It currently appears that other large mammal immigrants from the East (giraffids, the machairodontine felid *Machairodus*, and the suine *Propotamochoerus*) could have dispersed into Western Europe at about the same time as *Hippotherium* (Alba et al., 2022; McKenzie et al., 2023). The fact that *T. priscus* follows the same pattern reinforces this view, particularly given that morphological evidence does not support a closer phylogenetic link with the older *T. telleri*. These two species differ in the dimensions of the teeth (with *T. telleri* being smaller than *T. priscus*) and in some occlusal traits, with *T. telleri* being characterized by the absence or reduction of labial cingula on the upper teeth (an apomorphic feature in Ceratomorpha), the reduction of the metastylid on the lower teeth, and by a Wp similar in value to Wa on m3 (Hofmann, 1893: pls. VII–VIII; Eisenmann & Guérin, 1992: pl. 1; Zapfe, 1996: figs. 1–3; Van der Made & Stefanovic, 2006: pl. 1). *Tapirus priscus* shows instead greater morphological similarities with the Eastern Asian *Tapirus hezhengensis* Deng et al., 2008 from the early Late Miocene (Bai et al., 2020; Deng et al., 2008), e.g., by having a well-developed parastyle, a strong but discontinuous labial cingulum, and strong mesial and distal cingula on the upper molars.

Throughout the Vallesian and early Turolian, *T. priscus* attained a broader geographic distribution than previously thought, as shown by the remarkable discovery of a tooth from Udabno 1, Georgia (Bukhsianidze, 2019), which is currently correlated to the early Turolian (MN11), with an estimated age of 8.1–7.1 Ma based on biostratigraphic and paleomagnetic data (Agustí et al., 2020). Based on currently available data from the Vallès-Penedès Basin, *T. priscus* went extinct after the earliest late Vallesian (MN10) in the Iberian Peninsula, whereas in Central Europe it persisted until the early Turolian (MN11; Franzen, 2013), in further agreement with its occurrence in Georgia (Bukhsianidze, 2019) (Fig. 2). This leaves a gap in the *Tapirus* record during MN12 and MN13, given that *T. arvernensis* is not recorded until the Mio-Pliocene boundary (Pandolfi et al., 2023). During MN12 and MN13, European tapirids are exclusively represented by *Ta. pannonicus* and *Ta. balkanicus* from Central and Eastern Europe, while neither *Tapirus* nor *Tapiriscus* are recorded in Western and Southern Europe. *Tapirus arvernensis* seems to be more derived than *T. priscus*, but it is not possible to conclude that the two taxa are closely related within a single lineage, with *T. arvernensis* more likely representing an independent, later dispersal from Asia into Europe (Pandolfi et al., 2023).

Paleoenvironmental implications

Extant tapirs are closely related to dense forests (primary or secondary forests, riparian forests, or palm forests, depending on the species), and their distribution is strongly affected by the presence of water bodies (García et al., 2012 and references therein). *Tapirus terrestris* occurs in a variety of lowland moist swamp forests, dry and moist shrublands and grasslands, but the most important habitats are moist, wet or seasonally inundated areas (Varela et al., 2019). *Tapirus bairdii* inhabits forested areas with ponds, streams, and swamps, but also narrow oak-forest strips (García et al., 2016). *Tapirus pinchaque* occurs in tropical montane forest, shrubland, wetlands and grassland from 1400 m to the snowline (Lizcano et al., 2016), while *Tapirus indicus* is restricted to tropical moist forest areas and occurs in both primary and secondary forest and wetland areas (Traeholt et al., 2016). All the extant tapir species are generally browsers with a broad diet, including leaves, fiber, twigs, and fruits (García et al., 2012 and references therein). In particular, South American tapirs (*T. bairdii*, *T. pinchaque*, and *T. terrestris*) have $\delta^{13}C$ values consistent with a predominantly C3 diet, with all values lower than $-12‰$, suggesting highly conservative dietary niches within forest environments (DeSantis, 2011). The Asian tapir species, *T. indicus*, is a selective browser, concentrating on young leaves and growing twigs and a considerable amount of fruit (Nizam et al., 2006; Williams & Petrides, 1980). Fossil tapirs are also considered browsers too, and stable isotopic analyses of their tooth enamel suggest they lived in forested stable environments. Indeed, $\delta^{13}C$ values of tapirs remain very negative and stable through protracted time intervals while coexisting mammals, such as camelids, modify their diets with changing climates and environments (DeSantis & MacFadden, 2007; DeSantis et al., 2009). However, isotopic studies were mainly focused on extant and fossil American *Tapirus* species, and a few of them considered European latest Miocene-Pliocene species (e.g., *T. arvernensis* in Kovács et al., 2015, *T.* cf. *arvernensis* in Nelson & Rook, 2016). A recent study of occlusal surface area (OSA) in extant and fossil tapirs suggested that European and early North American species probably occupied a niche as fruit and leaf eaters and seed dispersers, similarly to South American taxa (Dumbá et al., 2022). However, the latter study showed that *T. priscus* does not significantly differ from *T. indicus* in both upper and lower tooth row OSAs, suggesting that, like *T. indicus*, *T. priscus* would have been a seed predator that processed seeds more successfully than American extant species and other Turolian and Pliocene species from Europe, inferred to be more successful seed dispersers (Campos-Arceiz et al., 2012; Dumbá et al., 2022; Van Linden et al., 2022). Accordingly, similar habitat and dietary preferences as *T. indicus* may be inferred for *T. priscus*, which would thus be indicative of the presence of humid conditions, water bodies, and productive dense forests.

The presence of *T. priscus* at CLL1 is thus in accordance with paleoenvironmental inferences for this locality based on previous faunal and paleobotanic evidence, indicating the presence of humid and densely-forested environments, and in further agreement with the documented presence of a frugivorous and suspensory great ape (Moyà-Solà & Köhler, 1996; Almécija et al., 2007; Alba et al., 2010; DeMiguel et al., 2014). In particular, ecometric analyses based on functional crown types of large herbivorous mammals are indicative of a tropical seasonal forest or tropical rainforest (Arranz et al., 2023), while the flora indicates the presence of a dense wetland/riparian forest (Marmi et al., 2012), probably with more open wetlands nearby (see discussion in Arranz et al., 2023). It is likely that, by the time of CLL1, densely-forested environments in the Vallès-Penedès Basin were highly fragmented and restricted to the wetlands, with more open areas in between (Marmi et al., 2012; Arranz et al., 2023). Such environments, with persisting (sub) tropical plant elements suitable for frugivorous mammals, would have eventually disappeared during the late Vallesian (MN10) due to an ongoing trend toward cooling and increased seasonality, eventually leading to the local extinction of hominoid primates, listriodontine suids, and other forest-adapted taxa—such as tapirids—shortly thereafter (Agustí et al., 2003; Casanovas-Vilar et al., 2010, 2011; Marmi et al., 2012; DeMiguel et al., 2014; Van der Made et al., 2022; Arranz et al., 2023). In any case, the material from CGS-I5 attests to the persistence of *T. priscus* in the Vallès-Penedès Basin until the early late Vallesian (MN10), in further agreement with the last records of other forest-adapted taxa such as hominoid and pliopithecoid primates at ~9.5 Ma and ~9.1 Ma, respectively (Casanovas-Vilar et al., 2011, 2014, 2016a, b; Alba et al., 2018). Thus, the presence of tapirids at CGS-I5 strengthens the view that the so-called Vallesian Crisis did not imply an abrupt extinction of forest-adapted taxa at the early/late Vallesian boundary but was rather a more protracted extinction event that appears abrupt because of the biases of the record (Casanovas-Vilar et al., 2014).

In turn, the presence of *T. priscus* at CCN20 is apparently at odds with the fact that this site, where primates have yet to be recorded, displays considerable faunal differences with the site of Castell de Barberà, which is roughly coeval (~11.2 Ma) based on magnetostratigraphic data and can be further correlated to the Vallesian based on the presence of hipparionins (Alba et al., 2019). Although a large portion of the fauna from CCN20 remains unpublished—except for small mammals (Casanovas-Vilar et al., 2006), barbourofelids (Robles et al., 2013), and suids (McKenzie et al., 2023)—currently available data are indicative of a more open and less humid environment as compared with the closely-forested environment inferred for Castell de Barberà (McKenzie et al., 2025). The latter is one of the few sites in Europe where hominoid and pliopithecoid primates co-occur, further recording more abundant castorids and arboreal rodents (Casanovas-Vilar & Agustí, 2007; Casanovas-Vilar et al., 2006), as well as a much higher diversity of suids and much scarcer hipparionin remains than CCN20 (Alba et al., 2019; McKenzie et al., 2023, 2024). Although the presence of *T. priscus* at CCN20 seems to contradict such an interpretation, the presence (though scarce) of the small semiaquatic beaver *Euroxenomys minutus* (Casanovas-Vilar et al., 2006) indicates the presence of stable water bodies. Furthermore, this apparent paradox might simply stem from the fact that currently published remains from CCN20 were presumably recovered from higher levels of the site. Excavations since 2016 have shown that the site encompasses multiple levels within a short (~5 m-thick) section. The lower levels, including CCN20F and CCN20E (which yielded the tapirid fossil described herein) have produced more abundant remains of forest-adapted taxa linked to water bodies (e.g., tragulids, castorids, and freshwater turtles), which are absent or very rare in the uppermost levels (authors' pers. obs.). The tapirid tooth described herein—which comes from CCN20E and can be unambiguously correlated to the earliest Vallesian based on the presence of hipparionin horses—supports this interpretation. The stratigraphic distance between CCN20E and the uppermost levels indicative of more open and arid environments is very short (1–2 m) and, based on local sedimentation rate, it would imply an age difference of a few thousand years. This suggests that previously noted paleoenvironmental differences between Castell de Barberà and CCN20 (based on data previously available for the upper levels) might not be attributable to local physiographic differences but rather to rapid temporal shifts in paleoenvironmental conditions at a more regional scale. Under this interpretation, the earliest Vallesian in the Vallès-Penedès Basin might have been characterized by less open and arid conditions than previously assumed (e.g., Casanovas-Vilar et al., 2006), in further agreement with paleoenvironmental inferences from Castell de Barberà (Alba et al., 2019).

Conclusions

Miocene tapirid species are poorly documented in Europe, being mainly represented by isolated and scanty dental remains. Tapiridae teeth are very conservative in morphology and sometimes it is very difficult to distinguish between deciduous and permanent dentition or among various species. The new specimens reported here, attributed to *T. priscus*, increase our knowledge on the deciduous dentition of this species and further evince some dental characters useful to discriminate not only between deciduous and permanent teeth, but also between juveniles of *Tapirus* species from the Neogene. In the future, these data will be helpful to revise some *Tapirus* occurrences from Europe and to better understand the phylogenetic relationships among Vallesian and Turolian tapirid species as well as *T. arvernensis*. The described remains further extend the chronostratigraphic range of *T. priscus* in Western Europe, which, based on currently available data, was recorded throughout the early Vallesian (MN9)—since the arrival of hipparionin horses—and persisted until the late Vallesian (MN10), whereas in Central Europe this species did not become extinct until the beginning of the Turolian (MN11). From a paleoenvironmental viewpoint, the described remains support the persistence of humid and forested environments in the Vallès-Penedès Basin sometime into the late Vallesian (MN10) and further indicate that earliest Vallesian (11.2 Ma) paleoenvironments in this basin were more closed and less arid than previously assumed based on the CCN20 fauna—in further agreement with data from the roughly coeval site of Castell de Barberà.

Supplementary Information

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Supplementary Material 1.

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Author contributions
LP and DMA designed the research; LP and SGA collected data (measurements and/or photographs); SA, ÀHL, MP, AU, ICV, and DMA excavated part of the fossil material; LP performed the descriptions and comparisons; ICA and JG provided the biostratigraphic and geological data for CGS-I5; LP, SGA, ICV, and DMA prepared the figures; LP and DMA wrote the manuscript with input from the remaining authors.

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Availability of data and materials
Data is provided within the manuscript or supplementary information files.

Declarations

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The authors declare no competing interests.

Author details
[1]Dipartimento di Scienze della Terra, Università di Pisa, via S. Maria, 53, 56126 Pisa, Italy. [2]Division of Anthropology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA. [3]New York Consortium in Evolutionary Primatology, New York, NY 10024, USA. [4]Institut Català de Paleontologia Miquel Crusafont (ICP-CERCA), Universitat Autònoma de Barcelona, Edifici ICTA-ICP, c/ Columnes s/n, Cerdanyola del Vallès, 08193 Barcelona, Spain. [5]Universitat Autònoma de Barcelona, Campus de la UAB, Cerdanyola del Vallès, 08193 Barcelona, Spain. [6]Departamento de Ciencias de la Vida, Universidad de Alcalá, Cátedra de Otoacústica Evolutiva y Paleoantropología (HM Hospitales-UAH), Alcalá de Henares, 28871 Madrid, Spain.

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