A new gigantic carnivore (Carnivora, Amphicyonidae) from the late middle Miocene of France (#68485)

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A new gigantic carnivore (Carnivora, Amphicyonidae) from the late middle Miocene of France

Floréal Solé [1] , **Jean-François Lesport** [2] , **Antoine Heitz** [3] , **Bastien Mennecart** Corresp. [3]

[1] Royal Belgian Institute of Natural Sciences, Brussels, Belgium

[2] Private, Sainte-Hélène, France

[3] Naturhistorisches Museum Basel, Basel, Switzerland

Corresponding Author: Bastien Mennecart
Email address: mennecartbastien@gmail.com

Serravallian terrestrial vertebrate are very uncommon in the northern margin of the Pyrenean Mountains. A mandible of a new large size amphicyonid (ca. 200 kg) is here described from the marine deposits of Sallepisse (12.8-12.0 Mya). Despite that this new taxon is close in size to some European amphicyonids from the Miocene (e.g., *Magericyon, Agnotherium*, and *Tomocyon*), the novel morphology of its p4, unknown in this clade, allows the erection of the new genus *Tartarocyon cazanavei* nov. gen. & sp. This taxon may be closely related to *Pseudocyon*, *Amphicyon*, and possibly *Magericyon*. This restricted to Europe group seems to have acquired the adaptations to bone-crushing mesocarnivory and hypercarnivory (in *Magericyon*) in convergence with the Thaumastocyoninae (e.g., *Agnotherium*, *Peignecyon*, *Ysengrinia*). The description of this new taxa highlights the polyphased ecological and diversity erosion of the Amphicyonidae in response to well-known Miocene events.

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Solé F.[1], Lesport J.-F.[2], Heitz A.[3], and Mennecart B.[3]

[1] D.O. Earth and History of Life, Royal Belgian Institute of Natural Sciences, Rue Vautier 29, B–1000 Brussels, Belgium, floreal.sole@naturalsciences.be;

[2] 220 allée des cailles, F-33480 Sainte-Hélène, France, jf.lesport@free.fr;

[3] Natural History Museum Basel, Augustinergasse 2, 4001 Basel, Switzerland, mennecartbastien@gmail.com.

Corresponding Author:
Mennecart Bastien
Augustinergasse 2, 4001 Basel, Switzerland
Email address: mennecartbastien@gmail.com

Abstract

Serravallian terrestrial vertebrate are very uncommon in the northern margin of the Pyrenean Mountains. A mandible of a new large size amphicyonid (ca. 200 kg) is here described from the marine deposits of Sallepisse (12.8-12.0 Mya). Despite that this new taxon is close in size to some European amphicyonids from the Miocene (e.g., *Magericyon, Agnotherium*, and *Tomocyon*), the novel morphology of its p4, unknown in this clade, allows the erection of the new genus *Tartarocyon cazanavei* nov. gen. & sp. This taxon may be closely related to *Pseudocyon*, *Amphicyon*, and possibly *Magericyon*. This restricted to Europe group seems to have acquired the adaptations to bone-crushing mesocarnivory and hypercarnivory (in *Magericyon*) in convergence with the Thaumastocyoninae (e.g., *Agnotherium*, *Peignecyon*, *Ysengrinia*). The description of this new taxa highlights the polyphased ecological and diversity erosion of the Amphicyonidae in response to well-known Miocene events.

Key words. Miocene, Europe, Carnivora, Amphicyonidae, Ecology.

Introduction

The middle Miocene (15.97-11.63 Ma) is a period of ~~extreme~~ interest concerning climate ~~changes~~ and faunal dispersal ~~through~~ Eurasia and Africa (Rögl, 1999; Hilgen, 2012). The Langhian (ca. 15.97-13.65 Mya) encompasses the ~~Mid-Miocene~~ Climatic Optimum, a global increase ~~of the~~ temperature of ca. 5°C, while during the Serravallian, cooler temperatures occurred (Hilgen, 2012). These events ~~lead~~ to important environmental changes and faunal renewals and exchanges (Costeur, 2005). Despite the very abundant invertebrate fossil record, ~~few~~ ~~are~~ currently known about the faunal connections between the northern and southern part of the ~~Pyrenean Mountains~~ during the middle Miocene due to lack of continental vertebrate remains. Indeed, the Southwestern part of France was ~~several times~~ flooded by the sea during the early and middle Miocene (Cahuzac et al., 1992) and the continuing ~~to rise Pyrenean Mountains~~ formed a natural barrier between the Iberian Peninsula and the rest of Europe.

The last transgression in Aquitaine occurred during the Serravallian (middle Miocene, ca. 13.82-11.63 Mya). This sea deposited in the Orthez area (Southwestern France) a famous and abundant marine fauna found in ~~shell~~ sandy deposits named “Faluns bleus”

(Delbos, 1848), also known as Blue Faluns of Orthez (Lesport, Cluzaud & Verhecken, 2015). ~~Early in the paleontological history~~, ~~this~~ formation attracted scientists. In 1833, the naturalist Dufour made an excursion in this area (Dufour, 1836) and gave indications to his palaeontologist friend Grateloup who ~~could~~ ~~published~~ soon after new fossil gast~~e~~ropod~~s~~ species (Grateloup, 1835; 1845-1847). Since then, numerous authors contributed to the knowledge of the malacofauna from the Orthez area, including in Sallespisse (see Lesport, Cluzaud & Verhecken, 2015 for an extensive literature). These bioclastic accumulations (thanatocenos~~i~~is) may represent a nearshore environment in a subtropical to tropical climate. In 1993, JFL and Philippe Renard ~~have~~ found a mandible of a very large carnivoran in a transgressive microconglomerate layer from the Crousquillière locality in Sallespisse. It was, at that time, the only terrestrial remain among the entire fauna in this layer. This ~~new~~ specimen belongs to an Amphicyonidae (Carnivora, Caniformia).

The Amphicyonidae, which are colloquially referred to as "bear-dogs", represent~~ed~~ one of the most characteristic groups of carnivorans in the European faunas (Solé et al., 2018). They first appeared during the Eocene (Priabonian, MP18, ca. 37-36 Ma; de Bonis, 1978; Sole et al. 2018). Nevertheless, the Miocene is particularly interesting for studying the evolution of this family. These carnivorous mammals ~~contained~~ numerous species during the early and middle Miocene in Europe with a maximum of nine contemporaneous species (Viranta, 1996), but went extinct before the end of the Miocene, the last amphicyonids being known ~~during~~ late Tortonian (*Amphicyon pannonicus*; Kretzoi, 1985; Viranta, 1996). European Miocene amphicyonids were also ecologically diverse: taxa ranged from 9 kg to 320 kg and displayed typical mesocarnivorous, omnivorous, bone-crushing, and hypercarnivorous diets (Viranta, 1996; Ginsburg, 1999). They started to decline from MN7/8 with only few taxa recorded during MN9-MN12 (Viranta, 1996). The amphicyonids ~~might~~ have ~~strongly~~ ~~suffer~~ from the Vallesian Crisis, with only rare and specialized taxa known in the late Vallesian and early Turolian ~~located~~ in some parts of Central Europe (Agustí, Cabrera & Garcés, 2013; Viranta, 1996). Therefore, the description of this new Amphicyonidae from the ~~South Western Europe~~ Serravallian is crucial in order to better understand the diversity and geographic distribution of the last amphicyonids and their abrupt decline in Europe.

Geological settings and location

Location and paleontological content. During the Serravallian, the sea expanded into the gulf of Chalosse (Southwestern France), which was delimited by the “Diapir de Dax”, the “Ride de Tercis”, and the “Dôme de Clermont”, and the anticline of Louer, and penetrated further south, constituting the Gulf of Orthez/Salies-de-Béarn. (Figure 1). The Blue Faluns in the area of Orthez are found in many places, mainly in the South part of Sallespisse, at an altitude ~~comprised~~ between 120 and 140 meters (Le Paren, Houssé, Pouchan, Labarthe, Carré; see Karnay, 1997). All these localities are in line with a ~~S~~outhwest/~~N~~ortheast orientation. The proximity and a global similitude in the ~~fauna~~ taxonomic composition and sedimentological content allowed previous authors to consider all these localities as synchronous and were grouped under the locality name of Sallespisse (Daguin, 1948). Nevertheless, very small differences in ~~proportion~~ within the different mollusc communities are ~~noticed~~ indicating small local environmental ~~discrepancies~~ (Degrange-Touzin, 1895). The most common gastropod~~s~~’ ~~family~~ are the Naticidae, Epitoniidae, Ocenebrinae, Nassariidae, Cancellariidae, Conidae, Turridae, and Acteonidae, which for the most part are predators, scavengers, or commensals. Among many species of bivalves, the most ~~represented~~ genera are *Acanthocardia, Megacardita, Anadara, Pecten*, and *Clausinella*. These bivalves and the profusion of a species of scaphopod collected in a soft bioclastic sand matrix currently live on a sandy-muddy bottom of the SFBC type (“[Sables Fins Bien Calibrés” = fine sands well calibrated, Peres & Picard, 1964). The current SFBC biocenosis, which occupies large areas along the coasts and bottom of the Mediterranean gulf, are remarkable for the absence of algae and marine phanerogams, which seems to agree with the deposits at the Carré site. This is confirmed by the abundant associated marine life (e. g. Nolf & Steurbaut, 1979; Chaix & Cahuzac, 2005). However, some brackish and freshwater species may be found (e.g. *Theoxodus*), may indicate sediments of continental origin~~s~~.

The locality of Crousquillière (Figure 1), misspelled in Lesport, Cluzaud & Verhecken, 2015 as La Croustillère, is located ~~in~~ the Carré farm property (also known as Carrey) own by the Cazanave family in Sallespisse. The fossiliferous Blue Faluns grey-blue sands may be found along a small stream that flows into a brook called Le Moussu, ~~S~~outh to the Carré farm (coordinates 43.512705; -0.717866). This locality ~~has been~~ poorly exploited for its fossiliferous contains before the 1990’. From 1993, J.-F. Lesport and P. Renard systematically excavated numerous fossils from these layers (crustaceans, bryozoans, echinoderms, foraminifers, scleratinians, fishes, and more than 200 species of molluscs; Lesport, Cluzaud & Verhecken, 2015). A new excavation campaign during the summer of 2021 completed the malacofauna but unfortunately did not bring new bone elements from carnivorous mammals.

Sedimentological succession (Figure 2). The succession is relatively similar to the one observed in the other Blue Faluns outcrop from Sallespisse. The complete studied outcrop measures 3.5m. It is composed from base to top of:

- Molasse~~s~~ deposits observed on more than 10 meters high along the stream. They are made of continental/lacustrine whitish to greyish marly limestone with nodules. These sediments are apparently azoic. Nevertheless, the broad sedimentation of this molassic Formation may be ~~comprised~~ between the middle Eocene and the Burdigalian in this area (Karnay, 1997). Being at the very end of this sequence may indicate an age ~~comprised~~ between the late Oligocene and the early Miocene. The top of this formation is heterogeneous, incised by shallow depressions forming small bowl (ca. 1 meter in depth).

- Blue Faluns of Orthez (1 to 2 meters) deposits with an evolution in colour and sedimentation from base to top. The basal transition between the molasse~~s~~ deposits and the falun deposits is marked by broken molluscs and black pebbles that may be pierced by lithophagous bivalves, characteristic of a transgressive event. The studied mandible ~~has been~~ found in this layer. New remains (an isolated molar and an astragalus) of ruminant coming from this layer are currently under study. The basal basins are ~~field~~ with blue to black clayey sand containing a diversified fauna of large molluscs (e.g. *Pelecyora*, *Procardium*, *Megacardita*, *Hexaplex*, *Conus*). This level is sealed with few centimetres of ~~a~~ fine blue to black sand containing rare fossils. Then, the grey-blue falun has a thickness of ca 1 meter containing many well-preserved mollusks. The Faluns deposits end with a yellow to orange sandstone characteristic to ~~oxidant~~ conditions. This Formation clearly corresponds to the Faluns de Sallespisse (Karnay, 1997). The age of these deposits is discussed ~~hereafter.~~

- A multicolored clay layer of 20 cm is found above the Faluns deposits. The top of the layer ends with fine ferruginous sandstone (2 cm), also called garluche. Lignified wood remains have been found during ~~the~~ excavation in this section.
- Coarse yellowish clay sand (80 cm) ending with a ferruginous conglomerate (ca. 10 cm) that may correspond to Pliocene deposits. Daguin (1948), without differentiating the different terrestrial levels, calls this formation "Sables Fauves".

Age of la Crousquillière (in Sallespisse) locality. The age of the Falun deposits in the ~~area of~~ Orthez have been ~~many times~~ interpreted from the late Eocene (d'Orbigny, 1852) to the late Miocene (Delbos, 1848; Raulin, 1852), including an early Miocene age (Grateloup, 1845-1847). Nevertheless, the very diverse mollusc fauna ~~permitted to constrain~~ the age attribution of these deposits to the middle Miocene, characterizing the lithofacies Vindobonian (Poignant, 1967); the Sallomacian, a local name for middle Miocene marine deposits (Fallot, 1893Poignant, 1967; Nolf & Steurbaut, 1979); or the sedimentological facies "Helvetian", which encompass the Langhian and Serravallian (Benoist, 1884; Degrange-Touzin, 1895; Cossman & Peyrot, 1909-1914; 1909-1924; 1917-1924; Peyrot 1925-1935; 1927-1932). Magné, Gourinard & Wallez (1987), Cahuzac & Poignant (1993), and Karnay (1997) proposed a Langhian age for these deposits.

However, recent studies based on diverse marine fauna (benthic foraminifers, ostracods, pteropods) and strontium isotopic analyses ~~leaded~~ to a revaluation of the age of the Faluns deposits from Sallespisse and Othez to the Serravallian (Cahuzac, Janin & Steurbaut, 1995; Cahuzac & Poignant, 1996; Ducasse & Cahuzac, 1997; Cahuzac & Janssen, 2010). These sediments are now attributed to the marine biozones Martini NN6/7, Blow N11/13, Janssen & King NSB19, with an isotopic age ~~comprised~~ between 12.8 and 12.0 Mya. This corresponds to the European Land Mammal Ages MN7/8 (Duranthon & Cahuzac, 1997).

Materials & Methods

Specimen, nomenclature and measurements. The specimen has been ~~given~~ by JFL to the Natural History Museum of Bordeaux (France): it is now register under the number MHNBx 2020.20.1. A cast of the specimen is available at the Natural History Museum Basel. Moreover, MHNBx 2020.20.1 has been surface scanned. The 3D model of the specimen is downloadable ~~on~~ the open access article~~s~~ Mennecart et al. (accepted).

The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The LSID for this publication is: urn:lsid:zoobank.org:pub:9FE7C271-9402-4062-B9B5-2087C8ACDC04. The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central SCIE and CLOCKSS.

The dental nomenclature of premolars follows Ginsburg (1999). The measurements, taken by ~~a calliper~~, have a precision of 0.1 mm.

Body Mass. We used the equation of Van Valkenburgh (1990) in order to estimate the body mass of some amphicyonids including *Tartarocyon cazanavei* nov. gen. & sp.: Log^{10}(BM) = [2,97 x Log^{10}(Lm1)] – 2,27; with BM: the estimated body mass in kg; Lm1: the length of the first lower molar in millimeters.

Biochronology. The biostratigraphic framework is based on geological time scales for the Miocene provided by Hilgen et al. (2012).

Systematic Palaeontology

CARNIVORAMORPHA Wyss & Flynn, 1993
CARNIVORAFORMES Flynn, Finarelli & Spaulding, 2010
Order CARNIVORA Bowdich, 1821
Suborder CANIFORMIA Kretzoi, 1943
Family Amphicyonidae Trouessart, 1885
Genus *Tartarocyon* nov. gen.

ZooBank LSID. urn:lsid:zoobank.org:act:70359DC0-49E9-4E87-BC90-B02D5CFAFBB1

Type species. *Tartarocyon cazanavei* nov. gen. & sp.; monotypic, see below.

Etymology. Tartaro is the name of a man-eater giant living in the Southwestern French ~~Pyrenean Mountains,~~ including the Bearn where the fossil has first been described. –*cyon* is the Greek for dog.

Diagnosis. As for the type and only species.

Species *Tartarocyon cazanavei* nov. gen. & sp.

Figure 3

ZooBank LSID. urn:lsid:zoobank.org:act:C7BE021C-6434-4715-AB89-63E9A64E6178

Etymology. Dedicated to Mr Alain Cazanave, owner of the locality, who helped ~~during many years~~ with the excavation.

Diagnosis. The taxon is characterized by the following features: long diastemata between the premolars, low p2 and p3, absent mesial cusp on p4, large distal accessory cusp on p4, and unreduced m2 and m3. The taxon differs from all the other European amphicyonids from the Miocene by the individualization of the distal accessory cusp from the main cusp on p4. It also differs from *Pseudocyon*, *Amphicyon*, and *Cynelos* – ~~its~~ closest genera – by the absence of distal shelf and cingulum on p4.

Specimen. MHNBx 2020.20.1, right mandible bearing p2-p4, alveoli of i1-i3, c, p1, m1-m3.

Measurements. Tables 1 & 2.

Description. The mandible is mesiodistally elongated. Large diastemata are present between the canine, p1, p2, p3, and p4; the longest diastema is between the p2 and p3. The symphysis is oval ~~in shape~~ and nearly horizontally oriented; it is high and extends posteriorly up to the distal root of ~~the~~ p2. A mental foramen lies beneath the p1-p2 diastema; it is in a high position on the mandibular ramus. The ramus of the mandible is shallower anteriorly than posteriorly, the highest portion being below the m3. The ventral margin of the ramus below the toothrow is relatively straight but~~,~~ beneath the anterior extremity of the large, deep masseteric fossa~~,~~ it becomes convex. An incisura vasorum is present on the ventral margin of the mandible anterior to the angular process. The angular process is robust but very short; it projects medially. The mandibular condyle is at the level of the tooth row. It is cylindrical and mediolaterally elongate. The coronoid process is tall and distinctly oriented backwards; it arises at a 50° angle relative to the horizontal ramus. The posterior margin of the coronoid is vertical and straight, while the cranial margin is rounded. The masseteric fossa, on its labial side, is deep and wide. The mandibular foram~~ina, on its lingual side~~, is relatively circular, standing at the level of the incisura vasorum, at mid~~-~~height between the base of the mandible and the level formed by the tooth~~-~~row. The mandibular foramen opens midway between the m3 and the mandibular condyle.

The lower incisors are not preserved, but the alveoli of the i1, i2, and i3 are visible. Considering the size of the tooth sockets, the i3 seems to have been the largest and the i1 the smallest. The canine is also not preserved. It was ovoid in section and ~~important in~~ size. Its root ~~expends~~ in the mandible between p2 and p3. The p1 is not preserved; a single alveolus is visible but it appears that two mainly fused roots were present. The other teeth are two-rooted, except the m3, which is single-rooted. The p2 and p3 are very low in height. There is a prominent ridge on the mesial and distal margins of the main cuspid. The main cuspid is low and located mesially, which results in an asymmetric morphology in lateral view. Mesial to the protoconid, the lingual cingulum is thicker, but no individualized paraconid is present. On p3 and p4, the distal shelf forms the widest part of the crown; it is less clear on p2. There is a ~~distal~~ short cingulum, but no cuspid is present. The p4 is distinctly longer and ~~transversally~~ wider than the p2 and p3. However, the main cusp remains low. The tooth is less asymmetric, the apex of the protoconid being more mesiodistally centered. No real paraconid is present mesial to the protoconid. A distal accessory cusp is present: it is mostly individualized from the protoconid. The distal accessory cusp is ~~transversally~~ centered. The distal cingulum is thin and is almost completely absent at the distal part. The molars are not present, but the m1 was the largest tooth of the tooth-row. The m2 is larger than the m3.

Comparison. ~~The amphicyonids~~ are characterized by the presence of a pronounced, trenchant dentition (Morlo et al., 2020; Morales et al., 2021). Two subfamilies of Amphicyonidae are ~~well-~~recognized in the Miocene of Europe: the Haplocyoninae and the Thaumastocyoninae, the Amphicyoninae being supposedly paraphyletic (Morales et al., 2021).

The typical haplocyonines (*Haplocyon*, *Haplocyonoides*, *Haplocyonopsis*) are unknown in Europe after MN3 (Peigné & Heizmann, 2003; Morlo et al., 2020) – although they might have survived until the end of the Serravallian in Asia (Jiangzuo et al., 2021). The premolars of the typical haplocyonines (*Haplocyon*, *Haplocyonoides*, *Haplocyonopsis*; de Bonis, 1966; Peigné & Heizmann, 2003; Morlo et al., 2020) differ from those of MHNBx 2020.20.1 in being tall (i.e., tall protoconid) and short. Based on phylogenetic analysis, Jiangzuo et al. (2021), proposed to include ~~among~~ the Haplocyoninae the genera *Sarcocyon*, *Gobicyon*, and *Aktaucyon*. Among these genera, only *Gobicyon* is known ~~in~~ Europe (*G. serbiae*; Pavlovic & Thenius, 1959; Ginsburg, 1999; Jiangzuo et al., 2018). Nevertheles, ~~as~~ the other haplocyonines, the premolars of *Gobicyon* differ from those of MHNBx 2020.20.1 in being tall and short. Moreover, the p2 and p3 of *G. serbiae* ~~possess~~ individualized and large distal accessory cusp. Additionally, typical haplocyonines and *Gobicyon* have a short toothrow lacking diastema. These amphicyonids are thus relatively short-snouted compared to the taxon from Sallespisse.

The Thaumastocyoninae groups the genera *Thaumastocyon*, *Ysengrinia*, *Tomocyon*, *Crassidia*, *Agnotherium*, *Ammitocyon*, and possibly *Amphicyonopsis* (Morales et al., 2019; 2021; Morlo et al., 2020). All these taxa differ from MHNBx 2020.20.1 in having shorter diastemata between the premolars. The p2 and p3 preserved on MHNBx 2020.20.1 are similar to those of the oldest thaumastocyonines (*Ysengrinia*, *Crassidia*) in being low (i.e., their protoconid is noticeably lower than the p4~~'s~~ protoconid). The p4 of MHNBx 2020.20.1 also share with the thaumastocyonines the presence of a strong distal accessory cusp. The youngest thaumastocyonines – *Ammitocyon* and *Agnotherium* – however, differ from MHNBx 2020.20.1 in having no p1, p2, and p3 (Morlo et al., 2020; Morales et al., 2021). Compared to the fossil from Sallespisse, the thaumastocyonines have a reduced m3 relative to m1; the youngest thaumastocyonines (*Thaumastocyon*. *Ammitocyon*, *Agnotherium*) have even reduced m2 relative to m1 as well ~~as no~~ m3 (Morlo et al., 2020; Morales et al., 2021). As a consequence, MHNBx

2020.20.1 differs in having more developed premolars, a mesially elongated snout (i.e., diastemata between the premolars), and less reduced postcarnassial molars.

The hypercarnivorous amphicyonine *Magericyon* (Peigné et al., 2008) differs from MHNBx 2020.20.1 in the absence of p2, in having a single-rooted p3, and in the absence of a distal cusp on p4.

Two amphicyonids are regarded to be ~~apart~~ from those recorded in the Miocene: *Ictiocyon* and *Pseudarctos* (Ginsburg, 1992). These small amphicyonids are short-snouted (i.e., short diastemata between the premolars) and the p2 and p3 are distinctly taller. Moreover, the distal accessory cusp on p4 is reduced in *Ictiocyon* and *Pseudarctos*.

The Amphicyoninae as defined by Peigné et al. (2008) is now considered to probably be paraphyletic forming a grade and including several lineages more basal than the thaumastocyonines or ~~incuding~~ in this subfamily (Morales et al., 2019; 2021). The Miocene amphicyonines *Cynelos*, *Amphicyon*, and *Pseudocyon* share with MHNBx 2020.20.1 the presence of very long diastemata between the premolars, the presence of low p2, p3, and p4, and the unreduced m3 (the m3 indeed tends to reduce and ~~are~~ event absent in hypercarnivorous amphicyonids; Table 3) (Kuss, 1965; Peigné & Heizmann, 2003; Viranta, 1996). Despite sharing a characteristic slender ramus of the mandible, the p4 of MHNBx 2020.20.1 differs from that of the *Cynelos* species by a less developed mesial cusp (even it is [illegible] individualized in *Cynelos*) and a much more reduced distal shelf. MHNBx 2020.20.1 shares with the species of *Amphicyon* and *Pseudocyon* the reduction of the mesial cusp and the distal shelf compared to *Cynelos*. However, no species of *Amphicyon* and *Pseudocyon* has a p4 that displays a distal accessory cusp separated from the protoconid as it is on the p4 of MHNBx 2020.20.1; additionally, the mandible of *Amphicyon* and *Pseudocyon* appears more massive than ~~in~~ MHNBx 2020.20.1 (Kuss, 1965; Peigné & Heizmann, 2003; Viranta, 1996).

A canine has been described from the locality of Rimbez (France, MN5), a locality that is located 100 km to the north-west of Sallespisse (Ginsburg, 1967); this locality is the closest one that provided a Miocene amphicyonid specimen. This canine has been referred to *Pseudocyon sansaniensis*, an Amphicyonidae of similar size to MHNBx 2020.20.1. It is at the moment impossible to compare this canine with MHNBx 2020.20.1, but one can note that this tooth is close in size to the alveolus of the canine of MHNBx 2020.20.1. Moreover, because this canine is referred to *Pseudocyon*, one can image that the taxon from Rimbez could also be closely related to the taxon from Sallespisse.

To conclude, the fossil from Sallespisse show striking similarities with *Cynelos*, *Amphicyon*, and *Pseudocyon* (i.e., presence of long diastemata between the premolars, unreduced premolars and m3, low p2 and p3) but differs in having an individualized distal accessory cusp. Therefore, we erect the new genus and species *Tartarocyon cazanavei* nov. gen. & sp. for MHNBx 2020.20.1.

Discussion

Relationships of *Tartarocyon cazanavei* nov. gen. & sp. Because of the lack of information on the morphology of the molars, it is hard to discuss the relationships of *Tartarocyon cazanavei* nov. gen. & sp. within the amphicyonids; the molars actually provide numerous features (see for instance the diagnoses in Kuss, 1965; Viranta, 1996; Heizmann & Kordikova, 2000; Peigné & Heizmann, 2003; Peigné et al., 2008; Morales et al., 2019; 2021). Viranta (1996), Peigné et al. (2008), Morales et al. (2019, 2021) tackled the relationships among European amphicyonids. However, the aims as well as the characters and taxa lists used for the phylogenetic analyses are different in each analysis. Phylogenetic analysis ~~for~~ *Tartarocyon cazanavei* nov. gen. & sp. did not provide statistically significant results, adding noise to the topology, because the dentition of MHNBx 2020.20.1 is only represented by the p2, p3, and p4, including autapomorphic characters.

Nevertheless, as already highlighted, *Tartarocyon cazanavei* nov. gen. & sp. clearly differs from the Haplocyoninae ~~that~~ possess tall and short premolars without diastema. *Tartarocyon cazanavei* nov. gen. & sp. does not belong ~~either~~ to the Thaumastocyoninae, this family having reduced premolars and postcarnassial molars (Table 3). The youngest thaumastocyonine species, from the middle and late Miocene, are ~~even~~ characterized by the absence of m3 and of ~~the premolars~~ p1, p2, and p3 (Table 3) (Morales et al., 2019; 2021; Morlo et al., 2020). A reduction of ~~the~~ premolar~~s~~ size is also observed in amphicyonines; this is a common trend in European amphicyonids. However, as ~~visible~~ on Table 3 the premolar~~s~~ and molar~~s~~ ratio show that the premolars and postcarnassial molars tend to reduce more among the thaumastocyonines than in the amphicyonines *Pseudocyon*, *Cynelos*, and *Amphicyon* (Table 3). The values estimated ~~in~~ *Tartarocyon* nov. gen. are similar to those of *Pseudocyon*, *Cynelos*, *Amphicyon* (Table 3). Moreover, diastemata are still present between the premolars in these amphicyonines (e.g., *Pseudocyon sansaniensis*) as in

Tartarocyon cazanavei nov. gen. & sp. Interestingly, the ratio between the p4 and the m1 is ~~bigger~~ in the thaumastocyonines (excep~~ted~~ for *Ysengrinia depereti*, Table 3) than in *Pseudocyon*, *Amphicyon*, and *Tartarocyon* nov. gen.

The case of *Magericyon* is puzzling. This amphicyonid differs from the contemporaneous thaumastocyonines by the presence of ~~a~~ m3 but also by the presence of a reduced p4 compared to the m1 (Table 3) (Peigné et al., 2008; Morales et al., 2019; Morlo et al., 2020). ~~At the oppo~~site, its shoulder anatomy is relatively primitive and generalized~~; it is~~ similar to that of ~~the~~ *Cynelos lemanensis*. Its shoulder is intermediate between that of the ursid-like amphicyonines (*Amphicyon major*) and that of the markedly cursorial North American amphicyonids (Temnocyoninae and Daphoeninae) (Siliceo et al., 2015). Thus, *Magericyon* may ~~represent~~ a hypercarnivorous representative of an amphicyonid group that could include *Amphicyon*, *Pseudocyon*, *Cynelos*, and *Tartarocyon* nov. gen.

It appears that *Tartarocyon cazanavei* nov. gen. & sp. is morphologically similar to *Cynelos*, *Amphicyon*, and *Pseudocyon* in having premolars and postcarnassial ~~premolars~~ only slightly reduced in length. However, one can note that the mesial cusp area and the distal shelf are more reduced in *Tartarocyon cazanavei* nov. gen. & sp. compared to *Cynelos*. *Tartarocyon cazanavei* nov. gen. & sp. also differs from *Cynelos* by reduced p2, p3, and p4 (Table 3). This feature is shared with *Pseudocyon* and *Amphicyon*. Despite these similarities, *Tartarocyon cazanavei* nov. gen. & sp. differs from *Pseudocyon* and *Amphicyon* in the large and individualised distal cusp that is positioned distally on the p4. As a consequence, we think that *Tartarocyon cazanavei* nov. gen. & sp. derived from a *Cynelos*-type amphicyonine.

Cynelos, *Amphicyon*, and *Pseudocyon* are amphicyonines known from the early Miocene (Ginsburg, 1999). *Tartarocyon* nov. gen. seems to be more derived than *Cynelos* but more basal than *Amphicyon*, and *Pseudocyon*. A close relationship between *Tartarocyon* nov. gen., *Pseudocyon*, and *Amphicyon* can be considered, *Tartarocyon cazanavei* nov. gen. & sp. ~~following~~ a distinct evolutionary path from the other amphicyonids due to geographic~~al~~ isolation as shown by its unusual p4 morphology.

Ecology of *Tartarocyon cazanavei* nov. gen. & sp. The under-estimated body mass (based on the alveoli of the m1 of MHNBx 2020.20.1) is 194.91 kg. *Tartarocyon cazanavei* nov. gen. & sp. is distinctly larger than the *Pseudocyon* ~~species: the species of this genus~~ range from 118 to 130 kg (Viranta, 1996, Table 4). In being close to 200 kg, the estimated body mass of *Tartarocyon cazanavei* nov. gen. & sp. recalls those of *Amphicyon major* (212 kg, male), *A. pannonicus* (198 kg), *Magericyon castellanus* (198 kg), and *Agnotherium grivense* (190 kg) (Viranta, 1996, Table 4). ~~The amphicyonids~~ that are ~~well~~ larger than *Tartarocyon cazanavei* nov. gen. & sp. are few: *Amphicyon giganteus* (317 kg, male), *A. gutmanni* (246 kg), *A. eppelsheimensis* (225 kg), *Magericyon castellanus* (246 kg), and *Amphicyonopsis serus* (270 kg) (Viranta, 1996, Table 4). In this regard, the amphicyonid from Sallespisse is one of the largest amphicyonids ever recorded in Europe.

Viranta (1996) recognized four categories of amphicyonids based on feeding ecolog~~ies~~: omnivores, mesocarnivores, bone-crusher mesocarnivores, and hypercarnivores. The presence of the four premolars as well as the presence of large m2 and m3 (~~regarding~~ the m1) indicate that *Tartarocyon cazanavei* nov. gen. & sp. was not a hypercarnivore. Indeed, hypercarnivorous amphicyonid such as *Magericyon castellanus*, *Pseudocyon caucasicus*, *Thaumastocyon* spp. and *Agnotherium* spp. are characterized by ~~the~~ reduction of the premolars and of the m1 and m2 together with the development of slicing carnassials (i.e., P4 and m1) (Viranta, 1996). The ~~heavy~~ mass of *Tartarocyon cazanavei* nov. gen. & sp. ~~disagrees~~ with those of the omnivorous amphicyonids *Pseudarctos bavaricus* and *Ictiocyon socialis*, which were the smallest amphicyonids in the Miocene of Europe (Viranta, 1996). Moreover *P. bavaricus* and *I. socialis* are characterized by high-crowned teeth with blunt cusps and closely appressed premolars; these two features distinguish these small amphicyonids from *Tartarocyon cazanavei* nov. gen. & sp. Viranta (1996) regarded *Cynelos* spp. as a typical mesocarnivore. This amphicyonid is notably characterized by a primitive dentition (e.g., canine not especially robust, a premolar row quite crowded). *Tartarocyon cazanavei* nov. gen. & sp. clearly differs in having large diastemata between the premolars as well as a robust canine. Viranta (1996) considered *Amphicyon major* and *A. giganteus* as bone-crushing mesocarnivores. As noted by Viranta (1996, p.46), “There are no modern analogues for the dentitions of these species. They have well-developed molars and a sparsely distributed, complete set of premolars.” These features are also found in *Tartarocyon cazanavei* nov. gen. & sp. Moreover, the body mass of *Tartarocyon cazanavei* nov. gen. & sp. and the *Amphicyon* species are close (see above). Therefore, *Tartarocyon cazanavei* nov. gen. & sp. can be reconstructed as a predator with bone-crushing habits (Figure 4).

The evolution of ~~the~~ European amphicyonids during the Miocene. Viranta (1996) ~~realized~~ a comprehensive study on the systematics, ecology, and evolution of the European amphicyonids from the Miocene. The present discussion represents an update of the remarkable work of Viranta (1996) and underlines several periods to focus on.

Viranta (1996) did not consider the Haplocyoninae in her study. The inclusion of the Haplocyoninae, which were only present in Europe until MN3 ~~during the Miocene~~, ~~allows to find~~ a similar specific diversity during the entire lower Miocene with 9 to 10 contemporaneous Amphicyonidae species in Europe (Table 5). The diversity ~~visible~~ in MN4 and MN5 is thus due to a diversification of the remaining amphicyonids (Amphicyoninae and Thaumastocyoninae) with 10 species as already evidenced by Viranta (1996). Moreover, contrary to Viranta (1996), the diversity of the Amphicyoninae and Thaumastocyoninae is already ~~visible~~ in MN3 (9 species; Figure 5; Table 5). The amphicyonids were indeed taxonomically and ecologically diverse in MN3 (Figure 5; Table 5), as illustrated ~~notably~~ by the presence of the small ~~and~~ omnivore *Ictiocyon*, the mesocarnivore *Cynelos*, the hypercanivore *Peignecyon*, and the large bone-crusher mesocarnivores *Amphicyon* and *Janvierocyon*. The diversification of the Amphicyoninae and Thaumastocyoninae must be questioned because it ~~has~~ concomitant with the disappearance of the Haplocyoninae (the last European haplocyonines are from MN3; Peigné & Heizmann, 2003). The MN3 biozone hosts some of the most important climatic and faunal events including the Proboscidean Datum Events and Asiatic dispersals (e.g., Tassy, 1989; Van der Made, 1999). From arid environments throughout Western Europe during the Agenian, a latitudinal gradient ~~set~~ with wet and closed environments in France and Germany during the Orleanian (Costeur, 2005; Costeur & Legendre, 2008). Due to these environmental changes and the competition ~~of~~ the newcomers, nearly 60% of the ungulate fauna ~~have been~~ replaced during that time (Scherler et al., 2013). The ~~restructuration~~ of the community and of the environment may have been fatal to the Haplocyoninae ~~and, at the opposite,~~ favored the Amphicyoninae and Thaumastocyoninae.

The amphicyonids remained diversified during MN5 (8 species), MN6 (9 species), MN7/8 (6 species), and MN9 (6 species) (Table 5). The bone-crushing mesocarnivorous amphicyonids are taxonomically well-diversified in MN6 (4 species) and MN7/8 (3 species including *Tartarocyon* nov. gen.). ~~At the opposite, the~~ mesocarnivorous amphicyonids are unknown in Europe after MN6. Additionally, no amphicyonid between 50 kg and 100 kg ~~are~~ known after MN5. The disappearance of the mesocarnivorous amphicyonids and of amphicyonids of 50-100 kg is related to the disappearance of *Cynelos* from Europe (Figure 5; Table 5). One can note the reappearance of the haplocyonines in MN6 (occurrence of *Gobicyon serbiae*; Ginsburg et al., 1999; Jiangzuo et al., 2018; 2021). This taxon probably dispersed from Asia into Europe because this genus appeared earlier in Asia (ca. 17 Ma; Jiangzuo et al., 2021) than in Europe. Interestingly, its ~~weight~~ is close to that of the amphicyonids known in MN6 and not to those of the *Cynelos* species recorded in MN5~~; therefore,~~ it did not probably fill the same ecological niche. Nevertheless, *Gobicyon* was present in Europe only for a short period~~; it~~ is only known ~~in~~ one locality (Pavlovic & Thenius, 1959; Ginsburg, 1999). A small reorganization of the amphicyonid fauna thus occurred between MN5 and MN6. This biotic event might be related to the Middle Miocene Global Cooling Event or the middle Miocene Disruption, which results for instance in an increase ~~of~~ aridity in Spain (Menéndez et al., 2017).

From MN6 to MN11, the largest amphicyonids were all specialized as either hypercarnivorous or bone-crushing mesocarnivorous predators. However, the taxonomic diversity of the bone-crushing ~~mesocarnivorous~~ starts to decrease after MN5, as exemplified by the presence of only one taxon during MN9 (Figure 5; Table 5). ~~At the opposite, the~~ hypercarnivorous amphicyonids were still taxonomically diverse in MN9 with 4 species. Viranta (1996) estimated that the decline of the Amphicyonidae started ~~at~~ MN7/8 and considered that MN9 marked the probable disappearance of ~~the~~ amphicyonids in Western Europe. However, the recent descriptions of ~~amphicyonid as~~ *Magerocyon anceps* Peigné et al., 2008, *Ammitocyon kainos* Morales et al., 2021 in MN9 and MN10 Spanish localities and *Tartarocyon* nov. gen. greatly changed our ~~vision~~ of the latest amphicyonid evolution (Figure 5; Table 5). Indeed, the amphicyonids, notably the Thaumastocyonines, were still diversified in MN7/8 (6 species) and MN9 (6 species) although less than in MN6.

The amphicyonid~~s~~ community changed considerably from MN9 to MN11 (Figure 5). The omnivorous amphicyonid *Pseudarctos*, which was also the smallest and only omnivorous amphicyonid at that time, disappeared from Europe (last record in MN9) (Figure 5; Table 5). As a consequence, the European amphicyonids are only represented by large to very large forms ~~weighting~~ at least 100 kg during MN10 and even 200 kg during MN11 (Figure 5). This modification of the amphicyonid fauna also resulted in the presence of only specialized amphicyonids: the latter were either hypercarnivores or bone-crushing mesocarnivores. Moreover, the number of hypercarnivorous amphicyonid species known during MN10 and MN11 distinctly decrease in comparison to MN9 (Figure 5; Table 5). This modification of the amphicyonid fauna between MN 9 and MN10 could be related to the Vallesian Crisis. This crisis ~~coinciding~~ with the early/late Vallesian boundary (at 9.7 Ma) (Figure 5). First ~~time~~ recognized in Spain (Agustí and Moyà-Solà, 1990; Agustí, Cabrera & Garcès, 2013), the Vallesian Crisis is now described as the major extinction event in the history of the Western European mammalian faunas (Jaeger and Hartenberger, 1989) (but see Casanovas-Vilar et al., 2014 for a critical analysis). The Vallesian crisis was a time of major environmental change that led to a substantial turnover of mammals in Western Europe (Fortelius et al. 1996; Agustí, Cabrera & Garcès, 2013). The environmental change, notably characterized by an ~~extension~~ of open habitats and retraction of forests, led to a decrease in the diversity of browsers. The opening of the environments led to the disappearance of ~~the~~ small size predators.

Because Viranta (1996) extensively discussed the possible explanations ~~of~~ the decline of the amphicyonids (e.g., extinction of potential prey~~s~~, competition), we will not develop these discussions herein. Agustí, Cabrera & Garcès (2013) noted that the amphicyonids ~~have been~~ affected by this crisis in that only some poorly known amphicyonids persisted in the late Vallesian and early Turolian in some parts of Central Europe (*Amphicyon gutmanni* from Germany and Austria, and *Amphicyon pannonicus* from Hungary). Moreover, these amphicyonids were ~~only~~ very large forms that display bone-crushing mesocarnivorous dentition (Viranta, 1996; Figure 5). However, the recent description of the hypercarnivorous amphicyonids *Ammitocyon* in a Spanish locality close to MN10 (Morales et al., 2021) and *Magericyon* from Spanish localities close to

MN9 and MN10 (Peigné et al., 2008) indicate that amphicyonids were still present in Southwestern Europe at the end of the Vallesian. Therefore, despite a decrease in number of species, amphicyonids remained present in the entire Europe and display ecological diversity during MN10. As noted by Viranta (1996), only the largest amphicyonids were still present in Europe at the end of the Vallesian and beginning of the Turolian. No taxon ~~that weight~~ below 150 kg ~~are indeed~~ known after MN9. As a consequence, it appears that the Vallesian crisis was above all critical for the small and omnivorous *Pseudarctos* due to the opening of the environment and the ~~restructuration~~ of the mammalian communities. Regarding the other amphicyonids (i.e., bone-crushing mesocarnivorous and hypercarnivorous), the Vallesian crisis seem to have had profound effect (decrease ~~of~~ diversity) but was not fatal. However, because the decrease in taxonomic diversity is notable, the Vallesian crisis was not insignificant for the remaining hypercarnivorous amphicyonids.

Conclusions

Tartarocyon cazanavei nov. gen. & sp. is a new large amphicyonid ~~discovered in~~ the French locality Sallespisse (12.8-12.0 Ma, France). It ~~clearly~~ morphologically ~~differs~~ from the Thaumastocyoninae and Haplocyoninae. It ~~actually~~ seems that this amphicyonid is a part of the radiation of a group of amphicyonids ~~that corresponds to~~ the bone-crushing mesocarnivore~~s~~ genera *Pseudocyon*, *Cynelos*, *Amphicyon*, and possibly *Magericyon*.

Tartarocyon nov. gen. moreover illustrates the ~~period of~~ diversity of the amphicyonids in Europe: during MN7/8 amphicyonids were diversified in both the body mass and ~~the~~ diet. However, the ecological and diversity ~~erosion~~ of the Amphicyonidae is polyphased. A new comprehensive analysis of the taxonomic and ecologic diversity of the amphicyonids is necessary to better understand the impact of biotic and abiotic factors on the evolution of these predators.

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References

Agustí J., Moyà -Solà S., 1990. Mammal extinctions in the Vallesian (Upper Miocene). In Kauffman E.G., Walliser O.H. (Eds.), *Extinction Events in Earth History*, Proceedings of the Project 216, Global Biological Events in Earth. Lecture Notes in Earth Sciences 30, pp. 425–432.

Agustí J., Cabrera L., Garcés M., 2013. The Vallesian Mammal Turnover: A Late Miocene record of decoupled land-ocean evolution. *Geobios* 46, 151–157.

Bowdich T.E., 1821. *An Analysis of the Natural Classifications of Mammalia, for the Use of Students and Travellers*. J. Smith, Paris, 115 pp.

Benoist E.A. 1884. Observations sur la liste des fossiles recueillis dans les faluns de la métairie du Paren près d'Orthez. *Procès-Verbaux de la Société Linnéenne de Bordeaux*, *année 1884*, 38, 4e série, 8, 37–38.

de Bonis L., 1966. Sur l'évolution du genre *Haplocyon* Schlosser (Carnivora). *Bulletin de la Société Géologique de France* 8(1),114–117.

de Bonis L., 1978. La poche a phosphate de Ste-Néboule (Lot) et sa faune de vertébrés du Ludien Supérieur. 12. - Fissipèdes (Carnivores). *Palaéovertébrata* 8(2-4), 301–311.

Cahuzac B., Janin M.-C., Steurbaut E., 1995. Biostratigraphie de l’Oligo-Miocène du Bassin d’Aquitaine fondée sur les nannofossiles calcaires. Implications paléogéographiques. *Géologie de la France* 2, 57–82.

Cahuzac B., Janssen A.W., 2010. Eocene to Miocene pteropods (Gastropoda, Euthecosomata) from the Aquitaine Basin, southwest France. *Scripta Geologica* 141, 1–193.

Cahuzac B., Alvinerie J., Lauriat-Rage A., Montenat C., Pujol C., 1992. Paleogeographic maps of the Northeastern Atlantic Neogene and relation with relation with the Mediterranean sea. *Paleontologia i evolucio* 24-25, 279–293.

Cahuzac B., Poignant A., 1996. Foraminifères benthiques et microproblematica du Serravallien d'Aquitaine (Sud-Ouest de la France). *Géologie de la France* 3, 35–55.

Casanovas-Vilar I., van den Hoek Ostende L.W., Furió M., Madern P.A., 2014. The range and extent of the Vallesian Crisis (Late Miocene): new prospects based on the micromammal record from the Vallès-Penedès basin (Catalonia, Spain). *Journal of Iberian Geology* 40(1), 29–48.

Chaix C., Cahuzac B., 2005. Les faunes de Scléractiniaires dans les faluns du Miocène moyen d'Atlantique-Est (bassins de la Loire et d'Aquitaine) : paléobiogéographie et évolution climatique. *Annales de Paléontologie* 91(numéro spécial « faluns ») 33–72.

Cossmann M., Peyrot A., 1909–1924. Conchologie Néogénique de l'Aquitaine. *Actes de la Société Linnéenne de Bordeaux*, 1909, 63(2), 72–144; 63(3), 145–232; 63(4), 233–293; 1910, 64(4), 235–288; 64(5), 289–400; 1911, 64(6), 401–445; 65(2), 51–98; 1912, 65(3), 99–178; 65(4), 179–333; 66(2), 121–168; 66(3), 169–232; 1913, 66(4), 233–324; 1914, 68(1), 5–96; 68(2), 97–210; 1915, 68(4), 361–435; 1917, 69(3), 157–284; 69(4), 285–365; 1918, 70(1), 5–100; 70(2), 101–180; 1919, 70(3), 181–356; 70(4), 357–491; 1921 (publ. 1922), 73, 5–321; 1923, 74(3), 257–342; 1924, 75(2), 71–144; 75(3), 193–318.

Cossmann M., Peyrot A. 1909–1914. Conchologie Néogénique de l'Aquitaine. Edition 4 "Extrait des Actes de la Société Linnéenne de Bordeaux", ouvrage couronné par l'*Académie des Sciences, Arts et Belles–Lettres de Bordeaux*, 1909, 1(1), 1–220;

1911, 1(2), 221–428; 1912, 1(3), 429–718; 1913, 2(1), 1–204; 1914, 2(2), 205–410; 1914, supplément, 411–496.

Cossmann M., Peyrot A. 1917–1924. Conchologie Néogénique de l'Aquitaine. Edition 8 "Extrait des Actes de la Société Linnéenne de Bordeaux", ouvrage couronné par l'*Académie des Sciences, Arts et Belles–Lettres de Bordeaux*, 1917, 3(1), 1–384; 1919, 3(2), 385–695; 1922, 4(1), 1–322; 1924, 4(2), 323–610.

Costeur L., 2005. *Les communautés de mammifères d'Europe de l'Oligocène supérieur au Pliocène inférieur : paléobiogéographie et palébiodiversité des ongulés, paléoenvironnements et Paléoécologie évolutive*. Unpublished PhD thesis of the University of Lyon, 124 pp.

Costeur L., Legendre S. 2008. Mammalian communities document a latitudinal environmental gradient during the Miocene Climatic Optimum in Western Europe. *Palaios* 23, 280–288.

Daguin F., 1948. *L'Aquitaine Occidentale*. Hermann & Cie, Paris, 232 pp.

Degrange-Touzin A., 1895. Étude préliminaire des coquilles fossiles des faluns des environs d'Orthez et de Salies de Béarn (Basses-Pyrénées). *Actes de la Société Linnéenne de Bordeaux*, *année 1894*, 47(7). 333–457, pls. 8–9.

Delbos J., 1848. Notice sur les fahluns du sud-ouest de la France. *Bulletin de la Société Géologique de France*, 2e serie, 5, 417–444.

Ducasse O., Cahuzac B., 1997. Les ostracodes indicateurs des paléoenvironnements au Miocène moyen (Serravallien) en Aquitaine (Sud-Ouest de la France). *Revue de Micropaléontologie* 40, 141–166.

Dufour L., 1836. Botanique. III. Lettre à M. le docteur Grateloup sur des excursions au Pic d'Anie et au Pic Amoulat dans les Pyrénées. *Actes de la Société Linnéenne de Bordeaux*, *année 1836*, 8(45), 53–102.

Duranthon F., Cahuzac B., 1997. Éléments de corrélation entre échelles marines et continentales : les données du Bassin d'Aquitaine au Miocène. *Actes du Congrès Biochrom'97*, Montpellier, 21, 591–608.

Flynn J.J., Finarelli J.A., Spaulding M., 2010. Phylogeny of the Carnivora and Carnivoramorpha, and the use of the fossil record to enhance understanding of evolutionary transformations. In Goswami A., Friscia A. (Eds.), *Carnivoran evolution: new views on phylogeny, form, and function*. Cambridge University Press, Cambridge, pp. 25–63.

Fortelius M., Werdelin L., Andrews P., Bernor R., Gentry A., Humphrey L., Mittman H., Viranta S., 1996. Provinciality, diversity, turnover and paleoecology in land mammal faunas of the later Miocene of western Eurasia. In Bernor R.L., Fahlbusch V., Mittmann H.-V. (Eds.), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York, pp. 414–448.

Ginsburg L. ,1967. Une faune de Mammifères dans I'Helvétien marin de Sos (Lot-et-Garonne) et de Rimbez (Landes). *Société Géologique de France* 7(IX), 5–18.

Ginsburg L., 1999. Order Carnivora, in Rössner G. E. & Heissig K. (eds), *The Miocene Land Mammals of Europe*. Verlag Friedrich Pfeil, Munich, 109–148.

Ginsburg L., 1992. Les genres *Pseudarctos* et *Ictiocyon*, Amphicyonidae (Carnivora, Mammalia) du Miocène européen. *Bulletin du Muséum national d'histoire naturelle.*

Section C, Sciences de la terre, paléontologie, géologie, minéralogie 14(3-4), 301–317.

Grateloup J.-P.S., 1835. Tableau (suite du) des Coquilles fossiles qu'on rencontre dans les terrains tertiaires grossiers (faluns) du bassin géologique de l'Adour (Landes). 12e article. *Actes de la Société Linnéenne de Bordeaux 1835*, 7(39), 101–114.

Grateloup, J.-P. S., 1845-1847. *Conchyliologie fossile des terrains tertiaires du Bassin de l'Adour (environs de Dax).* 1, Univalves. Atlas. Lafargue, Bordeaux. 1845, 45 plates (1, 3, 5-10, 12-48). 1847, 3 plates (2, 4, 11).

Heizmann E.P.J., Kordikova E.G., 2000. Zur systematischen Stellung von "*Amphicyon*" *intermedius* H. v. Meyer, 1849 (Carnivora, Amphicyonidae). *Carolinea* 58, 69–82, 6 figs.

Hilgen F.J., Lourens L.J., van Dam J.A., 2012. The Neogene Period. In: Gradstein F.M., Ogg J.G., Schmitz M., Ogg G. (eds.), *The Geologic Time Scale 2012*, pp. 923–978.

Hunt R.M. Jr., 2003. Intercontinental Migration of Large Mammalian Carnivores: Earliest Occurrence of the Old World Beardog *Amphicyon* (Carnivora, Amphicyonidae) in North America. *Papers in the Earth and Atmospheric Sciences* 545, 77–115.

Jaeger J.J., Hartenberger J.L., 1989. Diversification and extinction patterns among Neogene perimediterranean mammals. *Philosophical Transactions of the Royal Society of London B* 325, 401–420.

Jiangzuo Q.G., Li C.X., Zhang X.X., Wang S.Q., Ye J., Li Y., 2018. Diversity of Amphicyonidae (Carnivora, Mammalia) in the Middle Miocene Halamagai formation in Ulungur River area, Xinjiang, Northwestern China. *Historical Biology* 32(2), 187–202.

Jiangzuo Q., Wang S., Li C., Sun D., Zhang X., 2021. New material of *Gobicyon* (Carnivora, Amphicyonidae, Haplocyoninae) from northern China and a review of Aktaucyonini evolution. *Papers in Palaeontology* 7, 307–327.

Karnay G. 1997. *Notice explicative de la feuille Arthez-de-Béarn à 1/50 000*. Editions du BRGM, Orléans, 48 pp.

Kretzoi M., 1943. *Kochictis centennii* n. g. n. sp., ein altertuümlicher Creodonte aus dem Oberoligozän Siebenbürgens. *Földtani Közlöny* 73, 190–195.

Kretzoi, M., 1985: New Amphicyonid from the Early Pannonian of Pees, South Hungary. *Annales Historico Naturales Musei Nationales Hungarici* 77, 65–68.

Kuss S.E., 1965. Revision der europäischen Amphicyonidae (Canidae, Carnivora, Mamm.) ausschliesslich der voroberstampischen Formen. *Sitzungsberichte der Heidelberger Akademie der Wissenschaften. Mathematisch-naturwissenschafthiche Klasse 1*, 1–168.

Lesport J.-F., Cluzaud A., Verhecken A., 2015. The Cenozoic Plesiotritoninae (Mollusca: Neogastropoda: Cancellarioidea: Cancellariidae) of the Aquitaine Basin, southwestern France. *Palaeontos* 27, 1–64, pls 1–13.

Van der Made J., 1999. Intercontinental relationship Europe-Africa. In Rössner G.E., Heissig K. (Eds), *The Miocene land mammals of Europe*. Verlag Dr. Friedrich Pfeil: München, pp. 457–472.

Magné J., Gourinard Y., Wallez, M.J., 1987. Comparaison des étages du Miocène inférieur définis par stratotypes ou par zones paléontologiques. *Strata* l(3), 95–107.

Menéndez I., Gómez Cano A.R., García Yelo B.A., Domingo L., Domingo M.S., Cantalapiedra J.L., Balanco F., Hernández Fernández M., 2017. Body-size structure of Central Iberian mammal fauna reveals semidesertic conditions during the middle Miocene Global Cooling Event. PLoS ONE 13(8), e0202612. DOI 10.1371/journal.pone.0186762

Mennecart B., Tissier J., Lesport J.-F., Heitz A., Solé F., accepted. 3D models related to the publication: A new gigantic carnivore (Carnivora, Amphicyonidae) from the late middle Miocene of France*.* MorphoMuseuM.

Morales J., Fejfar O., Heizmann E., Wagner J., Valenciano A., Abella J., 2019. A new Thaumastocyoninae (Amphicyonidae, Carnivora) from the early Miocene of Tuchořice, the Czech Republic. *Fossil Imprint* 75(3–4), 397–411.

Morales J., Abella J., Sanisidro O., Valenciano A., 2021. *Ammitocyon kainos* gen. et sp. nov., a chimerical amphicyonid (Mammalia, Carnivora) from the late Miocene carnivore traps of Cerro de los Batallones (Madrid, Spain). *Journal of Systematic Palaeontology* 19(5), 393–415.

Morlo M., Bastl K., Habersetzer J., Engel T., Lischewsky B., Lutz H., von Berg A., Rabenstein R., Nagel D., 2020. The apex of amphicyonid hypercarnivory: solving the riddle of *Agnotherium antiquum* Kaup, 1833 (Mammalia, Carnivora). *Journal of Vertebrate Paleontology* 39(5). DOI: 10.1080/02724634.2019.1705848.

Nolf D., Steurbaut E., 1979. Les otolithes de téléostéens des faluns sallomaciens d’Orthez et de Sallespisse (Miocène Moyen d'Aquitaine méridionale, France). *Palaeontographica* A 164, 1–23.

Orbigny A. D', 1852. *Prodrome de Paléontologie stratigraphique universelle des animaux mollusques & rayonnés*. Masson, Paris, 3, 196 pp.

Pavlovic M, Thenius E. 1959. *Gobicyon macrognathus* (Canidae, Mammalia) aus dem Miozan Jugoslawiens. *Anzeiger Österreichische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse* 11, 214–222.

Peigné S., Heizmann E.P.J., 2003. The Amphicyonidae (Mammalia: Carnivora) from the Early Miocene locality of Ulm-Westtangente, Baden-Württemberg, Germany: systematics and ecomorphology. *Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie)* 343, 1–133.

Peigné S., Salesa M.J., Antón M., Morales J., 2008. A new amphicyonine (Carnivora: Amphicyonidae) from the upper Miocene of Batallones-1, Madrid, Spain. *Palaeontology* 51(4), 943–965.

Peres J.M., Picard J., 1964. Nouveau manuel de bionomie benthique de la mer Méditerranée. *Recueil des travaux de la station marine d'Endoume* 31(17), 5–137.

Peyrot A. 1925–1935. Conchologie Néogénique de l'Aquitaine. *Actes de la Société Linnéenne de Bordeaux*, 1925, 77(2), 51–194; 1927, 78, 199–256; 1928, 79, 5–264; 1931, 82(2), 73–126; 83, 5–116; 1932,84(1), 5–128; 1933, 84(2), 129–288; 1933, 85(1), 5–71; 1935, 86(2), 257–352.

Peyrot A. 1927–1932. Conchologie Néogénique de l' Aquitaine. Edition 8 "Extrait des Actes de la Société Linnéenne de Bordeaux", ouvrage couronné par l'*Académie des Sciences, Arts et Belles-Lettres de Bordeaux*, 1927, 5(1), 1–206; 1928, 5(2), 207–465; 1931, 6(1), 1–294; 1932, 6(2), 295–541.

Poignant A. 1967. *L'Oligo-Miocène d'Aquitaine méridionale*. Unpublished PhD thesis of the University of Paris, 385 pp.

Raulin V. 1852. Note relative aux terrains tertiaires de l'Aquitaine. *Bulletin de la Société Géologique de France*, 2e série, 9, 406–422.

Rögl F. 1999. Circum-Mediterranean Miocene Paleogeography. In Rössner G.E., Heissig K. (Eds), *The Miocene Land Mammals of Europe*. Verlag Dr Friedrich Pfeil., München, 39–48.

Scherler L., Mennecart B., Hiard F., Becker D., 2013. Evolution of terrestrial hoofed-mammals during the Oligocene-Miocene transition in Europe. *Swiss Journal of Geosciences* 106, 349–369.

Siliceo G., Salesa M.J., Antón M., Pastor J.F., Morales J., 2015. Comparative Anatomy of the Shoulder Region in the Late Miocene Amphicyonid *Magericyon anceps* (Carnivora): Functional and Paleoecological Inferences. *Journal of Mammalian Evolution* 22, 243–258.

Solé F., Dubied M., Le Verger K., Mennecart B., 2018. Niche partitioning of the European carnivorous mammals during the Paleogene. *Palaios* 33(11), 514–523.

Tassy P. 1989. The ''Proboscidean Datum Event'': How many Proboscideans and how many events? In Lindsay E.H., Fahlbusch V., Mein P. (Eds), *European Neogene mammal chronology: Proceedings of a NATO advanced research workshop*. New York, Plenum Press, pp. 237–252.

Trouessart E.L., 1885. Conspectus systematicus et geographicus marnmalium tam viventium quam fossil. -Catalogue des Mammiferes vivants et fossilies. *Bulletin de la Société d'Études scientifiques d'Angers* 15, 4.

Van Valkenburgh B.V., 1990. Skeletal and dental predictors of body mass in carnivores. In Damuth J., MacFadden B.J. (Eds), *Body Size in Mammalian Paleobiology.*

Estimation and Biological Implications. Cambridge University Press, Cambridge, England, 181–206.

Viranta S. 1996. European Miocene Amphicyonidae –taxonomy, systematics and ecology. *Acta Zoologica Fenica* 204, 1–61.

Wang X.M., Wang H.J., Jiangzuo Q.G., 2016. New record of a haplocyonine amphicyonid in early Miocene of Nei Mongol fills a long-suspected geographic hiatus. *Vertebrata PalAsiatica* 54(1), 21−35.

Wyss A.R., Flynn J.J., 1993. A phylogenetic analysis and definition of the Carnivora. In Szalay F.S., Novacek M.J., McKenna M.C. (Eds), *Mammal phylogeny*. Springer-Verlag, New York, pp.32–52.

Figures

Figure 1. Geographic~~al~~ position of the fossiliferous locality of Sallespisse (Close-up ~~on~~ ~~the~~ Southwest France~~,~~ redrawn from Cahuzac, Janin & Steurbaut, 1995). The light grey area represents the maximum ~~of extension~~ of the Serravallian Sea.

Figure 2. Sedimentological succession of the Sallespisse outcrop with the location ~~where~~ the specimen MHNBx 2020.20.1.

Figure 3. Holotype (MHNBx 2020.20.1) of *Tartarocyon cazanavei* nov. gen. & sp. from Sallespisse (MN7/8, Southwest France), in occlusal, lingua, and labial views. Scale bar~~e~~ is 5 cm.

Figure 4. ~~Reconstitution~~ of *Tartarocyon cazanavei* nov. gen. & sp. hunting small ruminant moschids along the Serravallian sea. Drawing ~~from~~ Denny Navarra.

Figure 5. Body mass and diet distribution of the amphicyonid during the Miocene biozones. The horizontal dashed lines refer~~red~~ to the biotic events discussed in the text.

Tables

Table 1. Measurements of the teeth of the holotype (MHNBx 2020.20.1) of *Tartarocyon cazanavei* nov. gen. & sp. from Sallespisse (MN7/8). *: based on alveoli.

Table 2. Several measurements of the teeth and mandible of the holotype (MHNBx 2020.20.1) of *Tartarocyon cazanavei* nov. gen. & sp. from Sallespisse (MN7/8). MD: Mandible height.

Table 3. Ratios estimated based on premolars and molars for several amphicyonines and thaumastocyonines known ~~in~~ the Miocene of Europe. Grey font: Thaumastocyonina; white font: Amphicyoninae.

Table 4. List of ~~the~~ Amphicyonidae known ~~in~~ the Miocene of Europe with indication of their stratigraphic distribution, body mass, and diet. Diet estimated based on similarities with the ones proposed by Viranta (1996). The Haplocyoninae are here considered as hypercarnivores because they display a hypercarnivorous dentition (see Wang et al., 2016). *: bodymass and diet based on Viranta (1996).

Table 5. Number of taxa by MN level~~s~~ in totality and based on diet after Table 4.

Figure 1

Geographic~~al~~ position of the fossiliferous locality of Sallespisse (Close-up on the Southwest France, redrawn from Cahuzac, Janin & Steurbaut, 1995).

The light grey area represents the maximum ~~of extension~~ of the Serravallian Sea.

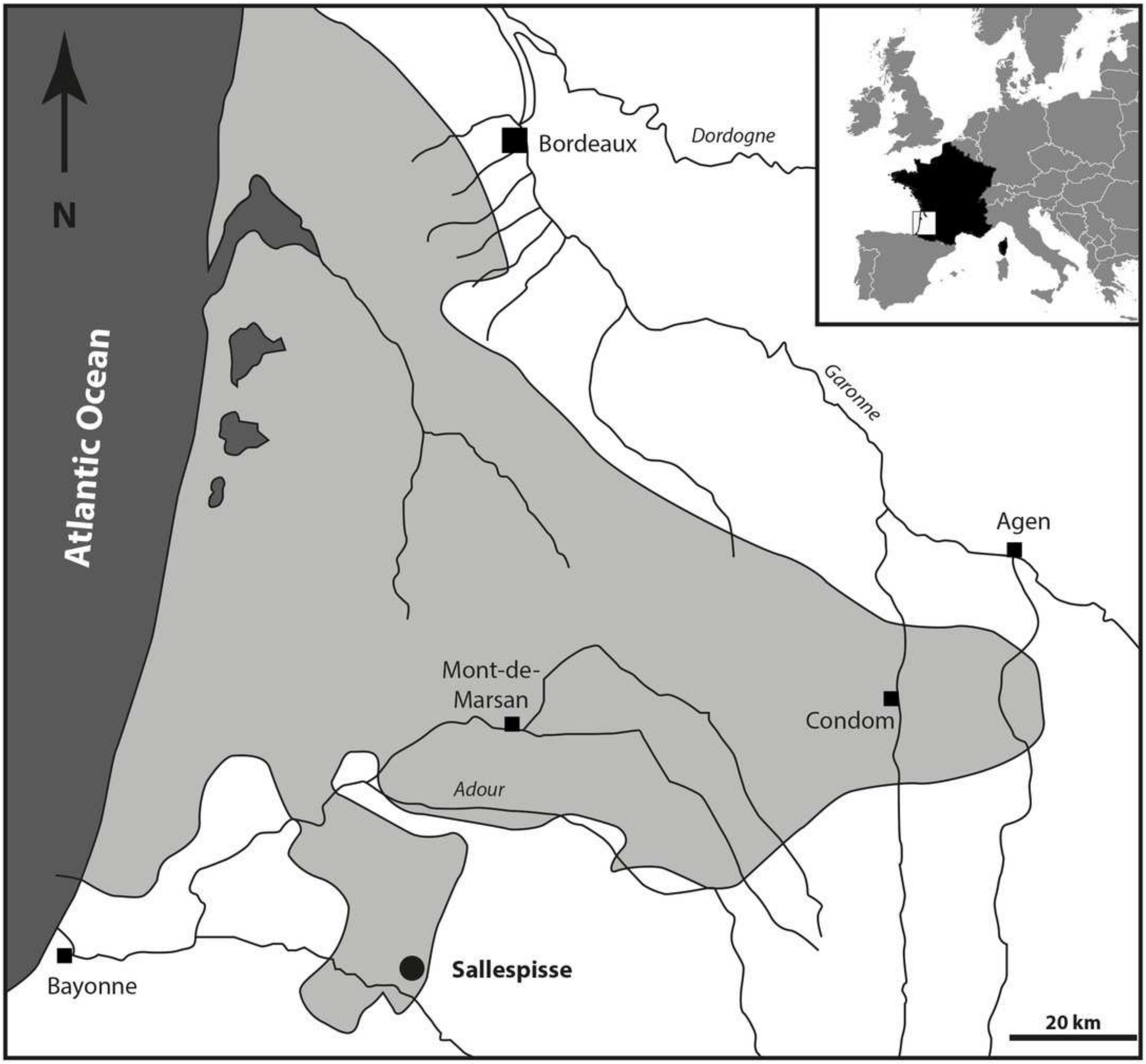

Figure 2

Sedimentological succession of the Sallespisse outcrop with the location ~~where~~ the specimen MHNBx 2020.20.1.

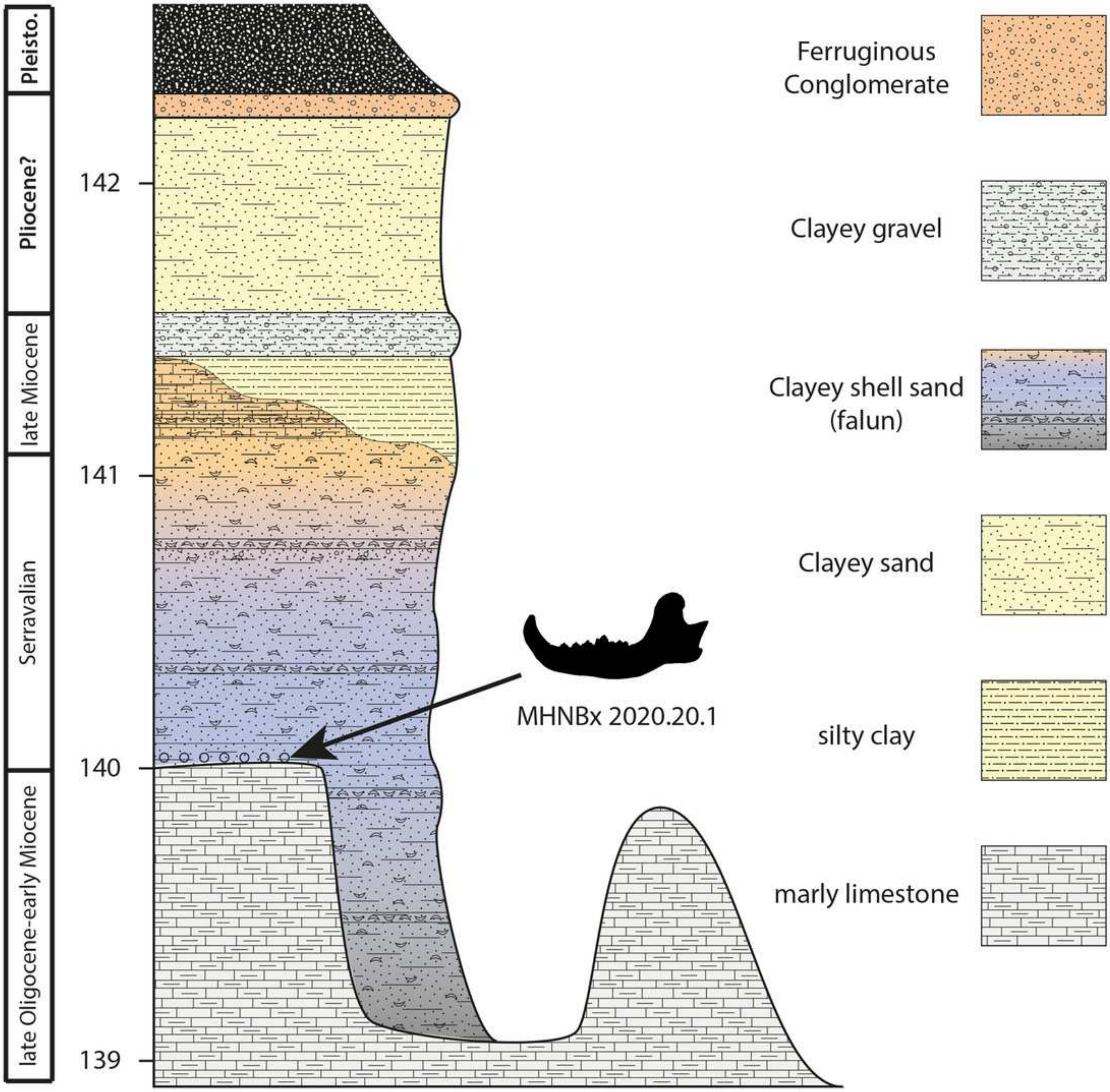

Figure 3

Holotype (MHNBx 2020.20.1) of *Tartarocyon cazanavei* nov. gen. & sp. from Sallespisse (MN7/8, Southwest France), in occlusal, lingua, and labial views. Scale bare is 5 cm.


5 cm

Figure 4

~~Reconstitution~~ of *Tartarocyon cazanavei* nov. gen. & sp. hunting small ruminant moschids along the Serravallian sea.

Drawing ~~from~~ Denny Navarra.

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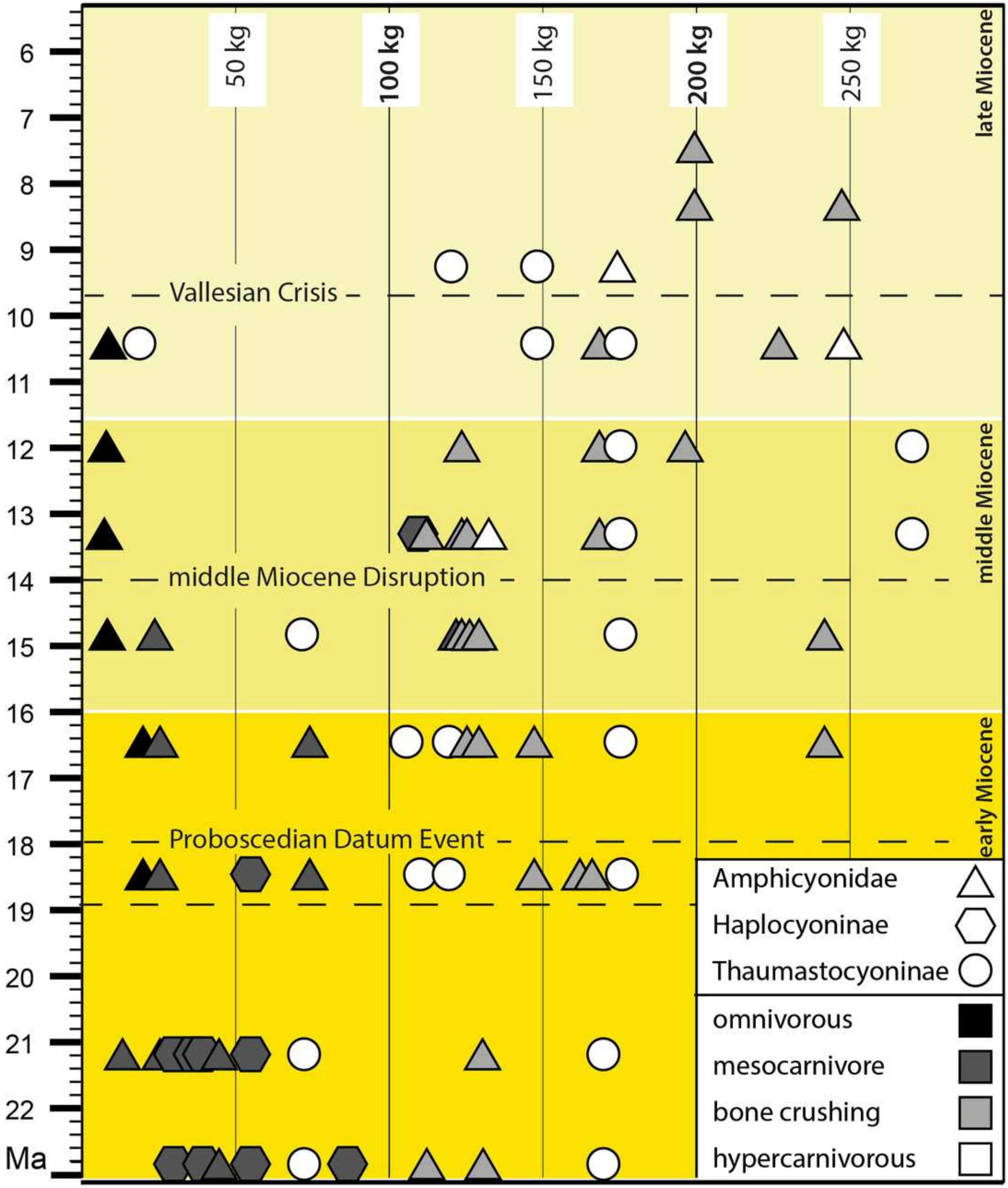
Body mass and diet distribution of the amphicyonid during the Miocene biozones.

The horizontal dashed lines refer~~red~~ to the biotic events discussed in the text.


6
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22
Ma
50 kg
100 kg
150 kg
200 kg
250 kg
late Miocene
middle Miocene
early Miocene
Vallesian Crisis
middle Miocene Disruption
Proboscedian Datum Event
Amphicyonidae △
Haplocyoninae ⬡
Thaumastocyoninae ○
omnivorous ■
mesocarnivore ■
bone crushing ■
hypercarnivorous □

Table 1(on next page)

Measurements of the teeth of the holotype (MHNBx 2020.20.1) of *Tartarocyon cazanavei* nov. gen. & sp. from Sallespisse (MN7/8).

*: based on alveoli.

Tooth locus	Length	Width
i1	7.58*	3.19*
i2	9.88*	5.02*
i3	11.51*	5.15*
c	-	18.02*
p1	7.87*	3.86*
p2	8.27	4.63
p3	11.14	6.35
p4	18.58	9.67
m1	34.30*	13.88*
m2	24.26*	14.22*
m3	17.21*	11.93*

Table 1. Measurements of the teeth of the holotype (MHNBx 2020.20.1) of *Tartarocyon cazanavei* nov. gen. & sp. from Sallespisse (MN7/8). *: based on alveoli.

Table 2(on next page)

Several measurements of the teeth and mandible of the holotype (MHNBx 2020.20.1) of *Tartarocyon cazanavei* nov. gen. & sp. from Sallespisse (MN7/8).

MD: Mandible height.

Length p1-p4	69.94
Length m1-m3	78.67
MD below p2	39.69
MD below m1	48.97
MD below m3	53.25

Table 2. Several measurements of the teeth and mandible of the holotype (MHNBx 2020.20.1) of *Tartarocyon cazanavei* nov. gen. & sp. from Sallespisse (MN7/8). MD: Mandible height.

Table 3(on next page)

Ratios estimated based on premolars and molars for several amphicyonines and thaumastocyonines known in the Miocene of Europe.

Grey font: Thaumastocyonina; white font: Amphicyoninae.

Taxon	Stratigraphic distribution	Ratio Lp2/Lm1	Ratio Lp3/Lm1	Ratio Lp4/Lm1	Ratio Lm2/Lm1	Ratio Lm3/Lm1
Cynelos lemanensis MNHNL-La85	MN1-MN2	0.43	-	0.67	0.63	-
Crassidia intermedia SMNS 46684	MN1-MN2	0.47	0.43	0.63	0.58	0.38
Ysengrinia gerandiana FSL 213828	MN1-MN2	0.44	0.47	0.62	-	-
Cynelos rugosidens BSP-1881-IX-14, 581	MN2	-	-	0.67*	0.65	0.42
Peignecyon felinoides TU 7391147	MN3	-	-	0.55	0.49	-
Amphicyon lathanicus Fossil from Hommes	MN3	0.35	0.53	0.59	0.71	-
Cynelos helbingi BSP-II-1937-12293	MN3-MN4	-	-	0.57*	0.64	0.39
Ictiocyon socialis Ginsburg (1992, p. 311)	MN3-MN4	0.41	0.51	0.62	0.72	0.42
Ysengrinia depereti MSNO.785	MN3-MN4	0.25	0.43	0.48	0.62	0.34
Cynelos schlosseri BSP-1937-12369	MN3-MN5	0.37	0.48	0.61	0.59	0.36
Tomocyon grivense UCBL-FSL 213797	MN3-MN9	-	-	-	0.6	-
Amphicyon giganteus Specimen from Vienna & Basel SO6521 (Hunt 2003,	MN4-MN5	0.3	0.42	0.58	0.71	-

table 4.7)						
Pseudocyon sansaniensis MNHN.F.Sa207	MN4-MN6	-	-	0.51	0.6	-
Thaumastocyon bourgeoisi Cast MNHN	MN5	?	?	-	0.45	No m3
Pseudocyon steinheimensis SMNS 4808	MN5-MN7/8	-	-	0.44	0.64	-
Pseudarctos bavaricus Ginsburg (1992, p. 309)	MN5-MN9	-	-	0.61	0.71	0.61
Amphicyon major MNHN.F.Sa844	MN6-MN9	0.31	0.36	0.54	0.7	0.56
Tartarocyon cazanavei MHNBx 2020.20.1	MN7/8	0.24	0.32	0.54	0.71	0.5
A. eppelsheimensis Holotype	MN9	-	-	0.47	0.67	-
Magericyon castellanus LVF 206y	MN9	No p2	-	0.42	0.45	-
Agnotherium antiquum *NMB CM 242 & MNHM Epp 117-2017*	MN9-MN10	No p2	No p3	0.62	0.37	No m3
Ammitocyon kainos BAT-3'08 604	MN10	No p2	No p3	0.71	0.54	No m3
Magericyon anceps	MN10	No p2	0.15	0.38	0.54	-

Mean

Table 3. Ratios estimated based on premolars and molars for several amphicyonines and thaumastocyonines known ~~in~~ the Miocene of Europe. Grey f~~ont~~: Thaumastocyonina; white f~~ont~~: Amphicyoninae.

Table 4(on next page)

List of ~~the~~ Amphicyonidae known ~~in~~ the Miocene of Europe with indication of their stratigraphic distribution, body mass, and diet.

Diet estimated based on similarities with the ones proposed by Viranta (1996). The Haplocyoninae are here considered as hypercarnivores because they display a hypercarnivorous dentition (see Wang et al., 2016). *: bodymass and diet based on Viranta (1996).

Family-subfamily	**Taxon**	**Stratigraphic distribution**	**Body mass (in kg)**	**Diet**
Amphicyoninae	*Amphicyon astrei*	MN1	112	Bone-crushing mesocarnivores
	A. laugnacensis	MN1-MN2	130 (est.)	Bone-crushing mesocarnivores
	A. lathanicus	MN3	159	Bone-crushing mesocarnivores
	A. giganteus	MN4-MN5	157-317*	Bone-crushing mesocarnivores*
	A. lactorensis	MN4-MN5	132	Bone-crushing mesocarnivores
	A. major	MN6-MN9	122-212*	Bone-crushing mesocarnivores*
	A. eppelsheimensis	MN9	225	Bone-crushing mesocarnivores
	A. gutmanni	MN11	246*	Bone-crushing mesocarnivores*
	A. pannonicus	MN11-MN12	198*	Bone-crushing mesocarnivores*
	Cynelos lemanensis	MN1-MN2	42	Mesocarnivores*
	C. rugosidens	MN2	13	Mesocarnivores*
	C. helbingi	MN3-MN4	60-86*	Mesocarnivores*
	C. schlosseri	MN3-MN5	23*	Mesocarnivores*
	C. bohemicus	MN5	118	Mesocarnivores
	Euroamphicyon olisiponensis	MN3-MN4	147*	Bone-crushing mesocarnivores*
	Ictiocyon socialis	MN3-MN4	21	Omnivorous*
	Janvierocyon pontignensis	MN3	162	Bone-crushing mesocarnivores
	Magericyon	MN9	246	Hypercarnivores*

	castellanus			
	M. anceps	MN10	171	Hypercarnivores
	Pseudarctos bavaricus	MN5-MN9	9*	Omnivorous*
	Pseudocyon sansaniensis	MN4-MN6	126*	Bone-crushing mesocarnivores*
	P. steinheimensis	MN5-MN7/8	123*	Bone-crushing mesocarnivores*
	P. caucasicus	MN6	130*	Hypercarnivores*
	P. styriacus	MN6	118*	Bone-crushing mesocarnivores*
	Tartarocyon cazanavei	MN7/8	195**	Bone-crushing mesocarnivores
Thaumastocyoninae	*Agnotherium antiquum*	MN9-MN10	148	Hypercarnivores*
	Ammitocyon kainos	MN10	120	Hypercarnivores
	Crassidia intermedia	MN1-MN2	169	Hypercarnivores
	Amphicyonopsis serus	MN6?-MN7/8	270	Hypercarnivores
	Peignecyon felinoides	MN3	110	Hypercarnivores
	Thaumastocyon bourgeoisi	MN5	72	Hypercarnivores *
	T. dirus	MN9	35	Hypercarnivores*
	Tomocyon grivense	MN3-MN9	174	Hypercarnivores*
	Ysengrinia gerandiana	MN1-MN2	72	Hypercarnivores*
	Y. depereti	MN3-MN4	118	Hypercarnivores*
	Y. valentiana	MN4	106	Hypercarnivores*
Haplocyoninae	*Gobicyon serbiae*	MN6	109 kg	Hypercarnivores

	Haplocyon crucians	MN1-MN2	45 kg	Hypercarnivores
	H. elegans	MN1-MN2	29 kg	Hypercarnivores
	Haplocyonoides mordax	MN1-MN3	52 kg	Hypercarnivores
	H. suevicus	MN2	42 kg	Hypercarnivores
	Haplocyonopsis crassidens	MN1	85 kg	Hypercarnivores

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Table 5(on next page)

Number of taxa by MN level~~s~~ in totality and based on diet after Table 4.

MN level	Omnivores	Mesocarnivores	Bone-crushing mesocarnivores	Hypercarnivores	Totality
MN1		5	2	2	9
MN2		6	1	2	9
MN3	1	3	3	3	10
MN4	1	2	4	3	10
MN5	1	2	4	2	9
MN6	1	1	4	3	9
MN7/8	1		3	2	6
MN9	1		2	4	7
MN10			0	3	3
MN11			2		2
MN12			1		1

Table 5. Number of taxa by MN level~~s~~ in totality and based on diet after Table 4.