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New data on the mammalian fauna from the late middle Eocene (MP 15–16) of Mazaterón (Soria, Spain): The youngest presence of the genus *Prodissopsalis* (Hyaenodonta, Hyaenodontidae) in Europe

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Abstract

The Hyaenodonta were the most diverse carnivorous mammals in the European Eocene and were classically divided into three subfamilies: Sinopaninae, Arfianinae, and Proviverrinae, with this latter being the most successful of the three, as it exhibited a much larger geographic and temporal range. This classification is currently abandoned, as cladistic analyses of Hyaenodonta showed that several of these groups were paraphyletic. In any case, the former "proviverrines" were European endemic hyaenodontids which occupied the niche of small to medium-sized predators from the Ypresian (MP7) to the Priabonian (MP19). Recent phylogenetic proposals recognize the "*Eurotherium* clade" including this latter genus, besides *Cartierodon* and *Prodissopsalis.* A single species is known for *Prodissopsalis*, *Prodissopsalis eocaenicus*, previously recorded in European fossil sites of MP 12 to MP 14; nevertheless, the new material studied here, a mandible of a subadult individual from the late Middle Eocene (Bartonian, MP 15–16) site of La Solana (Mazaterón, Soria, Spain) constitutes a new species of *Prodissopsalis* and the youngest record of this genus up to now, extending its chronological range and remarking the shelter role of the northwestern region of the Iberian Peninsula during the Middle and Late Eocene. The new species, *Prodissopsalis jimenezi* provides new data not only on the eruption sequence of the genus, but also on the evolution of its dental adaptations, as the new species exhibits a more trenchant, hypercarnivorous dentition in comparison to the more primitive species *P. eocaenicus*, which would point toward a refining of the hunting abilities of this hyaenodont during the Middle Eocene.

KEYWORDS

Bartonian, endemic faunas, Eocene, Hyaenodonta, Spain

1 | INTRODUCTION

During the Paleogene (66–23 Mya), several lineages of mammals competed for occupy the niche of terrestrial carnivorous predators: Carnivoramorpha (where the modern order Carnivora is included), Hyaenodonta, Mesonychia, and Oxyaenodonta (Friscia & Van Valkenburgh, 2010; Radinsky, 1982; Savage, 1977; Solé et al., 2022; Van Valkenburgh, 1999). Although the former group was the only one to persist in the extant mammalian faunas, these four clades were sympatric in most of the ecosystems of North America and Eurasia from the beginning of the Paleocene to the Middle Eocene, when carnivoramorphans finally became the dominant predators (Flynn & Wesley-Hunt, 2005; Friscia & Van Valkenburgh, 2010; Morlo et al., 2010; Morlo & Nagel, 2007; Rose, 2006; Savage, 1977; Solé et al., 2022; Van Valkenburgh, 1999). Although members of these four clades are considered to have a primarily carnivorous diet, only three of them (Carnivoramorpha, Hyaenodonta, and Oxyaenodonta) developed "carnassial teeth," that is, at least one pair of specialized teeth (one upper and one lower), with elongated crests that, when occluding, function as scissors, slicing the meat and cutting the skin and tendons of prey (Ewer, 1973; Flynn & Wesley-Hunt, 2005; Solé & Ladevèze, 2017; Van Valkenburgh, 1989). The

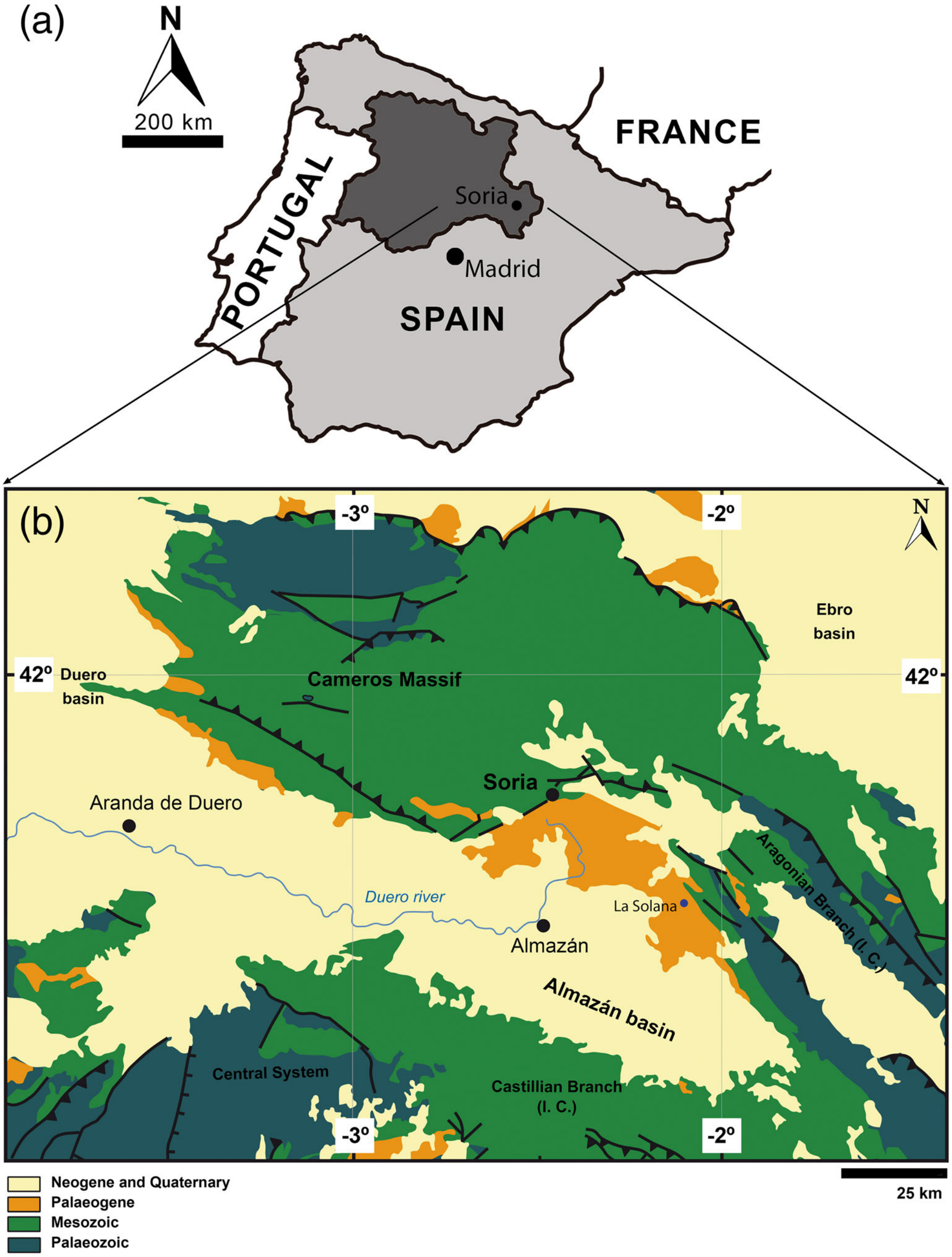

FIGURE 1 Geological map of the Duero Basin and location of the fossil vertebrate site of La Solana. (a) Location of Castilla y León autonomous community (dark gray) within Spain (light gray), showing the locations of Madrid and Soria cities. (b) Geological map of the Almazán Basin showing the location of the La Solana fossil site (modified from Ortega et al., 2022; Rodríguez Fernández et al., 2015).

fourth carnivorous clade, the Mesonychia, did not have proper carnassial teeth; instead, its members developed a peculiar molar morphology that showed a progressive modification toward a premolar-like structure (Russell, 1954).

Both Hyaenodontidae and Oxyaenodonta were previously considered superfamilies within the order "Creodonta," a heterogeneous group that was supposed to have a common origin (Ginsburg, 1999). Nevertheless, several studies strongly suggested that these two groups show similar morphological features and ecological roles by simply convergence, rather than due to a phylogenetical relationship (Morlo et al., 2009; Polly, 1994; Rose, 2006; Zack, 2019a). Solé (2013) proposed the use of the order Hyaenodonta, named by Van Valen (1967), which included the family Hyaenodontidae, although the use of Creodonta as an order was considered valid for other authors such as Friscia and Van Valkenburgh (2010). In this paper, we follow the proposal of Solé (2013), and we prefer to discard the use of the paraphyletic clade Creodonta.

The European mammalian faunas of the early Eocene (around 56 Ma) included Hyaenodontidae classically included in the subfamilies Sinopaninae, Arfianinae, and Proviverrinae, besides several genera of less clear adscription, such as *Cynohyaenodon*, *Eurotherium*, or *Matthodon* (Godinot, 1981; Godinot et al., 1987; Hooker, 2010; Rich, 1971; Smith & Smith, 2001; Solé, 2013; Solé et al., 2013). Nevertheless, sinopanines and arfianines went extinct during the Late Ypresian, around 50 Ma ago (Solé et al., 2014), whereas the rest of these European Hyaenodontoidea exhibited a much longer temporal range, in fact being recorded during the rest of the European Eocene (Solé et al., 2013, 2014). Nevertheless, the use of these subfamily-level names has been called into question due to several phylogenetic analysis that tried to clarify the actual relationships between the different groups (Borths & Stevens, 2017a, 2017c, 2019a, 2019b; Solé et al., 2020, 2021; Solé & Mennecart, 2019; Zack, 2019b). In fact, Solé (2013) already suggested that the use of Proviverrinae should be restricted to some European hyaenodontids with clear phylogenetic affinities, such as the genera *Proviverra*, *Allopterodon*, *Cynohyaenodon*, *Lesmesodon*, or *Prodissopsalis*, and later phylogenetic analyses (Borths et al., 2016; Borths & Seiffert, 2017; Borths & Stevens, 2017a, 2017c, 2019a) suggested that proviverrines could be a paraphyletic group. Also, in a recent revision of the group, Solé & Mennecart (2019) rejected the monophyly of "Proviverrinae" sensu Solé (2013), considering this group as part of the stem lineages of Hyaenodontinae, and grouping Hyaenodontidae, and "Proviverrinae" in Hyaenodontoidea (Solé et al., 2021; Solé & Mennecart, 2019). Finally, Solé et al. (2021) has proposed restricting the use of "Proviverrinae" to a clade within Hyaenodontoidea containing only *Proviverra*, *Allopterodon*, *Morlodon*, *Lesmesodon*, and *Parvagula*, which these authors called "*Proviverra*/*Allopterodon* clade," whereas the genera *Eurotherium*, *Prodissopsalis*, and *Cartierodon* would conform the "*Eurotherium* clade," with no close relationship to the "*Proviverra*/*Allopterodon* clade." Here, we will follow this taxonomical proposal of Solé et al. (2021). Within the *Eurotherium* clade, *Prodissopsalis eocaenicus* is recorded in European fossil sites from MP 12 to 14 (Calas, 1969, 1970; Lange-Badré, 1972; Lange-Badré & Haubold, 1990; Matthes, 1952; Morlo & Habersetzer, 1999; Solé & Mennecart, 2019), but the new material studied here, from the Spanish late middle Eocene (Bartonian, MP 15–16) site of La Solana (Mazaterón, Soria province) extends the chronological record of this genus up to around 41 Ma. This new taxon was a large to very large hyaenodont, following the categories by Morlo (1999), with an estimated maximum body weight of 30 kg (Morlo et al., 2010).

The Bartonian (late middle Eocene) fossil site of La Solana (Figure 1) is located 2.5 km northeast from the village of Mazaterón, in the Soria province (Spain), within the Mazaterón Formation of the Almazán Basin (Badiola et al., 2022). Although the inhabitants of this small village had known since many years ago about the existence of fossils in that spot, it was not until 1987 when the La Solana fossil site was intensively surveyed by Prof. Emiliano Jimenez (Cuesta Ruiz-Colmenares & Jiménez Fuentes, 1994). The vertebrate fossils from La Solana are found within a layer of gray marls that form part of a series of lacustrine-palustrine deposits, basically limestones and marls (Perales-Gogenola et al., 2021). These levels were formed in a shallow lacustrine system, which experienced recurrent flooding and drying processes (Alonso-Gavilán et al., 2004; Huerta & Armenteros, 2006). During the lower Ypresian (early Eocene), the faunal associations of mammals and reptiles from the Iberian Peninsula were very similar to those of the rest of Europe, which by that time, and due to a series of marine transgressions, had become a vast and fragmented archipelago (Egger et al., 2013; Rougier et al., 2016). But, in the lower Lutetian (lower middle Eocene, MP 11) the northwestern region of the Iberian Peninsula was isolated from both the eastern region and the rest of Europe, and thus, the known faunas from the latest middle and earliest upper Eocene (Bartonian and Priabonian) show a marked endemism (Bolet, 2017; Ortega et al., 2022).

2 | MATERIALS AND METHODS

2.1 | Studied specimen

The specimen studied in this paper is a mandible (catalogue number STUS-15077) from the late middle Eocene (MP 15–16) site of La Solana (Mazaterón, Soria province, Spain), housed at the paleontological collections of fossil vertebrates from the Duero Basin (Sala de las Tortugas) of the Universidad de Salamanca (Salamanca, Spain). We follow the dental nomenclature of Szalay (1969).

2.2 | Acquisition and processing of the data

The mandible STUS-15077 was scanned on a CTScan Nikon-XTH 160 at the Service of Non-Destructive Techniques of the MNCN-CSIC with the following parameters: 160 kv, 159 μA, and a resolution of 0.073 mm. The 3D virtual models were obtained through the software VGStudio MAX 3.0 (Volume Graphics GmbH) and 3D Slicer 4.10.1. To obtain 3D virtual models of different teeth the tomographs were processed following a semi-automatic protocol for segmentation based on the thresholding method.

Measurements of STUS-15077 were taken with a digital caliper to the nearest 0.1 mm. They are provided in Tables 1 and 2, besides those of different species of Hyaenodonta for comparison.

2.3 | Abbreviations

The following abbreviations are used throughout the text and figures: c, lower canine; i2, second lower incisor; i3, third lower incisor; dp4, deciduous fourth lower premolar; p1, first lower premolar; p1a, alveolus for p1; p2, second lower premolar; p3, third lower premolar; p4, fourth lower premolar; m1, first lower molar; m2, second lower molar; m3, third lower molar; BLW, buccolingual width; End, entoconid; Hyld, hypoconulid; Hyd, hypoconid; MDL, mesiodistal length; Med, metaconid; mf, mental foramina; tb, talonid basin; Pad, paraconid; PPac, postparacristid; PPrc, preprotocristid; Prd, protoconid; STUS, Sala de las Tortugas de la Universidad de Salamanca.

3 | SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758
Order Hyaenodonta Van Valen, 1967

TABLE 1 Measurements in mm of the m1 of different species of Hyaenodonta.

Species	Site	m1 MDL	m1 BLW	Data source
Prodissopsalis jimenezi	La Solana	11.33	6.05	This work
Eurotherium matthesi	Geiseltal	8.20	4.60	Lange-Badré and Haubold (1990)
Eurotherium matthesi	Geiseltal	8.90	4.70	Lange-Badré and Haubold (1990)
Oxyaenoides bicuspidens	Geiseltal	10.50	—	Lange-Badré and Haubold (1990)
Oxyaenoides bicuspidens	Geiseltal	10.90	5.50	Lange-Badré and Haubold (1990)
Oxyaenoides bicuspidens	Palassou	12.30	6.10	Lange-Badré and Haubold (1990)
Matthodon tritens	Geiseltal	11.20	6.40	Lange-Badré and Haubold (1990)
Matthodon tritens	Geiseltal	12.40	6.50	Lange-Badré and Haubold (1990)
Matthodon tritens	Geiseltal	12.40	6.70	Lange-Badré and Haubold (1990)
Prodissopsalis eocaenicus	Geiseltal	11.70	7.10	Lange-Badré and Haubold (1990)
Prodissopsalis eocaenicus	Geiseltal	12.70	6.10	Lange-Badré and Haubold (1990)
Cynohyaenodon trux	Egerkingen γ	6.30	—	Lange-Badré and Haubold (1990)
Cynohyaenodon trux	Egerkingen γ	5.50	3.20	Lange-Badré and Haubold (1990)
Proviverra typica	Egerkingen γ	4.30	2.50	Lange-Badré and Haubold (1990)
Cartierodon egerkingensis	Egerkingen γ	14.00	7.40	Solé and Mennecart (2019)
Paracynohyaenodon schlosseri	Les Clapiés	7.60	4.70	Lange-Badré and Mathis (1992)
Paracynohyaenodon schlosseri	Robiac	7.90	4.80	Lange-Badré and Mathis (1992)
Paracynohyaenodon schlosseri	Robiac	7.10	4.20	Lange-Badré and Mathis (1992)
Paracynohyaenodon schlosseri	Robiac	7.70	4.70	Lange-Badré and Mathis (1992)

TABLE 2 Measurements in mm of the m2 of different species of Hyaenodonta.

Species	Site	m2 MDL	m2 BLW	Data source
Prodissopsalis jimenezi	La Solana	14.81	5.67	This work
Eurotherium matthesi	Geiseltal	9.00	5.40	Lange-Badré and Haubold (1990)
Eurotherium matthesi	Geiseltal	9.20	5.50	Lange-Badré and Haubold (1990)
Eurotherium matthesi	Geiseltal	9.90	5.70	Lange-Badré and Haubold (1990)
Oxyaenoides bicuspidens	Geiseltal	12.30	6.20	Lange-Badré and Haubold (1990)
Oxyaenoides bicuspidens	Geiseltal	13.10	6.70	Lange-Badré and Haubold (1990)
Oxyaenoides bicuspidens	Palassou	12.70	8.10	Lange-Badré and Haubold (1990)
Matthodon tritens	Geiseltal	13.50	7.80	Lange-Badré and Haubold (1990)
Matthodon tritens	Geiseltal	14.30	8.10	Lange-Badré and Haubold (1990)
Matthodon tritens	Geiseltal	14.80	8.30	Lange-Badré and Haubold (1990)
Prodissopsalis eocaenicus	Geiseltal	12.70	7.20	Lange-Badré and Haubold (1990)
Prodissopsalis eocaenicus	Geiseltal	13.40	7.00	Lange-Badré and Haubold (1990)
Prodissopsalis eocaenicus	Geiseltal	13.90	7.20	Lange-Badré and Haubold (1990)
Prodissopsalis eocaenicus	Geiseltal	14.10	8.10	Lange-Badré and Haubold (1990)
Prodissopsalis eocaenicus	Geiseltal	14.40	7.90	Lange-Badré and Haubold (1990)
Cynohyaenodon trux	Geiseltal	6.20	3.40	Lange-Badré and Haubold (1990)
Cynohyaenodon trux	Geiseltal	6.00	—	Lange-Badré and Haubold (1990)
Cynohyaenodon trux	Geiseltal	7.10	—	Lange-Badré and Haubold (1990)
Cynohyaenodon trux	Geiseltal	—	4.10	Lange-Badré and Haubold (1990)
Cynohyaenodon trux	Egerkingen γ	5.80	3.70	Lange-Badré and Haubold (1990)
Proviverra typica	Egerkingen γ	4.40	2.70	Lange-Badré and Haubold (1990)
Proviverra typica	Egerkingen γ	4.60	3.10	Lange-Badré and Haubold (1990)
Cartierodon egerkingensis	Egerkingen γ	13.10	8.00	Solé and Mennecart (2019)
Cartierodon egerkingensis	Egerkingen γ	15.20	8.90	Solé and Mennecart (2019)

Family Hyaenodontidae Leidy, 1869

Genus *Prodissopsalis* Matthes, 1952

Type species. *Prodissopsalis eocaenicus* Matthes, 1952.

Type locality. Geiseltal-Obere Mittelkohle, Grube Leonhardt, Site III (MP 12, Germany).

Holotype. Leo III-94 (LH94), fragment of skull with right P1-P4 and M1-M3, and left M1-M3, figured in Matthes (1952, figs. 1–3).

Distribution. Geiseltal-Untere Mittelkohle (Lutetian, MP 12, Germany) and Geiseltal-Obere Mittelkohle (Lutetian, MP13, Germany); Issel (Lutetian, MP 14, France); Lissieu (Lutetian, MP 14, France); and Egerkingen α + ß (Lutetian, MP 14, Switzerland).

Emended diagnosis. Modified from Lange-Badré and Haubold (1990): "Proviverrine" of large size, with dental formula 2/? I, 1/1 C, 4/4 P, 3/3 M; P1, P2 and P3 with low and mesiodistally elongated crown, slightly separated but without defining a diastema; double-rooted P1 and p1 single or double-rooted depending on the species; crown of P3 distolingually expanded and shorter than that of P2; P4 with a lingually elongated protocone; p4 with hypoconid and entocristid; m1 and m2 with a moderately reduced metaconid, partially fused to the high and narrow protoconid, paraconid height larger than its mesiodistal length; high talonid with a swallow basin; hypoconid forming a buccal rib, widely separated from the hypoconulid; entoconid not distinct from the entocristid; presence of a postcingulid close to the hypoconulid; m3 with a more reduced metaconid and a longer and more mesially located paraconid than those of m1 and m2; triangular talonid with an entocristid contacting the hypoconulid. Upper molars with paracone smaller and lower than metacone; metastyle high in relation to the metastyle, and not aligned with the metacrista; length of metastyle similar to that of the two buccal cusps; protocone mesially located; M3 with a long parastyle and a very small metacone.

Prodissopsalis jimenezi new species

Figures 3–5, Tables 1 and 2

Type locality. La Solana (Mazaterón, Soria province, Spain), late middle Eocene (Bartonian, MP 15–16).

Holotype. STUS-15077, fragmented mandible with both right and left rami, with erupting left d4 and m2,

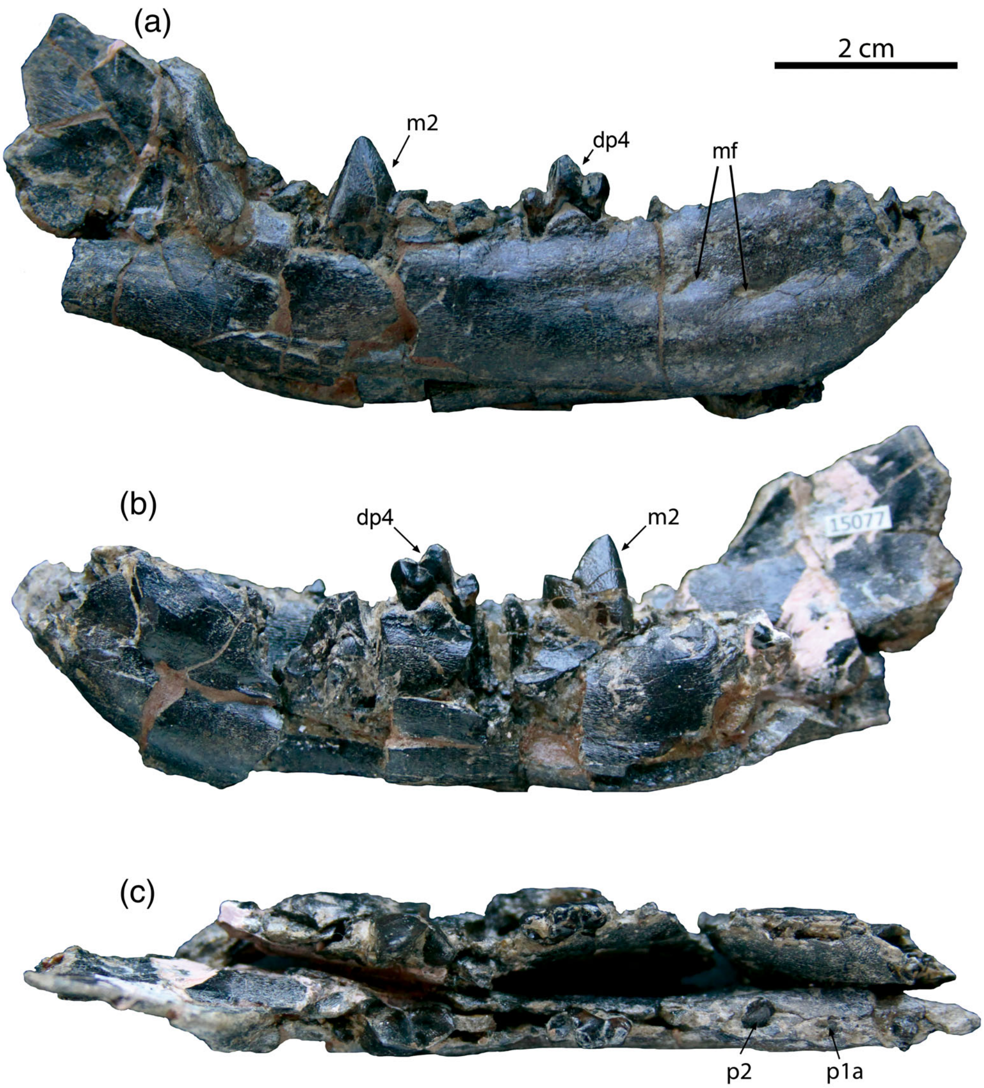

FIGURE 2 STUS-15077, mandible of *Prodissopsalis jimenezi* from La Solana: (a) right lateral view, (b) left lateral view, and (c) occlusal view. Abbreviations in Section 2.

and right dp4, m1 and m2; the c, p2, p3, p4 and m3 of both sides are still inside the mandibular bone, but only the right i2 and i3 are preserved; all of them were studied through CT Scanning of the piece.

Zoobank species LSID: urn:lsid:zoobank.org:act:87759DAB-B6DA-4D70-87FD-127AE66030DD.

Etymology. The species name is dedicated to Prof. Emiliano Jiménez Fuentes, who greatly contributed to the knowledge of the Eocene fossil record from Spain.

Diagnosis. Very similar size to *P. eocaenicus*, with dental formula ?/2 I, ?/1 C, ?/4 P, ?/3 M; dp4 with elongated and buccolingually compressed crown, without cingulids, paraconid lower than protoconid and mesially oriented, metaconid moderately developed, slightly higher that paraconid, low buccodistally oriented talonid, with a marked central basin, and talonid cuspids crested, with a hypoconid higher than entoconid and hypoconulid; single-rooted p1; p4 with hypoconid; m1 with low paraconid, much higher protoconid, well-developed metaconid located at the level of the distal border of the protoconid, paraconid mesiolingually oriented and with a vertical buccal ridge, talonid much shorter than trigonid, deep talonid basin, with entoconid, hypoconid and hypoconulid clearly individualized, the latter being slightly higher than the two others; m2 larger and relatively much higher than both m1 and dp4, with a mesiodistally elongated and buccolingually compressed crown, protoconid much higher than paraconid, which is mesiolingually oriented, very reduced talonid in comparison to m1, with round hypoconulid and a slightly lower hypoconid.

Differential diagnosis. *P. jimenezi* can be distinguished from *P. eocaenicus* by the following features: single-rooted p1, relatively more elongated paracristid in m1 and m2, relatively more compressed m1 and m2, relatively reduced talonid on m1.

4 | DESCRIPTION OF THE MAZATERÓN SPECIMEN

4.1 | Mandible

The specimen is very fragmented, and it lacks most of the coronoid process (Figure 2). The mandibular corpus is elongated, with a gently curved symphysis, and two mental foramina, similarly sized, slightly rostrocaudally elongated, and located at the level of p2 and p3 (Figure 2a). The caudal border is broken, but the remaining ventral border of the angular process shows the existence of a slightly curved outline. These two features (two mental foramina and curved caudal margin) are typical of Hyaenodontidae (Solé, Amson, et al., 2015).

4.2 | Lower dentition

The right i2 and i3 are partially unerupted; the crowns are formed but the roots were not fully developed when the animal died (Figure 3); the crown of both pieces is very similar in morphology and size: there is a main central cuspid, mesially displaced, a less developed distal cuspid, and a very small, vestigial mesial cuspid. The lower canines, with a blunt point, are in a very early development stage, so only a small portion of the crown is formed; this is buccolingually compressed, and showing a lingual longitudinal groove for the accommodation of the permanent canines, although there is no trace of them. The alveoli of both left and right p1 are visible, although these pieces are not preserved in the specimen; from the alveolus, it seems that the p1s were single-rooted (Figure 3c). The p2s have partially developed roots, as these teeth are in an early stage of development, showing only the tip of the main cuspid; their crowns are triangular, with a very elongated distal border, and are slightly buccolingually compressed and lingually curved; there are no mesial or distal cuspids, but there are soft mesial and distal ridges instead. Both p3s and p4s are unerupted. The p3s are much smaller than p2 and p4, but they seem to be in an earlier stage of development than these other premolars, which could explain their relatively smaller size; the crowns of both p3s are triangular, but more symmetrical than those of p2, as they lack the distal expansion seen on p2; also, the crown is not compressed but inflated. The p4s have a large and relatively high main cuspid, a very low buccodistal cuspid (a hypoconid for Lange-Badré & Haubold, 1990), and an

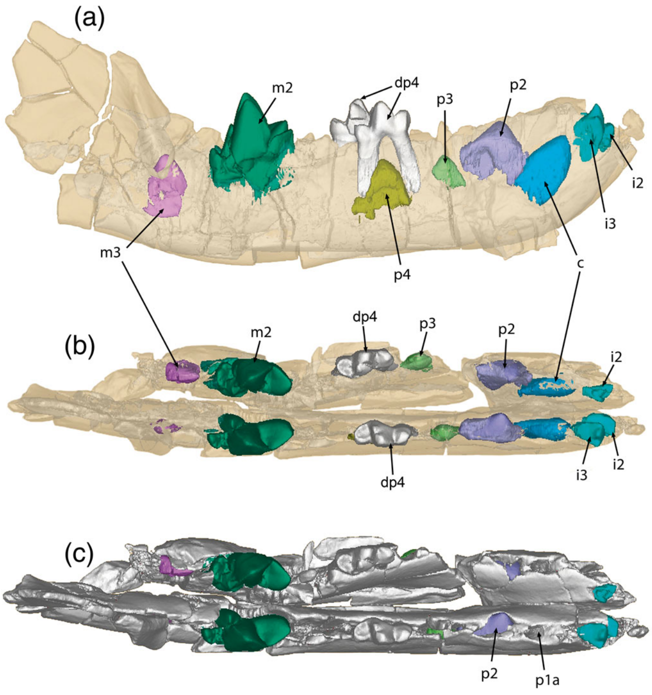

FIGURE 3 Rendering 3D image of STUS-15077, mandible of *Prodissopsalis jimenezi* from La Solana, rendered transparent to show the erupted and developing dentition in (a) right lateral view and (b) occlusal view. (c) Occlusal view of the rendered mandible to show the erupting dentition and alveoli. Abbreviations in Section 2.

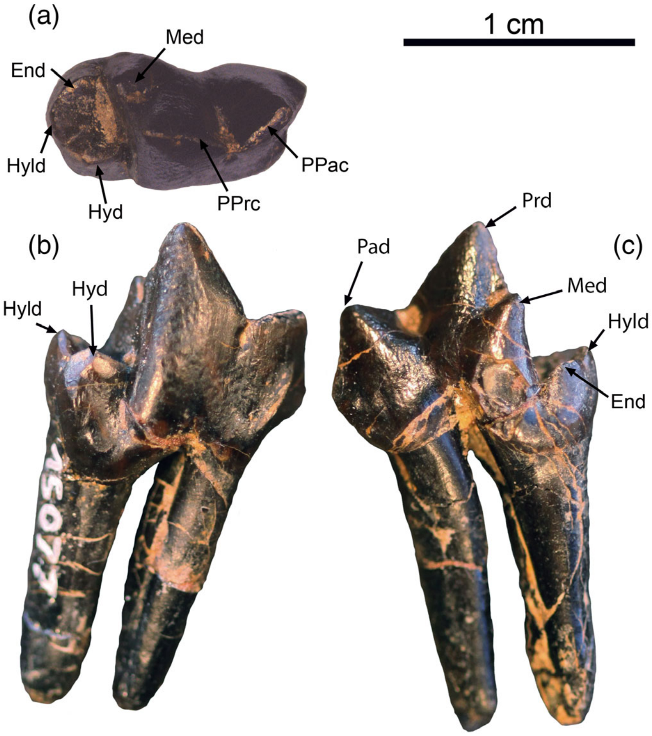

FIGURE 4 STUS-15077, right m1 of *Prodissopsalis jimenezi* from La Solana: (a) occlusal view, (b) buccal view, and (c) lingual view. Abbreviations in Section 2.

almost absent mesial cuspid; the crown is much larger than that of p3, but slightly smaller than p2; in a similar way to this latter tooth, the crown of p4 is buccolingually compressed. In this respect, it should be noted that p2, p3, and p4 are in different stages of development, but none of them has reached its definitive morphology, and thus the mentioned differences in relative size should be taken with caution until a mandible with a completely erupted adult dentition is found. The dp4s have elongated and buccolingually compressed crowns, without any trace of cingulids; the paraconid is lower than the protoconid and is mesially oriented; the metaconid is moderately developed, located slightly higher that the paraconid; the talonid is low, buccodistally oriented, with a marked central basin; the talonid cuspids are crested, with a hypoconid higher than entoconid and hypoconulid. The m1 (Figure 4) has a low paraconid and a much higher protoconid, with a well-developed metaconid located at the level of the distal border of the protoconid, slightly higher than the paraconid; this latter is oriented mesiolingually and its buccal surface develops a marked vertical ridge; the talonid is much shorter than the trigonid, and is distally oriented; the talonid basin is deep, and the entoconid, hypoconid and hypoconulid and are clearly individualized, with the latter being slightly higher than the two others. The dp4 and m1 are of similar size, both clearly smaller than m2. This latter molar is larger and relatively much higher than both m1 and dp4, and its crown is mesiodistally elongated and buccolingually compressed; the paraconid is much higher than the protoconid, which is mesiolingually oriented, although less so than the m1 protoconid; the talonid is very reduced in comparison to that of m1, and although it is severely broken, a round hypoconulid and a slightly lower hypoconid can be observed on the distolingual margin. The m3s are present, but unerupted and in a very early stage of development, and only the protoconid is clearly distinguishable in both sides.

4.3 | Eruption sequence in *P. jimenezi*

The study of the eruption sequence of mammals can provide important data for phylogenetical and ontogenetical analysis (Bastl et al., 2011, 2014; Bastl & Nagel, 2014; Borths & Stevens, 2017a). Nevertheless, for the description of the eruption sequence it is necessary to count with several specimens in different stage of development, which allows to infer the order of eruption of each dental piece. In general, to establish this eruption sequence, a tooth germ in a more advanced stage of formation is considered to erupt before other germs in an earlier stage, but for that purpose, a sample of fossils showing different phases of teeth development is necessary (Borths & Stevens, 2017a). In our case, only a single specimen is available from La Solana, and although it provides the first data on erupting teeth of a member of the *Eurotherium*-clade, the information is not enough to infer the complete sequence. The mandible STUS-15077 (Figure 3) does not preserve p1 (although the single-rooted alveolus confirms its presence), dp1, dp2, and dp3, but from the development stage of the permanent premolars and molars, it is clear that m1 and m2 were the first permanent teeth to erupt, and then probably the p2, which is located very close to the alveolar border of the mandible, and also shows a larger crown in a more advanced stage than those of p3 and p4; of these two latter premolars, the p3 shows a crown in a very early stage, as it is smaller than that of p4, which would suggest that the latter erupted earlier. Nevertheless, the crown of p3 is closer to the alveolar border than that of p4, and does not have a

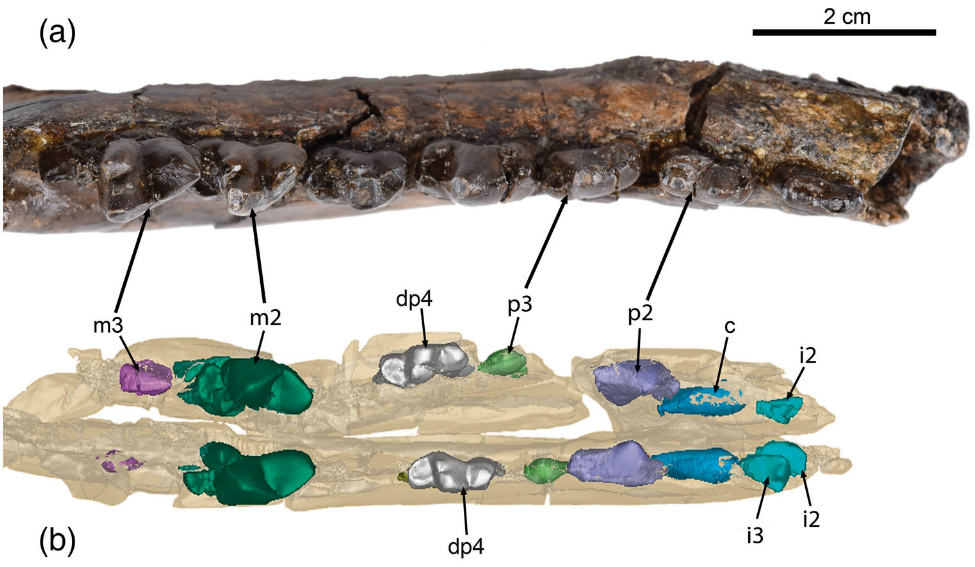

FIGURE 5 Comparison of the occlusal dentition in *Prodissopsalis*. (a) Occlusal view of GMH VI-211-1950, right hemimandible of *P. eocaenicus* from Geiseltal (MP 12–13, Germany). (b) STUS-15077, mandible of *P. jimenezi* from La Solana. Abbreviations in Section 2.

deciduous premolar delaying its eruption, which is the case of p4; thus, this could imply a p3 erupting earlier than p4. More problematic is the case of m3, which is very close to the alveolar border, but shows a very incomplete crown that seems to illustrate the protoconid, with no trace of talonid and mesial part of trigonid; this would suggest, rather than a very early stage of development, the loss of part of the crown due to the poor state of preservation of STUS-15077, and thus the m3 would be closer to erupt than p4. Finally, the lower canine crown is as large as that of p2, but there is no other indication of its place in the sequence.

Considering all this, the following tentative eruption sequence could be proposed for *P. jimenezi*: p1-m1-m2-p2-p3-m3-p4. This sequence is similar to those inferred by Borths and Stevens (2017a) for other Hyaenodonta, such as *Apterodon*, *Masrasector*, or *Metasinopa*.

5 | DISCUSSION

The fossil from La Solana shows several similarities with the material of *P. eocaenicus* from the older localities of Geiseltal (MP 12–13, Germany), and although the mandible studied here corresponds to a subadult individual, still far from the final adult stage, its overall shape and morphology, elongated and relatively slender, resemble those of the adult specimens from Geiseltal. The preserved dentition also illustrates the typical dental morphology of this genus and shows diagnostic features that allow its distinction from the closely related taxa *Cartierodon egerkingensis*, such as the smaller size, the relatively narrower lower premolars, and the absence of a mandibular foramen at the level of p4 (see Solé & Mennecart, 2019). Besides, the mandible from La Solana shows a very different morphology from that of other contemporary taxa such as *Matthodon tritens*, whose robust mandible and teeth (similarly to those of the genus *Quercytherium*) would point towards a scavenging, bone-cracking adaptation (Solé et al., 2014, 2015b). On the contrary, *P. eocaenicus* would belong to a group of more active hunters, which also included the more derived genus *Oxyaenoides*, this latter showing no trait of a metaconid in the lower molars and a strongly reduced talonid (Dubied et al., 2019). The m1 from La Solana shows a clearly individualized entoconid (Figure 4), a feature shared by other genera of hyaenodonts recorded in Ypresian and Lutetian localities from Europe, such as *Proviverra*, *Cynohyaenodon*, *Eurotherium*, *Prodissopsalis*, *Leonhardtina*, *Allopterodon*, *Alienetherium*, *Quercytherium*, and *Paracynohyaenodon* (Solé & Mennecart, 2019), but its larger size (Tables 1 and 2) and reduced talonid distinguishes the La Solana hyaenodont from other taxa with well-developed talonids on the lower molars, such as *Leonhardtina*, *Allopterodon*, *Eurotherium*, and *Paracynohyaenodon*. Following the phylogeny proposed by Solé & Mennecart (2019), *P. eocaenicus* is part of a clade containing the genera *Eurotherium* and *Cartierodon*, the three of them having a similar dental morphology, but also distinctive features: thus, *Prodissopsalis* shows a smaller size and a more reduced talonid on m1 and m2 than *Cartierodon*, traits also observed in the specimen from La Solana, whereas *Cartierodon* can be distinguished from *Prodissopsalis* by the presence of a second foramen located below the mesial root of the p4, wider lower premolars, mesiodistally shorter talonid on m3, and a protocone area more developed on P3 (Solé & Mennecart, 2019).

Nevertheless, the material of from La Solana shows a set of morphological differences that allow its distinction from the known fossils of *P. eocaenicus*, such as the single-rooted p1 (in contrast to the double-rooted p1 of the latter), a relatively more elongated paracristid in m1 and m2, relatively more compressed m1 and m2, and a strongly reduced talonid on m1 (Figures 5 and 6); these features indicate a derived dental morphology in relation to older specimens of this genus, something expectable given the great temporal gape existing between the last records of *P. eocaenicus* and the new fossils from La Solana site. Also, the dental differences suggest an evolution towards a more hypercarnivorous diet, with the reduction of p1 and more trenchant m1 and m2 (which both show elongated, sharper trigonids). Unfortunately, there are no published dp4 from *P. eocaenicus*, but this piece is known in other

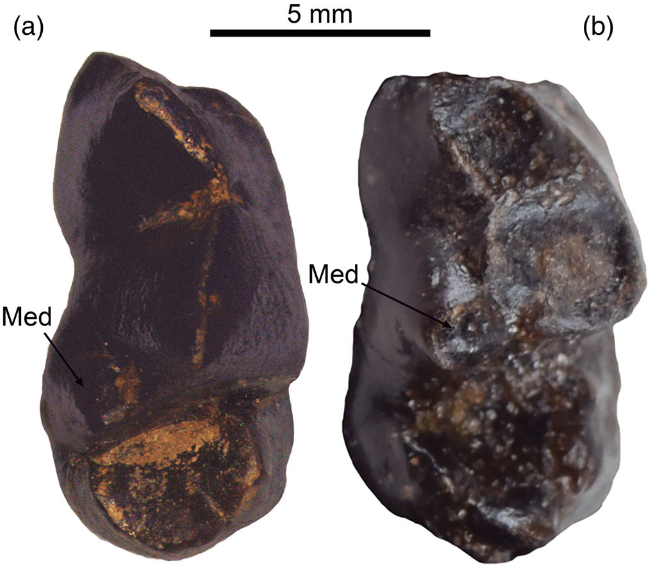

FIGURE 6 Comparison of the m1 in *Prodissopsalis* in occlusal view. (a) STUS-15077, right m1 of *Prodissopsalis jimenezi* from La Solana. (b) GMH VI-211-1950, right m1 of *P. eocaenicus* from Geiseltal (MP 12–13, Germany). Abbreviations in Section 2.

hyaenodonts, such as *Masrasector nananubis*, *Lesmesodon behnkeae*, *Metasinopa*, and *Hyaenodon* (Bastl et al., 2011, 2014; Borths & Stevens, 2017a; Morlo & Habersetzer, 1999). In this latter genus, the dp4 has a blade-like talonid, different from the wider, basined talonid of *P. jimenezi*, *M. nananubis*, *L. behnkeae*, and *Metasinopa*, something that would suggest a more carnivorous diet for *Hyaenodon*, although the microwear analysis by Bastl et al. (2012) found that the European species of this genus also included a high proportion of bone in their diet. The dp4 of *P. jimenezi* has a reduced talonid in comparison to those of *M. nananubis*, *L. behnkeae*, and *Metasinopa*, which show relatively more elongated talonids (Borths & Stevens, 2019a; Morlo & Habersetzer, 1999). Thus, the dp4 of *P. jimenezi* represents an intermediate morphology between that of *Hyaenodon* and that of the genera *Masrasector*, *Lesmesodon*, and *Metasinopa*, which probably had mesocarnivorous diets (Borths & Stevens, 2017c; Morlo & Habersetzer, 1999). In fact, Dubied et al. (2021) considered *P. eocaenicus* has having a diet that included primarily meat, but also bone, and the more sectorial dentition of *P. jimenezi* would suggest a much more meat-dominated diet.

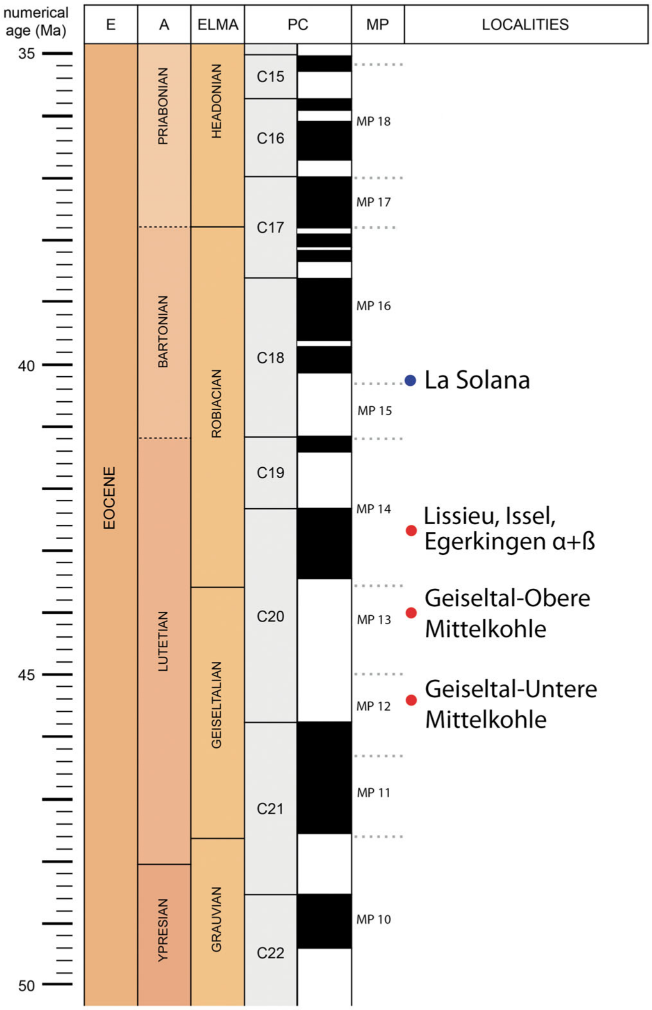

FIGURE 7 European fossil sites with *Prodissopsalis eocaenicus* (red dots) and *Prodissopsalis jimenezi* (blue dot). Columns are calibrated to International Chronostratigraphic Chart (Gradstein et al., 2012). A, age; E, epoch. Eocene European Land Mammal Ages (ELMA, see Vandenberghe et al., 2012) divided into mammal Paleogene (MP reference levels following Aguilar et al., 1997; Schmidt-Kittler, 1987). PC, Polarity Chron (Geomagnetic Polarity Scale; modified from Ortega et al., 2022).

The presence of *P. jimenezi* in the late middle Eocene (Bartonian, MP 15–16) of La Solana constitutes the youngest record of the genus *Prodissopsalis* in Europe (Figure 7), as this predator had not yet been detected after the Lutetian (MP 14) deposits of France (Calas, 1969, 1970; Lange-Badré, 1972; Lange-Badré & Haubold, 1990; Matthes, 1952; Solé & Mennecart, 2019). This gap in the fossil record poses interesting questions on the evolution of the hyaenodonts of the Iberian Peninsula during the Bartonian, a period for which very few data exist. During the Lutetian (MP 11–14), the only carnivorous mammals living in Europe were hyaenodonts and early carnivoraforms, as during the Ypresian, especially from MP 8 to 10, viverravids, oxyaenodonts, "sinopanine" hyaenodonts and mesonychids became extinct (Solé et al., 2022). Moreover, whilst the diversity of carnivoraforms decreased during the Ypresian and Lutetian, the endemic hyaenodonts experienced a strong radiation at the beginning of the Bartonian, coinciding with the Middle Eocene Climatic Optimum (Solé et al., 2022). Thus, the presence of *P. jimenezi* in MP 15–16 of La Solana suggests that the northwestern region of the Iberian Peninsula was not only a place for isolated evolution of endemic taxa (Badiola et al., 2009, 2022; Badiola & Cuesta, 2008; Perales-Gogenola et al., 2022), but also may acted as a refuge for taxa that went extinct in the rest of the continent, such as the genus *Prodissopsalis*. As widely discussed by Badiola & Cuesta (2008) and Badiola et al. (2009), the Middle and Late Eocene mammalian faunas from the western and central basins of the Iberian Peninsula (Duero, Almazán, Oviedo, and Miranda-Trebiño) were markedly different from those typical of the Southern Pyrenean basins and the rest of Europe (Casanovas & Moyà-Solà, 1992; Casanovas-Cladellas & Santafé-Llopis, 1987, 1989; Cuesta, 1991, 1999, 2003; Peláez-Campomanes, 1993). Among these taxa, there were several endemic genera of equoid Perissodactyla, such as *Cantabrotherium*, *Franzenium*, *Iberolophus*, and *Paranchylophus* (Badiola et al., 2022), all of them potential prey for *P. jimenezi*, at least the juvenile individuals. In fact, the transition from the middle to late Eocene is synchronic to a faunal change characterized by an increase in the diversity of hypsodont ungulates (Badiola et al., 2022; Franzen, 2003) probably due to a cooling process that caused the spread of open habitats, with increased aridity and a more marked seasonality (Badiola, 2004; Blondel, 2001; Franzen, 2003; Remy, 2004). This poses an interesting question regarding the locomotor adaptations of *P. jimenezi*, as, if this predator was favored by this aridification process and the appearance of less wooded environments, it would be very probable that it had a more or less slender appendicular skeleton, suitable for hunting fast ungulates. The more trenchant, hypercarnivorous dentition of *P. jimenezi* in comparison to the more primitive species *P. eocaenicus* would point toward a refining of its hunting abilities, but until new fossils of this interesting hyaenodont are found, this is just a speculation.

AUTHOR CONTRIBUTIONS

Manuel J Salesa: Conceptualization; investigation; formal analysis; funding acquisition; methodology; project administration; resources; writing-original draft. **Gema Siliceo:** Formal analysis; investigation; CT scanning processing, methodology; writing-original draft. **Mauricio Antón:** Formal analysis; investigation; writing-original draft. **Irene Martínez:** Preparation and restoration of fossils. **Francisco Ortega:** Formal analysis; investigation; methodology, writing-original draft.

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