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RESEARCH

Paleohistology and life history of *Procervulus* and *Eotragus* (Ruminantia, Artiodactyla) from the Middle Miocene site of els Casots (NE Iberian Peninsula)

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Abstract
The Miocene Climatic Optimum (MCO) event (ca. 16.9–14.7 Ma) was a period of increased warmth spanning more than 2 Myr that offers valuable insights into climate-driven ecological changes. The early Middle Miocene site of els Casots (MN5, ~15.9 Ma), in the Vallès-Penedès Basin (NE Iberian Peninsula), is of extraordinary importance due to the abundant vertebrate remains and its coincidence with the midpoint of the MCO. *Procervulus* (Cervidae) and *Eotragus* (Bovidae) are of particular interest among the recorded taxa due to their basal phylogenetic position within their respective clades and their (apparently) similar ecology. Dental histology can provide valuable information about an organism's life history (LH) through the analysis of its tissues, as their incremental development records growth rates and periods of physiological stress. To investigate possible LH differences between the two clades, we analyzed the enamel histology of their molars with a focus on their enamel daily secretion rate (DSR). Our results indicate that both species exhibited a particularly high DSR, which agrees with a fast LH strategy. The similarity in DSR between *Procervulus* and *Eotragus* further strengthens the similarity between cervids and bovids during their early evolutionary stages. Furthermore, *Procervulus* from els Casots shows no significant differences compared with *Procervulus* from Artesilla in central Iberia, where likely drier and more open habitats prevailed. However, the likely presence of open woodlands in the surroundings of the more forested environment of els Casots suggests that the two *Procervulus* spp. inhabited similar environments and might partially explain their ecological similarities.

Keywords Bovidae · Cervidae · Dental histology · Enamel · Miocene Climatic Optimum

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Introduction

The Miocene has been the subject of particular study with regard to climatic variations, which resulted in changes of the fauna and flora (DeMiguel et al. 2010; Steinthorsdottir et al. 2021a). A thermal maximum (the warmest since the Eocene), known as the Miocene Climatic Optimum (MCO) and lasting more than 2 Myr (ca. 16.9–14.7 Ma; Zachos et al. 2001; Westerhold et al. 2020; Steinthorsdottir et al. 2021a), has attracted the attention of the scientific community as a potential scenario for future climate projections (You et al. 2009; Steinthorsdottir et al. 2021a, b). During the MCO, it is believed that global temperatures were 5 to 7 °C higher than they are today (Westerhold et al. 2020; Steinthorsdottir et al. 2021a, b).

The stem cervid *Procervulus* is among the species that lived throughout this period of increased warmth (DeMiguel et al. 2010), until almost the Mid-Miocene Climate Transition (MMCT; 14.7–13.8 Ma), a long-lasting stepwise global cooling trend that followed the MCO (Steinthorsdottir et al. 2021a). This genus is first reported from the Early Miocene (MN3; ~19.5–17.2 Ma; Hilgen et al. 2012) of Western and Central Europe, primarily in France, Germany, and the Iberian Peninsula (Azanza 2000; Ginsburg 2005; Böhme et al. 2012; DeMiguel et al. 2012; Rössner et al. 2021). Its impressively long and well-documented Iberian record, spanning 4 Myr, makes it a useful taxon for inferring the effects of climate change on the physiology of mammals (see DeMiguel et al. 2010). *Procervulus* inhabited Europe alongside early bovids, likely overlapping their ecological niches (DeMiguel et al. 2008, 2010), although bovids constituted a minor component of the ruminant assemblages (DeMiguel et al. 2011), at least during the early and middle Aragonian (16.4–13.8 Ma; Hilgen et al. 2012). *Eotragus* is one of the earliest known members of the Bovidae (Bibi et al. 2009; Li et al. 2021; Mennecart et al. 2025) and, together with *Namacerus gariepensis*, the oldest known horn-bearing bovid (DeMiguel et al. 2014). The oldest European record of *Eotragus* dates back to the Early Miocene (MN4; 17.2–16.4 Ma; Van der Meulen et al. 2012) of France, with *Eotragus artenensis* (Bibi et al. 2009; Mennecart et al. 2025). In Asia, with an estimated age of 18 Ma, *Eotragus noyei* and *Eotragus minus* represent the oldest records of the genus (DeMiguel et al. 2014). Although the basal position of *Eotragus* is still a matter of debate (Bibi 2013), it is a key taxon for understanding the initial evolution of bovids during the Early Miocene (Mennecart et al. 2025). There are several European Miocene sites where *Procervulus* and *Eotragus* co-occur (Robles et al. 1991; Iñigo and Cerdeño 1997; Ginsburg 2001; Sach and Heizmann 2001; Augé et al. 2002; Kaiser and Rössner 2007; DeMiguel et al. 2014; Casanovas-Vilar et al. 2022a; Koufos 2024; Sánchez et al. 2024); however, evidence supporting their sympatry is only available from Artenay (France), Petersbuch 2 and Erkertshofen 2 (southern Germany), and Córcoles, Buñol and els Casots (Iberian Peninsula).

The early Middle Miocene site of els Casots (CS), located in the municipality of Subirats (less than 40 km away from Barcelona) within the Vallès-Penedès Basin (NE Iberian Peninsula) and dated to around 15.9 Ma (early Middle Miocene, MN5), reporting the presence of *Procervulus* cf. *dichotomus* and *E. noyei* (Casanovas-Vilar et al. 2022a), offers therefore a unique opportunity to study a specific moment within the early evolution of cervids and bovids. Furthermore, it allows us to study wetland ecosystems from southern Europe during the exceptionally warm MCO. In terms of their main features, both genera are brachyodont (DeMiguel et al. 2016), with *Eotragus* exhibiting slightly higher cheek teeth than *Procervulus*. Indeed, although their teeth are similar in size, there are some differences. Specifically, the persistence of the palaeomerycid fold and the central fold in *Procervulus*—respectively, a plesiomorphic feature typically found in the lower molars and an apomorphic feature typically found in the upper molars of primitive deer (Azanza 2000)—along with the morphological differences of the crests and styles/stylids in *Eotragus*, associated with the incipient hypsodonty of primitive bovids (DeMiguel et al. 2016). These differences include a reduced difference in height between the cones/conids and the styles/stylids in *Eotragus*—resulting in more vertical crests—and represent a transitional stage towards a more pronounced (even if incipient) hypsodonty, likely aimed at improving mechanical efficiency (DeMiguel et al. 2016). Besides these subtle dental differences (Ginsburg and Heintz 1968; Gentry 1994), the two taxa are very similar in size and postcranial morphology, and further share a low cranial appendage complexity. In fact, despite belonging to different families, the most prominent morphological differentiation between bovids and cervids occurred later during the Middle Miocene (Gentry et al. 1999; Badiola et al. 2001; DeMiguel et al. 2014).

The paleohistological analysis of fossilized tissues can provide valuable insights about development and physiology of an organism (Nacarino-Meneses et al. 2017; Orlandi-Oliveras et al. 2019; Chinsamy 2023; Cuccu et al. 2025). Among the hard tissues, dental enamel, dentine and cementum exhibit a periodic accretion that can be measured to map the developmental chronology of the tooth (Smith et al. 2006; Smith 2008; Hogg 2018). Specifically, enamel and dentine, periodically secreted by ameloblasts and odontoblasts, exhibit a typical incremental structure, result of periodical accretions, that reflects biological rhythms (Smith 2008; Nacarino-Meneses et al. 2025). Of the various incremental structures observed, laminations are the most prominent in ungulate enamel (Kierdorf et al. 2013, 2014; Orlandi-Oliveras et al. 2019; Emken et al. 2021). Described as incremental features that are parallel to the long-period ones found in the enamel of other mammals (referred to as Retzius lines), they represent the isochrone of the enamel formation front (Tafforeau et al. 2007; Kierdorf et al. 2013, 2014, 2019). Previous studies have demonstrated their daily nature (Iinuma et al. 2004; Kierdorf et al. 2013). Sub-daily incremental features have been reported in various studies on artiodactyls (Iinuma et al. 2004; Kierdorf et al. 2013, 2019; Emken et al. 2021; Cuccu et al. 2025; Nacarino-Meneses et al. 2025). However, while their presence in this group is well established, the detection of long-period incremental features cannot always be assumed. In fact, supra-daily incremental lines have not been found in the enamel of sheep and deer (Iinuma et al. 2004; Kierdorf et al. 2013; 2014; Cuccu et al. 2025). Nevertheless, such features have been reported in giraffes (Nacarino-Meneses et al. 2025) and suids (Kierdorf et al. 2019), albeit only limited to the outer enamel. Among the incremental features found in enamel the growth lines with circadian and supra-circadian periodicity have been widely studied to infer growth rates as well as disturbances during dental ontogeny (Kierdorf et al. 2012; Hogg 2018; Orlandi-Oliveras et al. 2019; Nacarino-Meneses et al. 2022, 2025). They have been also used to infer dental development in mammals, since it is closely associated with important life history events, such as age at weaning and age at skeletal maturity (Dean 2006; Smith et al. 2006; Dirks et al. 2012; Orlandi-Oliveras et al. 2019; Funston et al. 2022; Nacarino-Meneses and Chinsamy 2022). Here, based on the study of enamel incremental structures we investigate the lower molars of *P.* cf. *dichotomus* and *E. noyei* from els Casots and compare them with previously published data for other early *Procervulus* species (as no paleohistological data are currently available for other *Eotragus* species), with the aim to assess whether they exhibited similar life histories (LH).

Geological and faunal background

The site of els Casots (Subirats, Catalonia, Spain) is one of the richest terrestrial vertebrate sites from the early Middle Miocene of Europe. It was discovered in 1989 by an amateur collector, which led to systematic excavations from 1989 to 1995 (directed by Salvador Moyà-Solà; Moyà-Solà and Rius Font 1993) and from 2019 onward (Casanovas-Vilar et al. 2022a), and the protection of the site as a cultural heritage asset in 1995. More than 70 vertebrate species, represented by thousands of specimens, have been reported (Casanovas-Vilar et al. 2022a). These include well-preserved artiodactyl material that enabled the description of several new genera and species (Pickford and Moyà-Solà 1994, 1995; Duranthon et al. 1995; Orliac 2006; Pickford 2017)—the peccary-like suoid *Choeromorus ibericus*, the listriodontine suid *Eurolistriodon adelli*, and the paleomerycid *Ampelomeryx ginsburgi*. The material of some other artiodactyls from els Casots (tragulids, in particular) has been also described in detail (Alba et al. 2014), but the cervid and bovid material remains unpublished except for their brief account in Casanovas-Vilar et al. (2022a). The other large mammal remains from els Casots thus far described in detail correspond to the mustelid carnivora *Iberictis* (Valenciano et al. 2020) and the deinotheriid proboscidean *Prodeinotherium* (Gasamans et al. 2021).

Els Casots is located on the southern margin of the Vallès-Penedès Basin (Fig. 1), which is a half-graben formed during the late Oligocene-Miocene rifting of the Western Mediterranean (Roca et al. 1999; Casanovas-Vilar et al. 2016). The sedimentary infill of the basin consists mainly of Miocene continental deposits, with occasional marine transgressions (Casanovas-Vilar et al. 2016). Although the Early Miocene and early Middle Miocene deposits are generally less fossiliferous than the younger strata, recent systematic fieldwork has significantly expanded our knowledge of their chronology and paleoenvironment (Casanovas-Vilar et al. 2021, 2022a, b; Jovells-Vaqué and Casanovas-Vilar 2021). The site of els Casots corresponds to a shallow lacustrine system within the Subirats alluvial-lacustrine unit (Cabrera-Pérez 1981), which includes major fossil sites such as Can Julià, Can Martí Vell, and les Cases de la Valenciana (Crusafont et al. 1955; Agustí 1983; Jovells-Vaqué and Casanovas-Vilar 2021; Jovells-Vaqué et al. 2021). The Miocene succession at els Casots has been analyzed in detail through core drilling, revealing a ~35 m sequence (Casanovas-Vilar et al. 2022a). The basal unit consists of 4 m-thick breccias that directly overlie the pre-Miocene basement. This is followed by a 25 m-thick, cyclically arranged, mudstone/limestone lacustrine succession, and an uppermost sequence of 5 m of mottled, reddish silts, and sandstones, which are topped by carbonate-rich, pedogenic to palustrine facies (Casanovas-Vilar et al. 2022a). The lacustrine succession yielded an abundance of fossil vertebrates in the excavated area (Casanovas-Vilar et al. 2022a). Fossil remains of vertebrates have also been found in lacustrine levels outside of the site area, consisting of a 3.5 m-thick section with lutite and carbonate layers. Carbonate microfacies analysis on this section, together with recovered aquatic microflora, indicates a shallow freshwater mesotrophic to eutrophic lake (Sanjuan et al. 2023). The rare finding of abraded Miocene foraminifera, together with geological evidence, indicates that the lake system was situated near the coastline (Sanjuan et al. 2023). The stratigraphic succession shows that as global warming progressed, the lacustrine system disappeared and was overlaid by continental deposits consisting of red mudstones and green/gray sandstones corresponding to distal alluvial fan facies. This was followed shortly after by an oyster coquina and a bioclastic quartzarenite, which mark the Langhian marine transgression in this sector of the Vallès-Penedès Basin (Casanovas-Vilar et al. 2022a).

The biochronological correlation of els Casots within the European MN zones/units has been controversial, since the concept and definition of MN boundaries have long been debated. Following the zone boundary definition by selected single-taxon historical appearance events in Hilgen et al. (2012), the MN5 base is marked by the Last Historical Appearance (LHA) of the eomyid rodent *Ligerimys florancei*, which is the last recorded *Ligerimys* species in Central Europe. However, contrary to *L. florancei*, which

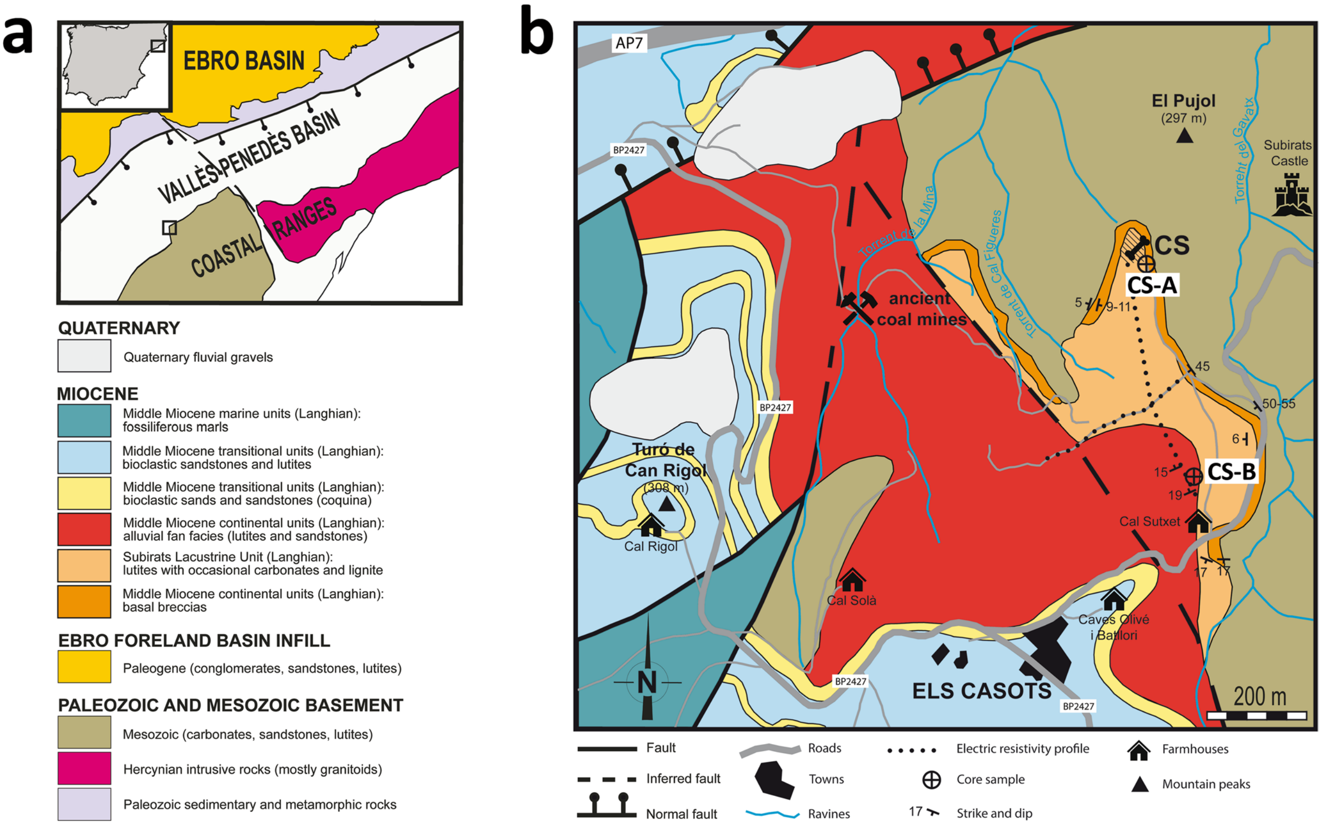

Fig. 1 Geographical (**a**) and geological (**b**) context of the Middle Miocene (MN5) els Casots site. The situation of the main excavation area (CS) as well as that of geological core samples (CS-A, CS-B) are indicated. Figure reproduced from Casanovas-Vilar et al. (2022a)

is last recorded from the site of Artesilla (16.49 Ma; Calatayud-Daroca Basin; Van der Meulen et al. 2012) at the base of the early Aragonian subzone Ca (16.63/16.49–16.30/16.15 Ma; Van der Meulen et al. 2012), *Ligerimys ellipticus* persists longer in the Iberian basins. Since only *L. ellipticus* is present at els Casots, the site is correlated to the early Aragonian subzone Cb (16.30/16.15–15.94/15.93 Ma; Casanovas-Vilar et al. 2022a), corresponding to the early MN5. This subzone was initially assigned to the MN4 unit (Van der Meulen et al. 2012), in agreement with the MN4 original concept based on the reference level of La Romieu (Mein 2000; Van der Meulen et al. 2012). This is because MN4/MN5 boundary was defined by the extinction of the genus *Ligerimys* without acknowledging that the Iberian endemic species *L. ellipticus* persisted for longer (Mein 1999). However, Hilgen et al. (2012) defined this boundary based on the LHA of *Ligerimys florancei*, which shows a minimal diachrony between Iberia and Central Europe (Van der Meulen et al. 2012). Magnetostratigraphic studies show that the entire sequence at els Casots exhibits reversed polarity (Casanovas-Vilar et al. 2022a) which, considering its correlation Aragonian subzone Cb, would correlate to the earliest part of chron C5Br (15.974–15.160 Ma; boundaries after Ogg 2020). This indicates an age of ~15.9 Ma, which corresponds to about the middle of the MCO.

The vertebrate assemblage at els Casots comprises over 75 taxa, including fish, amphibians, reptiles, birds, and mammals (see Casanovas-Vilar et al. 2022a for an updated review). The fossils, recovered from the upper part of the lacustrine succession, are exceptionally well-preserved, with articulated specimens and associated skeletal elements suggesting a parautochthonous assemblage at the lakeshore (Casanovas-Vilar et al. 2022a). The presence of thermophilic taxa such as crocodiles (*Diplocynodon*) and pythonid snakes indicates warm conditions. Herbivorous mammals include the cainotherid *Cainotherium*, the suoids *Choeromorus* and *Eurolistriodon*, the ruminants '*Dorcatherium*', *Ampelomeryx*, *Lagomeryx*, *Procervulus*, and *Eotragus*, the equid *Anchitherium*, at least three different rhinocerotids, and the proboscideans *Gomphotherium* and *Prodeinotherium*. The carnivorans include small to medium-sized mustelids, hyaenids, and herpestids, and larger felids, ursids, and two species of amphicyonids. The dominance of taxa that likely preferred humid environments, such as *Ampelomeryx* and some rhinocerotids, suggests wetland habitats. The small mammal fauna is dominated by cricetids

(*Democricetodon* and *Megacricetodon*) and presumably ground-dwelling glirids (*Simplomys* and *Peridyromys*). Arboreal forms are present, though noticeably rare. Preliminary paleoenvironmental studies indicate that the site of els Casots corresponds to a paleolake surrounded by lush vegetation, which developed in a tropical-subtropical and seasonally dry climate, where the water level would cyclically fluctuate (Casanovas-Vilar et al. 2022a; Sanjuan et al. 2023). This is consistent with slightly younger palynological data from the same area (Bessedik and Cabrera 1985; Rull et al. 2024), which document forested environments that were occasionally interspersed with increasingly open woodlands in the lowlands.

Materials and methods

Dataset, paleohistology, and measurements

The studied fossil sample comprises three lower molars of the bovid *E. noyei* (one m1 and two m3s) and four lower molars of the cervid *P.* cf. *dichotomus* (two m1s and two m3) from els Casots (Table 1). This material is housed in the Institut Català de Paleontologia Miquel Crusafont (ICP) in Sabadell (Catalonia, Spain). Comparative data for the extant cervid *Capreolus capreolus* and the extinct cervid *Procervulus ginsburgi* from the Early Miocene site of Artesilla (ART), based on material housed in the Museo de Ciencias Naturales de la Universidad de Zaragoza (MCNUZ), were taken from Cuccu et al. (2025). The material from els Casots was documented at the ICP, including linear measurements taken with a digital sliding caliper and digital pictures in occlusal, labial, and lingual views. Afterwards, it was sectioned at the Paleohistology Lab of the ICP, following standard protocols (Köhler et al. 2023). In particular, the dentognathic sample was embedded in epoxy resin Araldite® 2020 before being sectioned using a low-speed diamond saw (IsoMet, Buehler), along a plane transversely through the protoconid and metaconid of each molar. The resultant surfaces were then polished (using a MetaServ® 250, Buehler) and glued to frosted glass slides with epoxy resin. The mounted blocks were then sectioned with a diamond saw (PetroThin, Buehler) to a thickness of around 300 µm and ground until the incremental structures were visible at around 100 µm. Each histological section was then dehydrated in alcohol, rinsed with a histological clearing agent (Histo-Clear II), and covered with a glass slide using a DPX medium. The thin-sections were analyzed at the University of Zaragoza using a polarized light microscope (Leica DM2700 P), and histological tissue images were taken with Leica LASX microscope software. Enamel growth rate measurements were taken using LASX software, while Adobe Photoshop (version 23.5.2) was used for image composition.

Table 1 Dentognathic remains from els Casots included in the histological study

Catalog No.	Element	Species
IPS24251	left m1	*E. noyei*
IPS102728	right m3	*E. noyei*
IPS102843	left m3	*E. noyei*
IPS24352	right m1 and m3	*P.* cf. *dichotomus*
IPS24380	left m3	*P.* cf. *dichotomus*
IPS24755	right m1	*P.* cf. *dichotomus*

The base data for our study were incremental features matching the definition of lamination (Tafforeau et al. 2007; Jordana and Köhler 2011; Kierdorf et al. 2013, 2014, 2019), representing daily increments. Subdivisions of these incremental lines were considered of infradian nature. The amount of enamel formed per day, or daily secretion rate (DSR), was obtained by measuring the distance among successive laminations along the path of the enamel prisms and dividing this by the number of laminations. Normally, the pace at which the enamel extends (enamel extension rate; EER) along the enamel dentine junction (EDJ) and the time needed for the formation of the crown (crown formation time; CFT) are estimated. However, due to visibility issues, we could only obtain and study the DSR values. Moreover, growth rates were measured only in the cervical region (Fig. 2) due to the limited data availability resulting from visibility issues in the cuspal and middle regions of the enamel, without distinguishing between lingual and labial sides or among different locations (inner, central, and outer enamel) within the same region. This approach was adopted since previous studies (Cuccu et al. 2025) did not report significant differences in enamel DSR between the two sides of the tooth and among the different locations of the enamel band within the same region for *P. ginsburgi* (ART) and *C. capreolus*.

We also computed the hypsodonty index (HI) in the best-preserved specimens of *E. noyei* (IPS109472) and *P.* cf. *dichotomus* (IPS24352, IPS11946) from the ICP collections, as it is an important ecometric indicator (Eronen et al. 2010b). Increased hypsodonty (or relative crown height) is one of the best examples of innovation in response to environmental change (DeMiguel et al. 2014, 2016), being strictly tied to dietary behaviors associated with changes in habitat/vegetation structure (DeMiguel et al. 2016). Hypsodonty may be compared among different taxa using the HI, defined as the ratio between crown height and width (Janis 1988; Witzel et al. 2018). This index has already been employed in relation to dental growth parameters to test for a potential correlation between HI and DSR (Jordana et al. 2014). Nevertheless, this relationship remains unclear as

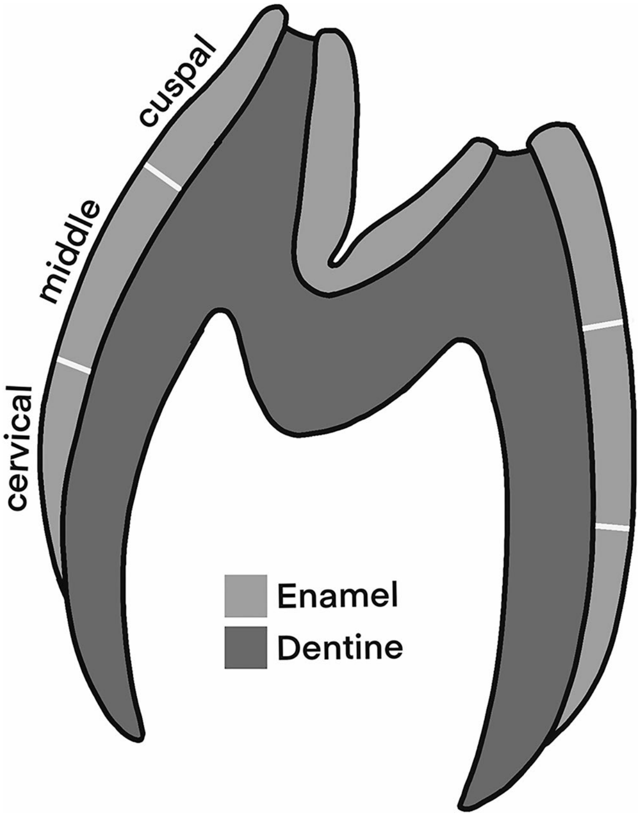

Fig. 2 Enamel regions considered when measuring DSR of each tooth (cervical, middle and cuspal). Figure modified from Cuccu et al. (2025)

some authors reported contrasting results (e.g. Jordana et al. 2014; Orlandi-Oliveras et al. 2019), which prompted us to test whether these two parameters are correlated. The HI of the m3 for *E. noyei* and *P.* cf. *dichotomus* (CS) was calculated following Janis (1988). In the case of *C. capreolus* and *P. ginsburgi* (ART), the HI values were taken from the literature (Janis 1988; DeMiguel et al. 2008). It is important to note that the HI value for *E. noyei* (CS) is based on a single slightly worn m3, so the actual value is expected to be somewhat higher. Once the HI was obtained, it was then assigned to specific categories following the classification proposed by Janis (1988) based on scores: brachyodont (HI less than 1.5), mesodont (HI between 1.5 and 3), hypsodont (HI above 3), and highly hypsodont (HI greater than 4.75).

Statistics

To compare enamel growth rates among the cheek teeth of the various species analyzed, we used RStudio version 2024.04.2 + 764 (Posit team, 2025). Since our sample is limited, we applied Kruskal-Wallis tests, a non-parametric alternative to analysis of variance that evaluates whether the various samples differ in median values (under the null hypothesis that the samples come from populations with equal medians; Hammer and Harper 2024). We also performed post-hoc pairwise comparisons using Dunn's test with Bonferroni correction, to determine which pairs of species significantly differ. All analyses were performed using a significance level of 0.05. To analyze the linear correlation between HI and DSR, we integrated our data with that from Jordana et al. (2014), plotted the points and calculated the regression lines for different groups, also with RStudio. *Myotragus balearicus*, an island fossil species, was excluded from the linear regression to avoid biasing the relationship among continental taxa.

Abbreviations

Institutional abbreviations: **ICP**, Institut Català de Paleontologia Miquel Crusafont; **IPS**, acronym of the ICP collections (formerly, Institut de Paleontologia Sabadell); **MCNUZ**, Museo de Ciencias Naturales de la Universidad de Zaragoza.

Other abbreviations: **ART**, Artesilla; **BM**, body mass; **CFT**, crown formation time; **CS**, els Casots; **DSR**, daily secretion rate; **EDJ**, enamel-dentine junction; **EER**, enamel extension rate; **HI**, hypsodonty index; **LH**, life history; **m1**, first lower molar; **m2**, second lower molar; **m3**, third lower molar.

Results

The most distinctly visible incremental lines identifiable in the enamel of *E. noyei* and *P.* cf. *dichotomus* (CS) are laminations (Fig. 3).

We also report infra-daily incremental lines for both species (Fig. 4), with a periodicity of 12 h (2 infra-daily lines within a lamination) for *E. noyei* and 12–8 h (2–3 infra-daily lines within a lamination) for *P.* cf. *dichotomus*. We do not observe long-period incremental lines for either taxon. The neonatal line is clearly visible in the lower half of the m1 crowns and runs in the same direction as the other incremental features, from the EDJ towards the outer enamel surface (Fig. 4). Hunter-Schreger bands are prominent and commonly found on the upper 2/3 of the crown, which considerably limits the visibility of any incremental structure (Kierdorf et al. 2013).

Concerning the cervical enamel DSR (Fig. 5), *C. capreolus* exhibits the lowest mean values for both tooth positions, while *Procervulus* spp. exhibits the highest (Table 2).

The Kruskal-Wallis test showed significant differences for both lower molars (Online Resource 1: Tables S1–S2). Concerning the m1, as observed in Cuccu et al. (2025), significant differences were only found between *C. capreolus*

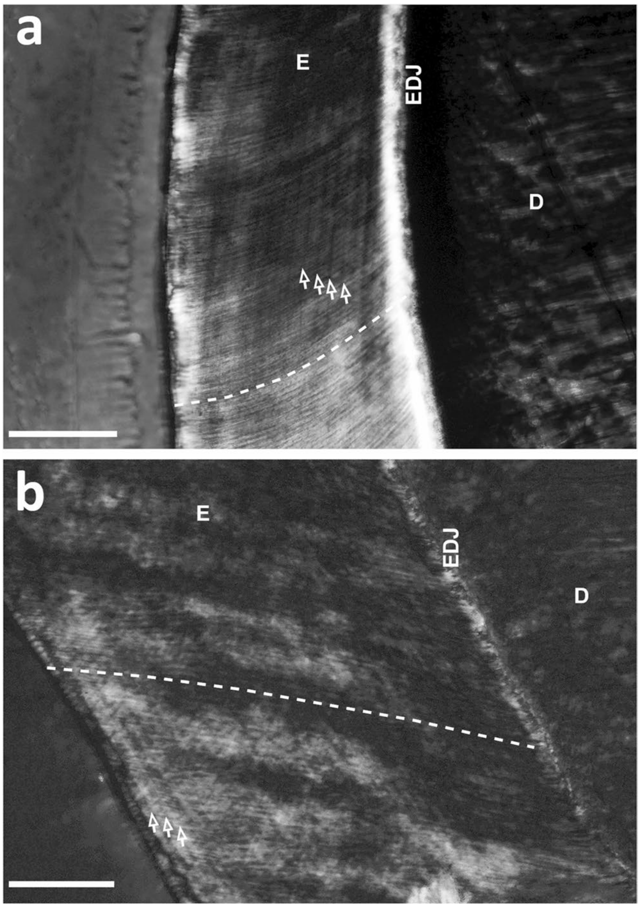

Fig. 3 Detailed picture showing the daily incremental features (arrowheads) in *P.* cf. *dichotomus* (**a**) and *E. noyei* (**b**) from els Casots. The dashed line represents the prism direction. Abbreviations: **D**, dentine; **E**, enamel; **EDJ**, enamel-dentine junction. Scale bars represent 100 µm

and *P. ginsburgi* (ART) in the adjusted p-values after running Dunn's post hoc tests (Online Resource 1: Table S1). For the m3, Dunn's test revealed significant differences (after adjusting the p-value) between *C. capreolus* and *Procervulus* spp. (CS, ART; Online Resource 1: Table S2). Finally, we performed a Kruskal-Wallis analysis to test for difference in the median values of the enamel DSR between m1 and m3 within each taxon. The results show significant differences in DSR between the two positions in *C. capreolus* and *P. ginsburgi* (ART), as observed in Cuccu et al. (2025), but not in *P.* cf. *dichotomus* and *E. noyei* (CS; Online Resource 1: Table S3).

With regard to the HI, it is 1.14 for *P.* cf. *dichotomus* (CS) and 1.06 for *E. noyei* (CS) (Table 3), although the latter is expected to be somewhat higher (see Materials and methods). The HIs of *P. ginsburgi* (ART) and *C. capreolus* obtained from previous literature (Janis 1988; DeMiguel et al. 2008) are 1.14 and 1.49, respectively (Table 3). Following Janis (1988), the four species are therefore classified as brachyodont (HI below 1.5).

In the bivariate plots of HI against DSR, based on data mostly taken from Jordana et al. (2014), the fossil ruminants from CS and ART (MN4/MN5) display lower HI than expected based on DSR, even though the latter falls well within the variation of Jordana et al.'s (2014) sample (Fig. 6). The regression line including only the extant species (Fig. 6a) displays the higher coefficient of determination ($r^2=0.31$; $p=0.01358$), while the regression including both the extant and extinct species (Fig. 6b) yielded a slightly lower coefficient ($r^2=0.26$; $p=0.01199$).

Discussion

Enamel incremental markings and daily secretion rate

As already reported for other extinct and extant artiodactyls (Iinuma et al. 2004; Jordana and Köhler 2011; Kierdorf et al. 2012, 2013, 2019; Emken et al. 2021), our histological study revealed the presence of laminations throughout the enamel of both *P.* cf. *dichotomus* (CS) and *E. noyei* (CS). In agreement with previous works on cervids and bovids (Ilnuma et al. 2004; Jordana and Köhler 2011; Kierdorf et al. 2012; Jordana et al. 2014), *E. noyei* and *P.* cf. *dichotomus* (CS) do not exhibit long-period incremental lines (i.e. Retzius lines), although in giraffids long periodicity lines are recorded in the outermost enamel (Nacarino-Meneses et al. 2025). Instead, sub-daily incremental markings (with a shorter periodicity) are reported for both taxa from CS, in accordance with what has been described for other ungulates (Kierdorf et al. 2012, 2013, 2019; Emken et al. 2021; Nacarino-Meneses et al. 2025).

The DSR of *E. noyei* (CS) and *P.* cf. *dichotomus* (CS) is similar among the lower molars, while *P. ginsburgi* (ART) and extant *C. capreolus* exhibit significant differences in the enamel DSR from the m1 to the m3 (Cuccu et al. 2025), which has also been observed in previous studies on hipparionin horses and giraffes (Orlandi-Oliveras et al. 2019; Nacarino-Meneses et al. 2025). The decline in the m3 enamel DSR has been associated with the attainment of skeletal maturity (Dean 2006), followed by a decline in growth rate. Orlandi-Oliveras et al. (2019) reported in *Equus* a uniform DSR in the different lower molars, but attributed this to the poor quality of the sample. Our sample has limitations that directly affect the amount of data retrieved. In particular, middle and cuspal visibility was lacking in most of the specimens, which significantly restricted the number of observations, precluding comparison between other regions of the crown, and therefore raising clear limitations to our study. Such limitations are further exacerbated when working with small samples, which is particularly common in

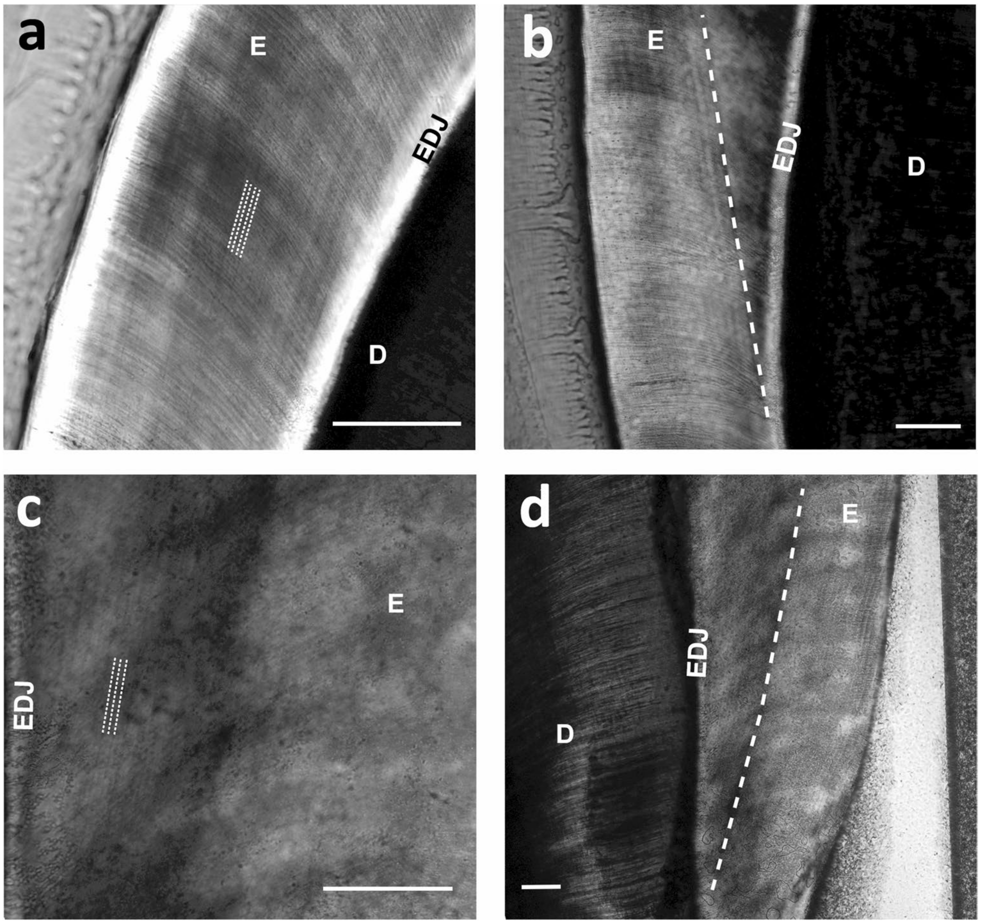

Fig. 4 Neonatal line (dashed lines) and sub-daily incremental features (dotted lines) in *P.* cf. *dichotomus* (**a**, **b**) and *E. noyei* (**c**, **d**) from els Casots. Abbreviations: **D**, dentine; **E**, enamel; **EDJ**, enamel-dentine junction. Scale bars represent 100 µm

paleontology due to preservation reasons, and even more common in paleohistology, due to the invasive nature of the technique (which limits the sample available for study).

Life history inferences

Our results contrast with those documented previously by Jordana et al. (2014), which showed a positive correlation between enamel DSR and HI in ruminants. *Eotragus noyei* and *P*. cf. *dichotomus* (CS; this work), and *P*. *ginsburgi* (ART; Cuccu et al. 2025) exhibit relatively high DSR despite being brachyodont. Moreover, *E. noyei* (CS), has a somewhat higher crown height and does not appear to differ significantly in DSR from either species of *Procervulus*. The opposite is true for *C. capreolus*, which has the highest HI among the examined taxa, despite having the lowest DSR. This suggests that the enamel DSR in ruminants is not clearly associated to the HI. The slope of the regression line (Fig. 6), as previously tested by Jordana et al. (2014), indicates a positive correlation between DSR and HI for extant species alone, as well as for both extant and extinct species included in the dataset, although with a lot of scatter (as indicated by the low determination coefficients). However, the Early Miocene species from CS and ART lie quite below the regression lines, to an extent that they can be considered as outliers (Fig. 6). That is, while a direct correlation between enamel DSR and HI may be true for extant species, showing a wide range of different HIs, this does not necessarily apply to early fossil brachyodont ones. Specifically, although Early Miocene bovids are defined to be as incipient hypsodont, they still exhibit brachyodont crowns (DeMiguel et al. 2014). Since hypsodonty increased considerably in bovids during the Middle Miocene (Gentry et al. 1999; Badiola et al. 2001; DeMiguel et al. 2014), the relationship between DSR and HI may be difficult to detect in early (MN4/MN5) ruminants. Besides, we consider that the relationship between hypsodonty and growth rates, even if significant, is not very tight (as indicated by the lower determination coefficients), and is possibly influenced by more factors. In this sense, Orlandi-Oliveras et al. (2019) also found no correlation between DSR and HI in hipparionin horses, indicating that an extended CFT and a long ameloblast lifespan are more likely to influence the formation of thicker and/or more hypsodont crowns.

In mammals, many aspects of dental development are associated with the pace of life (Dirks et al. 2009). The

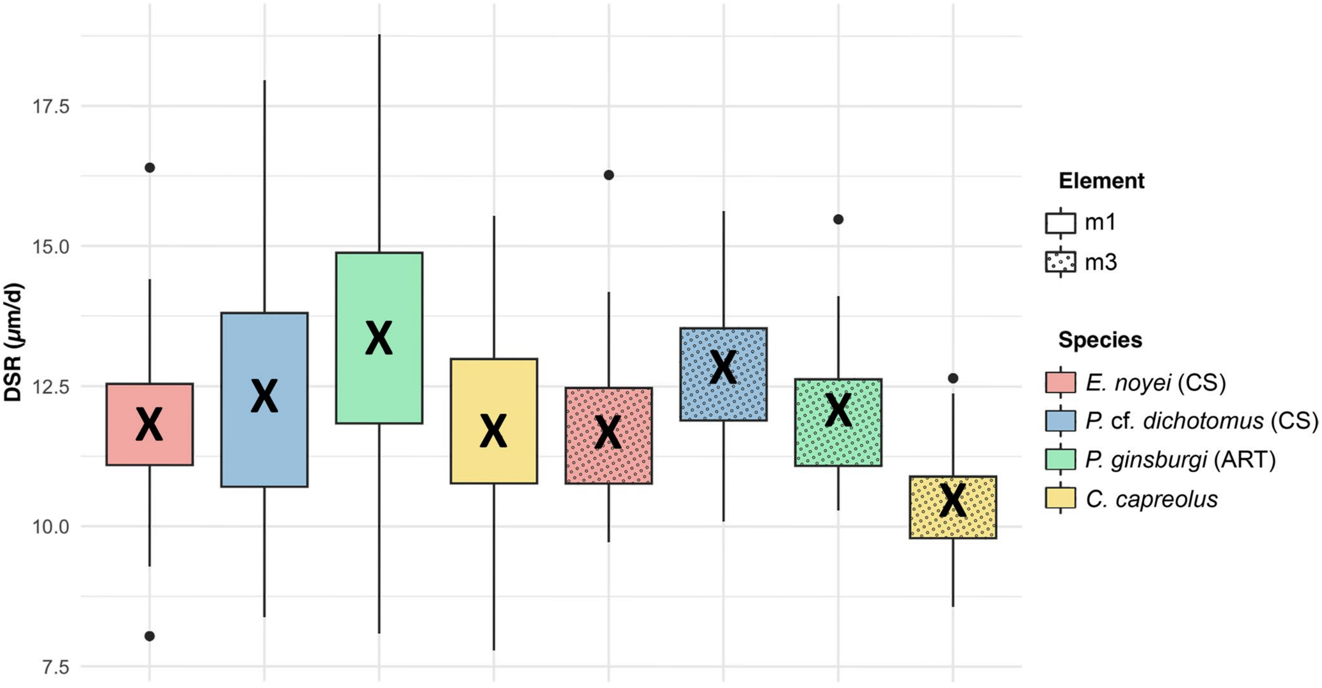

Fig. 5 Boxplot of the daily secretion rate (DSR, in µm/d) in the cervical enamel for the lower molars of *E. noyei* and *P.* cf. *dichotomus* from els Casots, *P. ginsburgi* from Artesilla, and extant *C. capreolus*. Black Xs denote the mean values, boxes represent the interquartile range (IQR; 25th −75th percentile) and whiskers represent the range up to 1.5 times the IQR over the 75th percentile and under the 25th percentile. Values out of these limits are represented as outliers (black circles). Data for *C. capreolus* and *P. ginsburgi* from Cuccu et al. (2025). Abbreviations: **ART**, Artesilla; **CS**, els Casots

Table 2 Descriptive statistics of enamel daily secretion rates (DSR, in µm/d) of the cervical region of the lower molars. Data for *C. capreolus* and *P. ginsburgi* from Cuccu et al. (2025). Abbreviations: **ART**, Artesilla; **CS**, els Casots; **n**, number of observations; **SD**, standard deviation

		n	Mean	SD	Median
C. capreolus	m1	21	11.74	1.66	11.92
	m3	31	10.47	0.97	10.38
E. noyei (CS)	m1	21	11.82	1.81	11.92
	m3	14	11.70	1.82	11.42
P. cf. *dichotomus* (CS)	m1	19	12.35	2.60	11.60
	m3	16	12.84	1.48	13.05
P. ginsburgi (ART)	m1	49	13.38	2.59	13.30
	m3	15	12.08	1.46	12.15

Table 3 Hypsodonty index and category for the species discussed in this work. The asterisk indicates that the specimen was slightly worn. Data of HI for *C. capreolus* were taken from Janis (1988) while HI data for *P. ginsburgi* from artesilla were taken from DeMiguel et al. (2008). Abbreviations: **ART**, artesilla; **CS**, els Casots; **HI**, hypsodonty index; **Hcat**, hypsodonty category; **n**, number of observations

	HI (*n*)	Hcat
C. capreolus	1.49 (1)	brachyodont
E. noyei (CS)	1.03*(1)	brachyodont
P. cf. *dichotomus* (CS)	1.14 (2)	brachyodont
P. ginsburgi (ART)	0.99 (5)	brachyodont

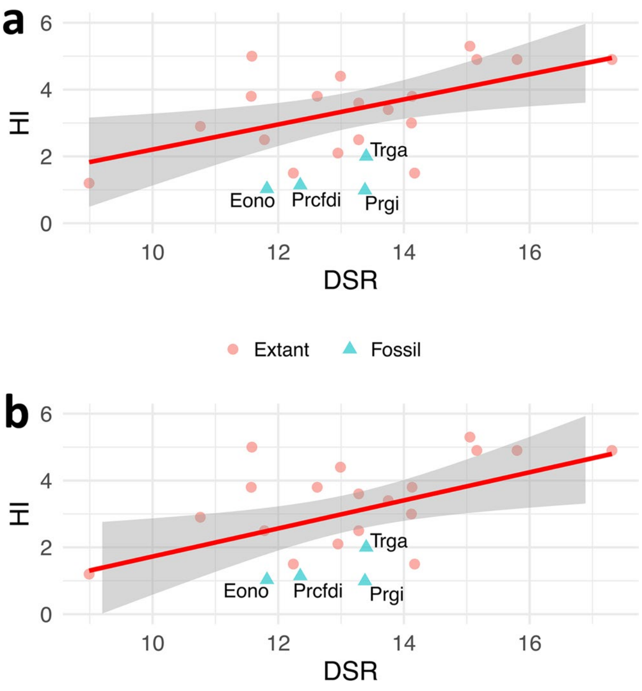

Fig. 6 Scatterplot of HI against DSR and regression line (in red) performed including only extant species (**a**), and both extant and extinct species (**b**). The 95% confidence interval for the linear model is in grey. Data for extant specimens and *Tragoportax gaudryi* from Jordana et al. (2014). Abbreviations: **Eono**, *E. noyei*; **Prcfdi**, *P.* cf. *dichotomus*; **Prgi**, *P. ginsburgi*; **Trga**, *T. gaudryi*

relationship between LH and enamel microstructure has been widely examined in primates (e.g. Schwartz et al. 2002; Dean 2006; Dirks and Bowman 2007; Hogg and Walker 2011; Bromage et al. 2012). The situation is different in artiodactyls, whose distinct enamel microstructure has previously resulted in the misidentification of their incremental features (Kierdorf et al. 2019; Emken et al. 2021), leading to inaccurate estimates of crown formation times (Macho and Williamson 2002). Nevertheless, a few studies on bovids and cervids (Jordana and Köhler 2011; Jordana et al. 2014) have found that the relationship between enamel development and LH is consistent with findings in primates. However, these values should not be compared across different groups of mammals (Jordana et al. 2014). Enamel DSR is considered to be influenced by different factors, including LH, tooth morphology, enamel thickness and phylogeny (Hogg and Walker 2011; Dirks et al. 2012; Kierdorf et al. 2014; Nacarino-Meneses et al. 2017; Orlandi-Oliveras et al. 2019). Enamel DSR has also been suggested to correlate with generic somatic growth rate (Orlandi-Oliveras et al. 2019; Nacarino-Meneses et al. 2025). Although enamel DSR may be considered a reasonable proxy for LH inferences, it does not offer the same level of insight as other variables, such as EER and CFT, which were not possible to estimate in this work. For this reason, interpretations should be taken with caution. Nevertheless, assuming that DSR yields indirect information about an individual LH, since it has also been linked to a fast pace of growth and early weaning (Hogg and Walker 2011), *P*. cf. *dichotomus* (CS) may have exhibited a fast LH, as previously found in *P*. *ginsburgi* (ART; Cuccu et al. 2025). In this line, similar inferences can be made for the bovid *E*. *noyei* (CS), which, in addition to exhibiting similar enamel DSR values, stands closer to the DSR values of extant cervid *C*. *capreolus*, considered to exhibit a fast life history (Cuccu et al. 2025).

Environmental factors are well known to influence the evolution of LH strategies (Reznick et al. 2001;). As such, the similarity between *P*. cf. *dichotomus* (CS) and *P*. *ginsburgi* (ART) does not seem to reflect the apparently marked differences in the environments they inhabited. Artesilla has been documented to record drier and more open conditions (DeMiguel et al. 2008) than CS, which is considered to be more forested and humid, including also the presence of a lake (Casanovas-Vilar et al. 2022a; Sanjuan et al. 2023). Although Europe experienced increased warmth during the MCO, the Iberian Peninsula was the first region to record increasingly arid conditions during the Early Miocene (Eronen et al. 2010a; DeMiguel et al. 2012). In this sense, the possibly more humid and closed environment of CS could have served as an ecological refuge for species ecologically closer to those of the central European habitats, such as the lagomerycid *Lagomeryx* (not recorded in ART), while more open and arid habitats spred in inner Iberia (DeMiguel et al. 2010, 2012). Open habitats are considered to be more erratic than closed ones (Southwood 1988) and the mortality associated with such environments favors the evolution of fast LH traits (Stearns 1977; Promislow and Harvey 1990). Conversely, a closed environment should favor the emergence of slow LH strategies (Cuccu et al. 2025), such is the case of *Procervulus praelucidus* from Wintershof-West (Germany, ~18.5 Ma; Böhme et al. 2012; Kolb et al. 2015). Nevertheless, *P.* cf. *dichotomus* (CS) and *P. ginsburgi* (ART) exhibit a similar DSR and likely a similar LH. The explanation might lie in the likely presence of more open drier woodlands further from the wetlands in CS, as suggested by small mammals (Casanovas-Vilar et al. 2022a). Given the trophic flexibility of *Procervulus* spp. (DeMiguel et al. 2010), including *P. ginsburgi* from ART, a similar habitat might then partially explain the similarities between the two *Procervulus* spp. from ART and CS. Microwear studies of *Eotragus sansaniensis* from the Middle Miocene (MN6) of Sansan (France) show signals typical of a browser (Solounias and Moelleken 1992), although it is thought this species switched from mixed-feeding towards a browsing behavior due to competition with other ruminants (DeMiguel et al. 2008). Based on this, *E. noyei* (CS) would likely dwell in a more closed environment. However, since the evolution of different LH strategies is affected by various factors (McNamara and Houston 1992; Hogg et al. 2011), we cannot exclude the influence of other factors in the shaping of the life histories of these species, such as a similar pration pressure. In this regard, both sites record several medium-to-large carnivores (Amphicyonidae, Felidae, and Hemicyonidae), which would likely exert a high predation pressure on both *Procervulus* spp. and *E. noyei*, given their similar body sizes. Establishing the exact predation pressure at the two sites would be too speculative and beyond the scope of this paper. Moreover, since both predation pressure and environment are tightly related, we believe that, given the similar environment inhabited, the two *Procervulus* spp. were subjected to similar selective pressures, which explain why these two species exhibited similar LH.

Conclusions

To date, the quantitative and qualitative description of the dental histology in fossil ruminants has largely been overlooked. This work provides, for the first time, paleohistological data for early bovids, thus contributing to a better understanding of the early evolutionary stages of this group. We report the presence of enamel daily incremental features in the Middle Miocene (MN5) *E. noyei* (Bovidae) and *P.* cf. *dichotomus* (Cervidae) from the site of els Casots. Both species exhibited relatively high DSR which may indicate a fast LH. Our results on the relationship between DSR and HI do not support a tight relationship between these variables, at least in early ruminants, suggesting that other factors, such as the ameloblast lifespan, may play a more significant role in determining hypsodonty than DSR alone in these species. Additionally, our study found no significant differences between *P.* cf. *dichotomus* from CS (Early Miocene, MN5) and *P. ginsburgi* ART (Early Miocene, MN4), despite seeming to inhabit different ecosystems. However, the dry woodlands likely present nearby the lake surroundings at CS, might partially explain why the two species seemingly displayed similar LH strategies.

Concluding, our findings of a similar enamel DSR in *Procervulus* spp. and *E. noyei*, strengthen the shared early evolutionary history of cervids and bovids, with marked differences between them, including an increase in crown height and postcranial anatomy, having only emerged later. Nonetheless, further studies are needed, particularly aimed at expanding the histological dataset of Miocene artiodactyls to encompass Iberian and Central European sites, to deepen our understanding of the evolution of these groups.

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Author contributions D.DM. and B.A. contributed to the study conception and design. A.C. performed data collection and analysis, and wrote the first draft of the manuscript, subsequently modified according to input from all authors. All authors read and approved the final version of the manuscript.

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Data availability All data generated during this study are included in this published article, in the supplementary information file, or available from the corresponding authors upon request. The fossil material studied in this paper is housed and adequately curated in the ICP.

Declaration

Competing interests The authors declare no competing interests.

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