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Hogs, hippos or bears? Paleodiet of European Oligocene anthracotheres and entelodonts

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ABSTRACT

Anthracotheres and entelodonts are large mammals with peculiar morphological characteristics that combine plesiomorphic and derived features. The unusual anatomy of anthracotheres shows a morphological resemblance to pigs and hippos and their bunoselenodont low-crowned molars have been interpreted as an adaptation to frugivorous/folivorous diets. Entelodonts share cranial and dental similarities to pigs and carnivores, and this has been interpreted as an adaption to opportunistic omnivore diets, hunting/scavenging, or bone-crushing (cf. hyenas). The objective of the present study is to use dental microwear analysis to test these assumptions and to infer the diet of anthracotheres and entelodonts. Dental microwear was quantified on the upper and lower molars using a stereomicroscope. To assess the dietary traits of the fossil samples, the results were compared to a dataset of extant large mammals covering ten dietary categories. The microwear features indicate different diets for *Anthracotherium* sp. and *Entelodon magnus*. Our sample of entelodonts shows an omnivorous diet similar to that of the wild boar, and it probably varied considerably between seasons. The anthracotheres we analysed were opportunistic browsing, frugivore, and grazing herbivores. During the Oligocene, these two taxa occupied ecological niches characterised by a large diversity of food resources. The results of the study offer further insights into the characteristics of the digestive system in fossil artiodactyls. The large dataset used in this research opens new perspectives for the dietary reconstruction of poorly known mammal taxa by considering a wide range of diets.

1. Introduction

Anthracotheriidae and Entelodontidae were widely diverse artiodactyl families. They were characterised by peculiar and easily distinguishable appearance that possessed features similar to those of modern-day pigs and peccaries, hippopotami, and even carnivores. The peculiar anatomical features of anthracotheres and entelodonts are of particular interest in the context of paleoecology.

The first representatives of the family Anthracotheriidae probably originated in Asia, after its members dispersed in latitudinal and longitudinal directions in Eurasia, Africa, and North and Central America (Carroll, 1988). Anthracotheriidae appeared in the Middle Eocene of Myanmar, in Eurasia and North America from the late Eocene to Miocene, in Central America in the Early Miocene, in Africa from the late Eocene to the terminal Miocene, and in the late Pleistocene of Asia, after which they died out (Carroll, 1988; Ducrocq and Lihoreau, 2006; Lihoreau et al., 2006, 2009; Rincon et al., 2013). Anthracotheriidae as a paraphyletic taxon is closely related to Hippopotamidae and Cetacea (Carroll, 1988; Boisserie et al., 2005). The morphological data suggest that extant Hippopotamidae are derived from the African branch of Anthracotheriidae (Carroll, 1988; Boisserie et al., 2005; Lihoreau et al., 2015).

The morphology of the anthracotheriid's skull, dentition, and postcranial skeleton is unique, though it has several plesiomorphic features that are similar to that of extant pigs and hippos (Fig. 1E). The skull is large and narrow with a long facial part (Orlov, 1962).

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Anthracotheriids had a plesiomorphic ungulate dental formula: $I\frac{3}{3}$, $C\frac{1}{1}$, $P\frac{4}{4}$, $M\frac{3}{3}$. The incisors were large and somewhat similar to pigs and the cheek teeth were low-crowned and often bunodont; however, in some advanced forms, the upper molars became almost square-like from an occlusal perspective and selenodont (or bunoselenodont) (Orlov, 1962; Carroll, 1988; Janis, 1995; Lihoreau et al., 2006; Tsubamoto et al., 2012). The limbs of anthracotheres were plesiomorphic: they were short, the forefoot has five digits and the hindfoot has four digits, the metapodials were short, the metacarpals and metatarsals of digits III and IV were not fused into a single cannon bone, and digits II and V were well-developed (Carroll, 1988; Ghezzo and Giusberti, 2016). The specificity of the sediment in which some derived anthracotheriids have been found suggests that they were semiaquatic (Carroll, 1988).

Entelodontidae, also known as 'hell pigs', were widespread in Eurasia and North America. The first representatives of the family emerged in the Middle Eocene of Mongolia, thereafter appearing in Eurasia and North America from the Eocene to Lower Miocene (Vislobokova, 2008). Traditionally, the Entelodontidae was considered members of the Suiformes clade (Simpson, 1945). However, recent studies have suggested that the family was closely related to the Anthracotheriidae, Hippopotamidae, and Cetacea (Spaulding et al., 2009).

The bizarre morphology of entelodonts consists of several plesiomorphic and derived features (Fig. 1D). The majority of Oligocene and early Miocene entelodontids were relatively large animals, with the largest representatives of the group reaching the size of extant bovines (Joeckel, 1990). Entelodontids were characterised by a large skull and a long facial part (Orlov, 1962); in adult *Daeodon* specimens, the skulls were around 90 cm long (Peterson, 1909). The zygomatic arches and the lower jaw typically had flanges and outgrowths. Entelodonts retained a plesiomorphic dental formula: $I\frac{3}{3}$, $C\frac{1}{1}$, $P\frac{4}{4}$, $M\frac{3}{3}$. Their incisors and canines were large; the premolars were triangular, with a large and conical main cusp; and the molars were relatively small, low-crowned, and bunodont, with four-five simple tubercules (Orlov, 1962; Joeckel, 1990). The lower jaw was very specialised, with a mandibular condyle at the level of the tooth row similar to that of carnivores and short coronoid processes (Fig. 1D). The skull was characterised by enlarged temporal fossae, a well-developed sagittal crest, a relatively small braincase, and rather forward-orientated orbits (Orlov, 1962; Joeckel, 1990). All these cranial features probably gave the entelodonts a powerful orthal bite and a very wide gape, similar to carnivores (Joeckel, 1990). The limbs were relatively long; the forefoot and hindfoot were mostly didactylous; the ulna and radius, as well as the tibia and fibula, were fused; and the metatarsals of digits III and IV were long but not fused into a single cannon bone (Kowalevsky, 1875; Orlov, 1962; Joeckel, 1990; Vislobokova,

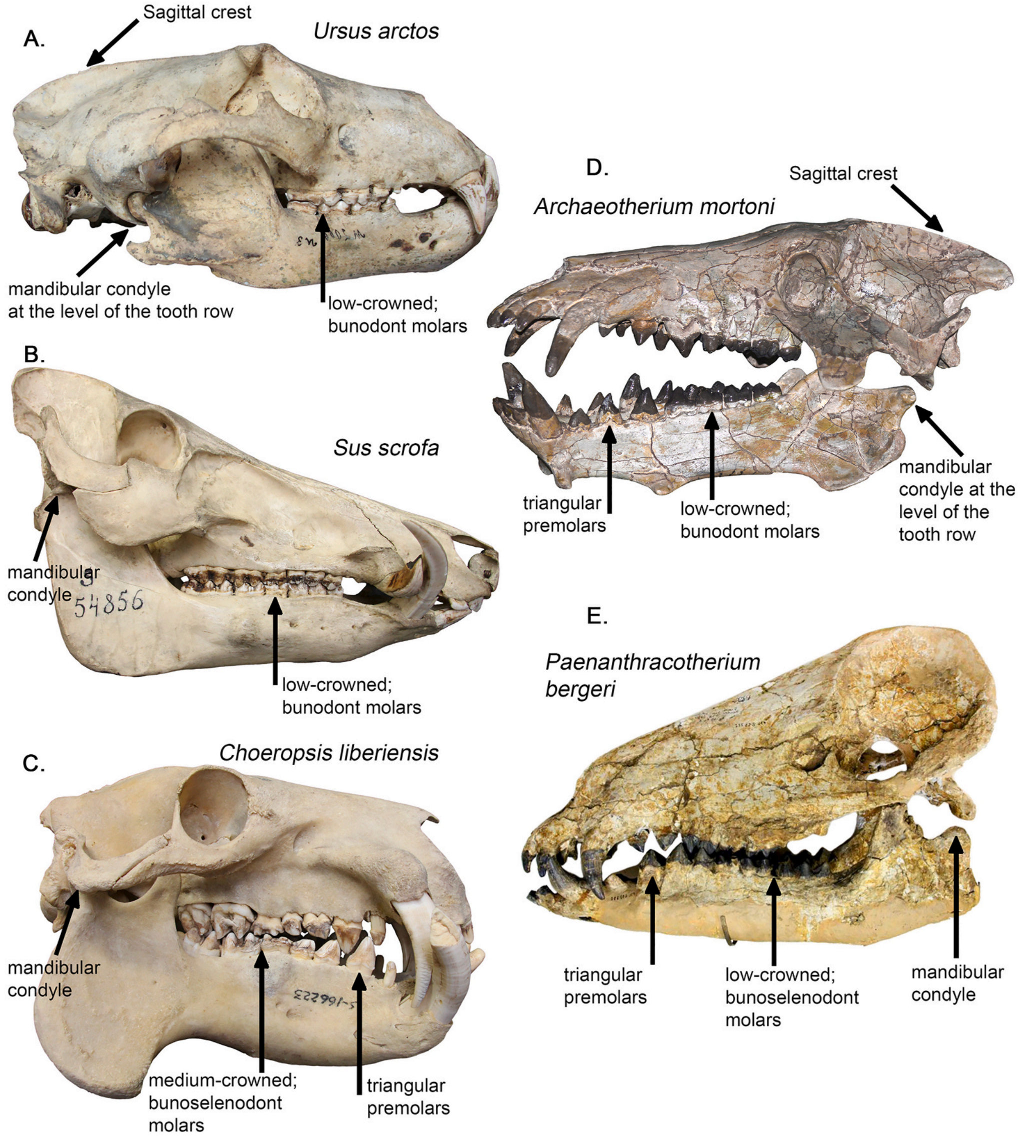

Fig. 1. Features of cranial morphology in anthracotheres, entelodonts and some modern-day species. (A) *Ursus arctos* (ZMMU S-34982); (B) *Sus scrofa* (ZMMU S-54856); (C) *Choeropsis liberiensis* (ZMMU S-166223); (D) *Archaeotherium mortoni* (State Museum of Natural History Karlsruhe [SMNK]) adapted from https://commons.wikimedia.org/wiki/File:Archaeotherium_mortoni_01.jpg (Credit: H. Zell, CC BY-SA 3.0, via Wikimedia Commons) (E) *Paenanthracotherium bergeri* (FSL-213772) modified from https://www.recolnat.org/en/nos-partenaires/pal-lyon (Credit: C. Vautey).

2008). Bite marks on the skulls of various entelodonts are suggestive of a high level of aggression and intraspecific competition (Foss, 2001).

The peculiar anatomy of anthracotheres resembles pigs and hippos, while that of the entelodonts resembles pigs and carnivores. The bunoselenodont structure of the anthracotheriid's low-crowned molars was previously considered to be an adaptation to frugivorous/folivorous diets (Janis, 1995; Blondel, 2001). The entelodont's cranial morphology and dentition have been interpreted as an adaption to an opportunistic omnivore diet similar to pigs and bears, hunting/scavenging (similar to large carnivores), or crushing bones (similar to hyenas) (Joeckel, 1990; Blondel, 2001; Foss, 2001). These morphological assumptions have not yet been tested using reliable methods for entelodonts. For anthracotheres, few studies applied stable isotope analysis and tooth wear to reconstruct the diet of three taxa, *Bothriogenys gorringei*, *Libycosaurus bahri* and *Anthracotherium* sp., but provided different results. For *Bothriogenys gorringei* from the early Oligocene of Egypt the very low $\delta^{18}O$ values indicated a semi-aquatic mode of life (Clementz et al., 2008). Combining stable isotopes, microwear and mesowear, similar results were obtained for *L. bahri* from the late Miocene of Toros-Menalla. It was reconstructed as a generalist species that fed on plants communities located in meadows near water bodies and had semi-aquatic specializations (Lihoreau et al., 2014). On the other hand, enamel $\delta^{13}C$ values for *Anthracotherium* sp. from the late Oligocene of Enspel (Germany) suggested that it foraged in forested habitats while the oxygen isotope values do not support a semi-aquatic mode of life (Tütken and Absolon, 2015). The objective of the present study was to test various assumptions about the paleodiet of anthracotheres and entelodonts using dental microwear analysis.

We investigated two genera: the anthracotheriid *Anthracotherium* Cuvier, 1822, and the entelodontid *Entelodon* Aymard, 1846. Both genera inhabited Europe in the late Eocene – early Oligocene (Kowalevsky, 1873, 1875; Vislobokova, 2008). *Entelodon* existed in Europe after MP20 (Gradstein et al., 2012), *Anthracotherium* appeared in Europe in MP21 and disappeared in MP29 (Ghezzo and Giusberti, 2016).

2. Material and methods

2.1. Materials

The material studied herein belongs to the collection of the Vernadsky State Geological Museum (VSGM), Moscow. The dental remains were obtained from the Quercy phosphorite Formation in southwestern France (Fig. 2). The Quercy phosphorites have been known since the last third of the 19th century, when sediment was excavated to extract phosphorite (used as a fertiliser for cultivation and farming; de Bonis et al., 2019). The appearance of phosphorite deposits is associated with the karstic system in Jurassic limestone. In the interval between the early Eocene and early Miocene, the karstic system was filled with sediment. The paleontological remains at Quercy were found in a large number of different fissures located across an area covering hundreds of square kilometers. In several locations, the sediment contained a large number of plants, insects, amphibians, reptilians, avian, and mammalian remains (Legendre et al., 1997). These were unearthed by workers in quarries and sold to brokers who were authorised by major museums or collectors (Legendre et al., 1997; de Bonis et al., 2019). Thus, it has not been possible to establish reliably the geological age of most of the old Quercy collections.

Fig. 2. Location of the Quercy phosphorite formation.

The geological age of the Quercy fauna extended from the early Eocene to the early Miocene. Most of the remains were found in ranges from the late Eocene to the beginning of the late Oligocene or from the MP16 to MP28 of the European land mammal Paleogene zones (Legendre et al., 1997; de Bonis et al., 2019).

The anthracothere teeth we studied belong to the collections #1809 and #1831 of the VSGM. The #1831 collection includes 37 teeth (incisors, canines, premolars, and molars) from the Oligocene *Anthracotherium alsaticum* Cuvier, 1822 (Fig. 3 A-H). The dental remains were donated to the museum by Rossignol in 1895. The entelodont teeth in collections #1762 include 33 teeth (incisors, canines, premolars, and molars) from the Oligocene *Entelodon magnus* (Fig. 3 —A-H). All of the fossils were catalogued by M.V. Pavlova (1910).

Given the above, it is not possible to state with confidence that the material we studied was found at a single location. The size of the teeth does not allow us to determine accurately the species of *Anthracotherium*. The mean width of M3 is very close to that stated by Ghezzo and Giusberti (2016) for *A. alsaticum* (43.8 vs 43 mm), but the length of the M3 is notably longer (41.6 vs 33.5 mm). Both are close in size to *A. monsvialense*. The size of M2 in anthracotheres is markedly smaller than the size of M3 (Ghezzo and Giusberti, 2016). However, the size of the VSGM 1831–08 specimen (M2) is larger than that of any M3 of the *Anthracotherium* genus outside of *A. magnum*. The mean length of m3 in *A. alsaticum* is ~40 mm; in our sample, 46–54 mm (Table 1). This length is also within the range of *A. monsvialense*. Thus, specimen 1831–08 (Fig. 3A) might have been from the large-sized *A. magnum* species, while the others specimens belong to the medium-sized *A. alsaticum* or *A. monsvialense* species. The other European species of *Anthracotherium* are characterised by notably smaller molars (Ghezzo and Giusberti, 2016).

All available upper and lower molars were selected for tooth microwear analysis. Premolars were excluded because the microwear signal is not consistent in comparison to the molars (Rivals et al., 2015; Xafis et al., 2017).

3. Methods

The microwear analysis was performed using the protocol established by Solounias and Semprebon (2002). It was carried out on the enamel surfaces using a stereomicroscope on high-resolution epoxy tooth casts. The surface of the tooth was cleaned using acetone and 96% ethanol and then moulded with high-resolution silicone (vinylpolysiloxane); finally the casts were created using clear epoxy resin. These were then carefully screened under the stereomicroscope. Those with poorly preserved enamel or taphonomic defects (i.e., features with an unusual morphology and size, or fresh features produced during the collecting process or storage) were excluded from the analysis (King et al., 1999; El-Zaatari, 2010; Uzunidis et al., 2021; Weber et al., 2022). The casts were examined under transmitted light with a Zeiss Stemi 2000C stereomicroscope at a 35× magnification. Microwear was quantified on the protocone or the protoconid of upper and lower teeth,

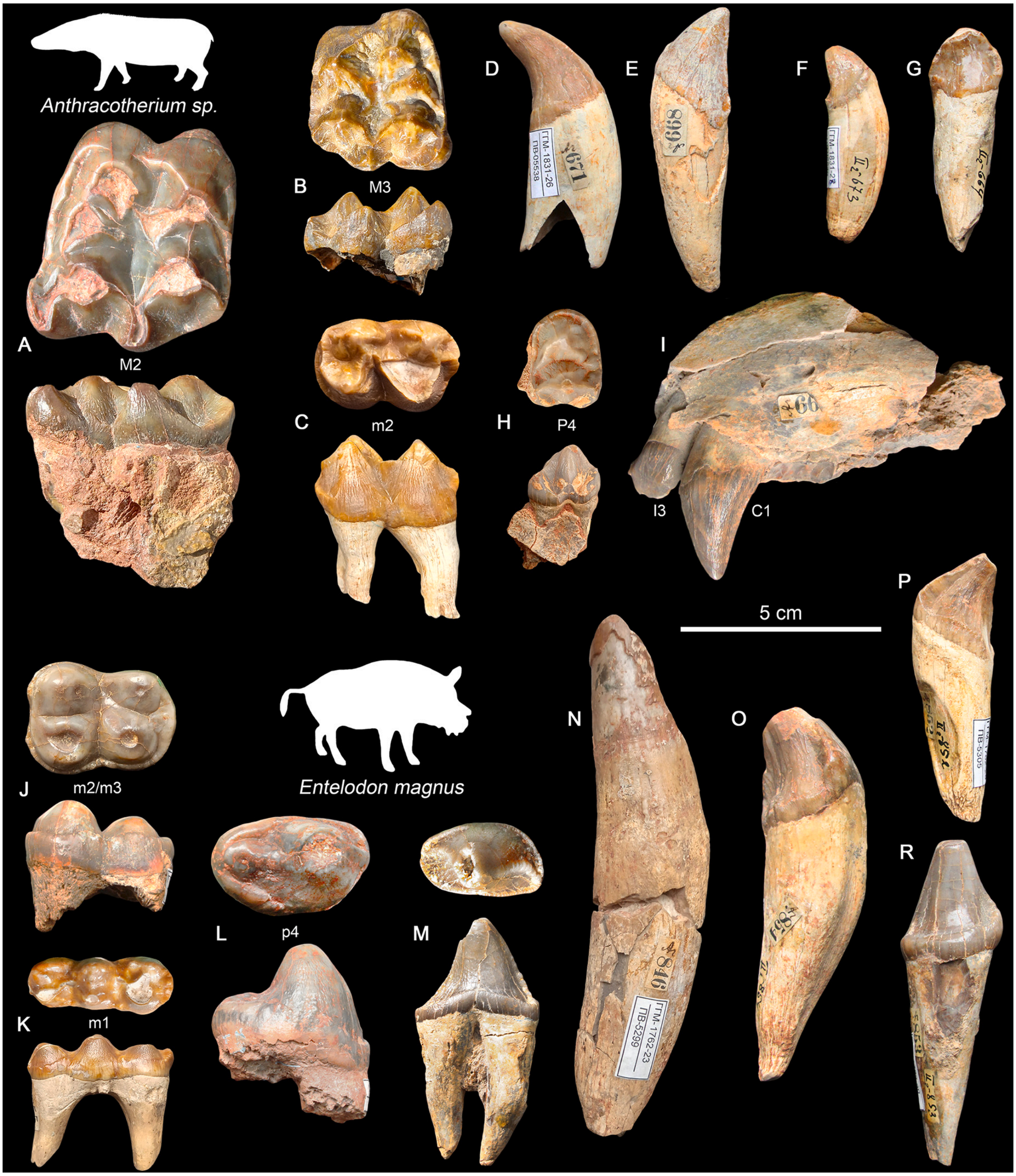

Fig. 3. Anthracothere and entelodont remains: *Anthracotherium magnum* M2 (1831–08) occlusal and labial view (A). *Anthracotherium* sp. M3 (1809–21) occlusal and labial view (B); m2 occlusal and labial view (C); canines (D, E); incisors (F, G); P4 (1831–04) occlusal and labial view (H); fragment of right maxilla (I3-C1; I); *Entelodon magnus* m2/m3 occlusal and labial view (J); m1 occlusal and labial view (K); p4 occlusal and labial view (L); p/P occlusal and lingual view (M); canine (1762–23) (N); incisors (P-R).

Table 1
Linear dimensions of the lower (m2, m3) and upper (M2, M3) molars of *Anthracotherium* sp. from the Quercy phosphorite formation.

Tooth	Length (mm)				Width (mm)			
	n	Min	Mean	Max	*n*	Min	Mean	Max
m2	2	41.8	42.3	42.8	2	27.7	28.35	29
m3	2	46.2	50.15	54.1	4	25	26.93	28.5
M2	5	32.3	38.94	49.7	5	38.2	43.8	56.1
M3	4	37.3	41.6	44	4	36.7	43.8	48.9

respectively. We adopted the classification of features defined by Solounias and Semprebon (2002), which distinguishes pits and scratches. We identified and quantified the number of small and large pits (circular or sub-circular scars), scratches (elongated microfeatures with parallel sides), gouges (large scars with irregular borders), and puncture pits (deep and large circular pits). We also classified the scratches according to their texture, that is, fine, coarse, or hypercoarse. The microwear features were quantified in a square area of 0.16 mm^2 using an ocular reticule. All data were collected by a single experienced observer (FR). The results were compared with a database containing data compiled from the literature that covers ten dietary categories in extant large mammals from a large range of habitats in Eurasia, Africa and America (with a total of 29 species and 542 individuals). The following dietary categories and species were selected: omnivorous (*Ursus arctos*, from Pappa et al., 2019; *Sus scrofa*, from Rivals et al., 2020); meat specialist (*Acinonyx jubatus*, *Panthera leo*; from Bastl et al., 2012); bone/meat (*Parahyaena brunnea*, *Hyaena hyaena*; *Crocuta crocuta*; from Bastl et al., 2012); mixed carnivorous (European and Asian *Vulpes vulpes*; from Bastl et al., 2012); mixed/fruit carnivorous (*Genetta genetta* and *Nandinia binotata*; from Bastl et al., 2012); piscivorous (*Lutra lutra*; from Bastl et al., 2012); leaf browser (*Alces alces*, *Boocercus euryceros*, *Giraffa camelopardalis*, *Litocranius walleri*; from Solounias and Semprebon, 2002); fruit browser (*Cephalophus dorsalis*, *C. niger*, *C. silvicultor*; from Solounias and Semprebon, 2002); grazer (*Alcelaphus buselaphus*, *Bison bison*, *Connochaetes taurinus*, *Equus burchelli*, *E. grevyi*, *Kobus ellipsiprymnus*, *Hippotragus niger*; from Solounias and Semprebon, 2002); and grazer/semi-aquatic (*Hippopotamus amphibius*, from Solounias and Semprebon, 2002). We conducted a linear discriminant analysis (LDA) based on the microwear variables to classify the extant species from the nine dietary groups. Using the R package MASS (Vernables and Ripley, 2002), we used the model derived from the LDA to classify the fossil species. We also ran a PCA using the R package factoextra (Kassambara and Mundt, 2020).

4. Results

The enamel surfaces were well preserved for *Anthracotherium* sp. Two teeth were excluded because their surfaces were damaged by taphonomic alterations. The final sample comprised 13 molars. For *Entelodon magnus*, 13 teeth were selected; five were discarded for taphonomic reasons and three because the teeth were unworn. The final sample comprised five teeth. The complete list of specimens and the quantitative data are available at https://doi.org/10.5281/zenodo.7432485 (Rivals, 2022).

The two species *Anthracotherium* sp. and *Entelodon magnus* had a small number of scratches but the other variables showed some differences (Fig. 4; Table 2). *Anthracotherium* sp. had a higher number of pits, more gouges, wider scratches with the presence of hypercoarse scratches, and fewer cross scratches and puncture pits than *Entelodon magnus* (Fig. 4).

The linear discriminant analysis (LDA) classified 87.85% of the extant species into their correct group. All five specimens of *Entelodon magnus* were classified similarly to the wild boar (*S. scrofa*), an omnivorous species (Table 3). The 13 specimens of *Anthracotherium* sp. were classified as belonging to three categories of extant herbivores: seven leaf browsers, three fruit browsers, and three grazers.

The PCA was performed using all the microwear features, revealing good discrimination amongst the extant species (Table 4; Fig. 5). The first principal component (PC1) explained 35.8% of the variation in microwear features and was mostly related to high numbers of pits, coarse, and hypercoarse scratches, and low numbers of scratches. The second principal component (PC2) explained 19.8% of the variation and was mostly related to high numbers of scratches and puncture pits and low numbers of pits. The PCA separated the individuals from the two fossil species, *Entelodon magnus* and *Anthracotherium* sp., and supported the dietary traits that were identified using LDA.

5. Discussion

One of the most prominent and acknowledged morpho-physiological features of artiodactyls is the foregut fermentation of cellulose, in contrast with the hindgut fermentation in perissodactyls (Sokolov, 1979; Wilson and Mittermeier, 2011). The increased complexity of the digestive system of artiodactyls is indicated principally in the stomach, which has extra chambers for the fermentation of plant food. The most complex stomachs are characteristic of ruminants. They consist of four compartments: the rumen, reticulum, omasum, and abomasum (the *true* stomach). A complex forestomach is also characteristic of other artiodactyls: Hippopotamidae, Tayassuidae, Camelidae, as well as cetaceans (Langer, 1976; Sokolov, 1979; Stevens and Hume, 1995; Wilson and Mittermeier, 2011). The only exceptions amongst even-toed ungulates are representatives of the Suidae, which do not have a complex stomach and are characterised by hindgut fermentation in the caecum (Wilson and Mittermeier, 2011). The anatomy of the digestive system correlates directly with dietary habits, which allows correlations to be established with the morpho-physiological features of extinct species.

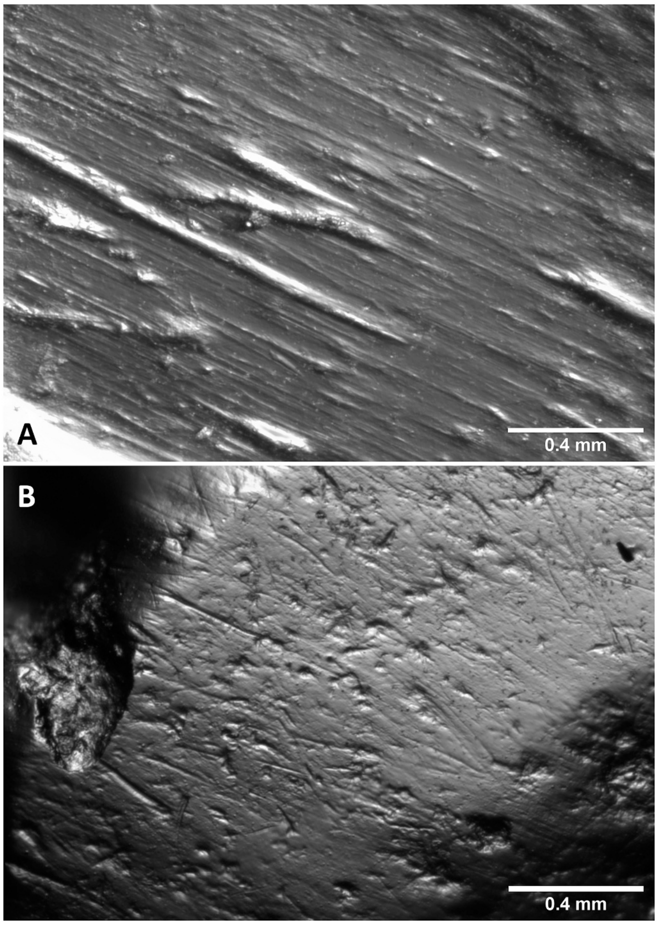

Fig. 4. Microphotographs of enamel surfaces of (A) *Anthracotherium* sp. (1831–10) and (B) *Entelodon magnus* (1762–04). Scale bar = 0.4 mm.

Entelodonts have been reported as having morpho-physiological features similar to those of pigs and carnivores (because they had a similar opportunistic omnivorous diet) or even hyenas (because they appear to have crushed bones) (Joeckel, 1990; Blondel, 2001; Foss, 2001). Our study shows that the microwear pattern quantified on entelodont enamel surfaces was similar to that of the wild *Sus scrofa* (with its omnivore diet) but different than that of *Ursus arctos*, the brown bear. Suidae have a more diverse diet than other artiodactyls and, as has been noted, are considered to be omnivorous and opportunistic. They do not have complex stomachs nor enlarged caecum and cannot digest cellulose very efficiently. Their digestion is rapid and adapted to the fast transition of food (Wilson and Mittermeier, 2011). Their teeth are low-crowned and bunodont, and they feed on fresh green grasses and forbs, palatable herbs and succulents, legumes, fruits, acorns, seeds, roots, bulbs, bark, fungi, invertebrates (worms, molluscs, beetles), fish, frogs, reptiles, small birds, rodents, newborn or injured mammals and carrion, and the eggs of ground-nesting birds and reptiles (Sokolov, 1979; Heptner et al., 1988; Baskin and Danell, 2003; Wilson and Mittermeier, 2011; Scandura et al., 2022; and references herein). Suidae food availability varies greatly depending on the area and seasonality. *Entelodon*

Table 2
Summary results of the microwear analysis on the anthracotheres and entelodonts. Abbreviations: *N* = number of specimens; *M* = mean; *SD* = standard deviation; Npit = number of pits; Nscr = number of scratches; %LP = percentage of individuals with large pits; %G = percentage of individuals with gouges; SWS = scratch width score; %XS = Percentage of individuals with cross scratches; %HC = percentage of individuals with hypercoarse scratches; Npp = number of puncture pits.

Species		*N*	Npit	Nscr	%LP	%G	SWS	%XS	%HC	Npp
Anthracotherium sp.	*M*	13	30.19	9.92	92.31	100	2.2	7.69	76.92	1
	SD		6.86	2.06						
Entelodon magnus	*M*	5	14.70	10.70	100	60	1.4	100	20	3.6
	SD		2.41	1.99						

Table 3
Summary of the linear discriminant analysis based on the quantitative analysis of microwear features.

Extant classification rate	87.85%	
	Fossil species	
Extant diets	*Anthracotherium* sp.	*Entelodon magnus*
Omnivorous (*S. scrofa*)	0	5
Omnivorous (*U. arctos*)	0	0
Meat specialist	0	0
Bone/meat	0	0
Mixed carnivorous	0	0
Mixed/fruit carnivorous	0	0
Piscivorous	0	0
Leaf browser	7	0
Fruit browser	3	0
Grazer	3	0
Grazer/semi-aquatic	0	0

Table 4
Eigenvalues and percentage of variance for the eight PCA axes.

	Eigenvalue	% variance
Dim.1	2.8667771	35.83
Dim.2	1.5859013	19.82
Dim.3	0.9343481	11.68
Dim.4	0.8528809	10.66
Dim.5	0.6816137	8.52
Dim.6	0.5958056	7.45
Dim.7	0.3168713	3.96
Dim.8	0.1658019	2.07

magnus differed from all carnivorous species and herbivorous ungulates in that they did not follow strict carnivorous or herbivorous diets. In the studied sample, it is also possible to discard the hypothesis that they hunted large herbivores and crushed bones because the microwear pattern does not fit with that of hyaenids. Nevertheless, the possibility of occasional scavenging behavior cannot be discounted because wild boar can feed on animal meat in this way (Giménez-Anaya et al., 2008; Scandura et al., 2022). Therefore, the microwear data obtained in our study suggest that large European *E. magnus* were omnivorous ungulates that probably did not possess yet the complex stomachs characteristic of most modern-day artiodactyls. This corresponds with the plesiomorphic low-crowned, bunodont structure of the molars found in entelodonts (Orlov, 1962; Joeckel, 1990).

The anthracothere *Anthracotherium* sp. was previously considered to have adapted to a frugivorous/folivorous diet because of the bunoselenodont structure of its low-crowned molars (Janis, 1995; Blondel, 2001). The morphological similarity to hippos and the specificity of the sediment in which some derived anthracotheriids have been found would suggest they may have been semiaquatic animals (Carroll, 1988). The microwear patterns quantified on the enamel surfaces classified the present sample of anthracotheres into the three dietary categories of extant herbivores: leaf browsers (53.8% of the individuals), fruit browsers (23.1%), and grazers (23.1%). In chalicotheres, the presence of coarse and hypercoarse scratches, which were associated with puncture pits in several individuals, has been associated to the consumption of ligneous plants (including bark) and fruits (Semprebon et al., 2011). Ligneous plants and bark consumption is characteristic of the wild boar's cold season diet (Heptner et al., 1988). The folivorous/frugivorous diet was supposed for 10 individuals (76.9% of the sample). The remaining 23.1% of the individuals were classified as grazers. This result is consistent with the presence of C_3 grasses in the European Oligocene (Strömberg, 2011). Finally, we can discard the possibility that the individuals herein followed a grazing diet and engaged in semi-aquatic behaviours characteristic of the hippopotamus, as none of the individuals were classified as semi-aquatic/grazer. Our results, added to previous analyses of the dietary traits in anthracotheres, suggest different behaviours. Dietary traits and behaviours were highly diverse in the Anthracotheriidae, with some species showing semi-aquatic mode of life like *Bothriogenys gorringei* from the early Oligocene of Egypt or *Libycosaurus bahri* from the late Miocene of Toros-Menalla (Clementz et al., 2008; Lihoreau et al., 2014), while *Anthracotherium* sp. from the late Oligocene of Enspel (Tütken and Absolon, 2015) and from the Quercy Phosphorites were not semi-aquatic taxa.

The presence of three dietary categories in the anthracotheres probably reflected the nature of the material studied. As it has been noted, it is not possible to establish the exact geological age and geographical location of the materials in the old collections from the Quercy phosphorite formation. Thus, the material we have examined most likely belongs to several species of *Anthracotherium* genera (see the Material section for details) that may have lived during different European land mammal Paleogene zones. As with the wild boar, the diet was variable, depending certainly on the part of the range and the availability of certain foods. Fruits, and in particular the oil-rich seeds are important for a variety of species of extant Suidae. Thus, in the genus *Sus*, mast fruiting of oak, Fagaceae and Dipterocarpaceae species provides an opportunity to fatten up and appears to be linked to its breeding cycle (Wilson and Mittermeier, 2011). A similar preference for feeding on fruits and seeds can be assumed for anthracotheres.

The diet of the anthracotheres described here is somewhat similar to the pygmy hippo. Pygmy hippos are believed to be browsers, feeding on leaves, aquatic plants, fallen fruits, roots, and tubers (Wilson and Mittermeier, 2011). Their cheek teeth are medium-crowned (mesodont) and considered as bunodont, with much taller main cusps than those of the Suidae. The premolars have a single large cusp, and the molars have four high cusps (Hillson, 2005).

The deviation from the omnivorous towards the leaf/fruit browser and grazer dietary categories in anthracotheres corresponds to the increased (cf. hogs and entelodonts) complexity of molar morphology (Janis, 1995). These shifts in dietary categories and molar morphology in anthracotheres may point to the increased complexity of the digestive system. Digestion and fermentation depend on the quality of the food. If the food contains a large proportion of digestible components (sugars, starch and proteins), then it is preferable to digest them rather than ferment them (Alexander, 1993). This case is characteristic of the omnivorous Suidae and, probably, entelodonts. If the food contains a low proportion of digestible material and a high proportion of cellulose material, fermentation become necessary, because cellulose is not digested by any of the enzymes secreted by mammals. This is the reason why various herbivorous mammals have foregut or hindgut chambers for bacterial fermentation of cellulose (Alexander, 1993). Thus, dietary

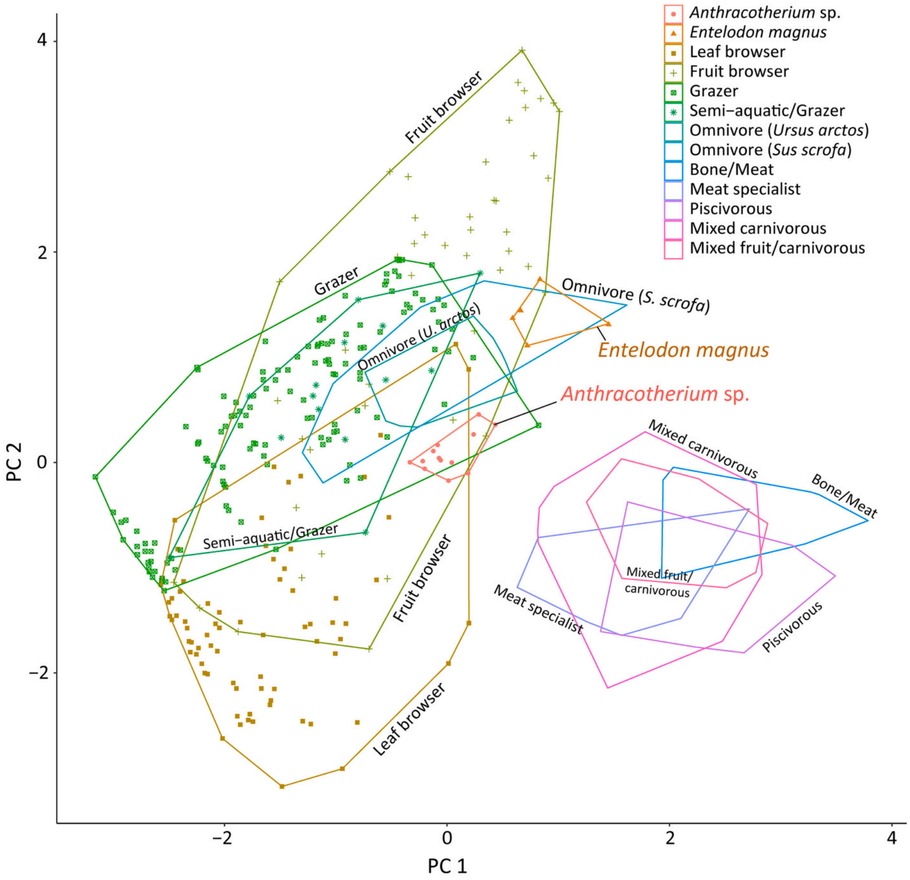

Fig. 5. PCA established on the eight microwear variables. The convex hulls correspond to the fossil *Anthracotherium* sp. and *Entelodon magnus* and the dietary categories of extant mammals selected: omnivorous, meat specialist, bone/meat, mixed carnivorous, mixed/fruit carnivorous, piscivorous, leaf browser, fruit browser, grazer and grazer/semi-aquatic.

traits in *Anthracotherium* may indicate the presence of a complex stomach, which is characteristic of most artiodactyls.

The two species under present consideration lived in relatively arid and open conditions. After relatively hot and humid conditions in rather forested environments in the Eocene, the beginning of the Oligocene marked a deterioration in the environment, which became more arid and open, corresponding with climatic cooling (Legendre, 1989). At the end of the early Oligocene, conditions improved but without returning to the subtropical/tropical conditions of the late Eocene (Legendre et al., 1997). During the Oligocene, both anthracotheres and entelodonts occupied habitats where a large diversity of resources was available.

6. Conclusions

The microwear analysis of *E. magnus* and *Anthracotherium* sp. from the Quercy phosphorite formation made it possible to identify their probable dietary preferences and their habitats and ecological niches.

The dietary traits of the taxa were considered in relation to their morpho-physiological adaptations. Entelodonts had an omnivore diet similar to that of the wild boar but not that of the brown bear. Similarly, for the Suidae, entelodonts were opportunistic, but food availability varied depending on the season and location. These features fit with the plesiomorphic low-crowned and bunodont molars of the entelodonts. Anthracotheres were opportunistic herbivores; most of the individuals were browsers, some were frugivorous, and some were grazers. Given the possibility that the sample contained different species, the diet of the anthracotheres varied depending on the geographic area, the chronology of the deposits, and the season(s) of the year when the animals died.

This is the first study of anthracothere and entelodont paleodiets based on dental microwear on (the limited) material from southern France. Future research will investigate how far the diet of anthracotheriids and entelodontids differed in different parts of their range, body size groups, and geological epochs.

Author contributions

Florent Rivals: Conceptualization, Formal analysis, Data curation, Writing - original draft; Ruslan I. Belyaev: Conceptualization, Writing - original draft, Writing - review and editing; Vera B. Basova: Writing - original draft, Writing - review and editing; Natalya E. Prilepskaya: Conceptualization, Writing - original draft, Writing - review and editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data are available on Zenodo: 10.5281/zenodo.7259210. Datasets related to this article can be found at https://doi.org/10.5281/zenodo.7432485, an open-source online data repository hosted at Zenodo (Rivals, 2022).

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