

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

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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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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 Sallespisse (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

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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 gasteropods 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 (thanatocenosis) 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", represented 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 Southwest/Northeast 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 gastropods' 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 origins.

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, South 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:

- Molasses 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 molasses 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 filled with blue to black clayey sand containing a diversified fauna of large molluscs (e.g. *Pelecypora*, *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, 1893; Poignant, 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 led 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 registered 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 articles [Mennecart et al. \(accepted\)](#).

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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.: $\text{Log}^{10}(\text{BM}) = [2,97 \times \text{Log}^{10}(\text{Lm1})] - 2,27$; 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 foramina, 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 extends 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). Nevertheless, 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 including 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 even 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 not 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 imagine 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 premolars size is also observed in amphicyonines; this is a common trend in European amphicyonids. However, as visible on Table 3 the premolars and molars 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 (excepted 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 opposite, 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 postcanassial 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 geographical 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 ecologies: 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 hypercarnivore *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 Orléanian (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 amphicyonids 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 preys, 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 mesocarnivores 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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Figures

Figure 1. Geographical 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.

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 referred 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).

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Figure 1

Geographical 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.

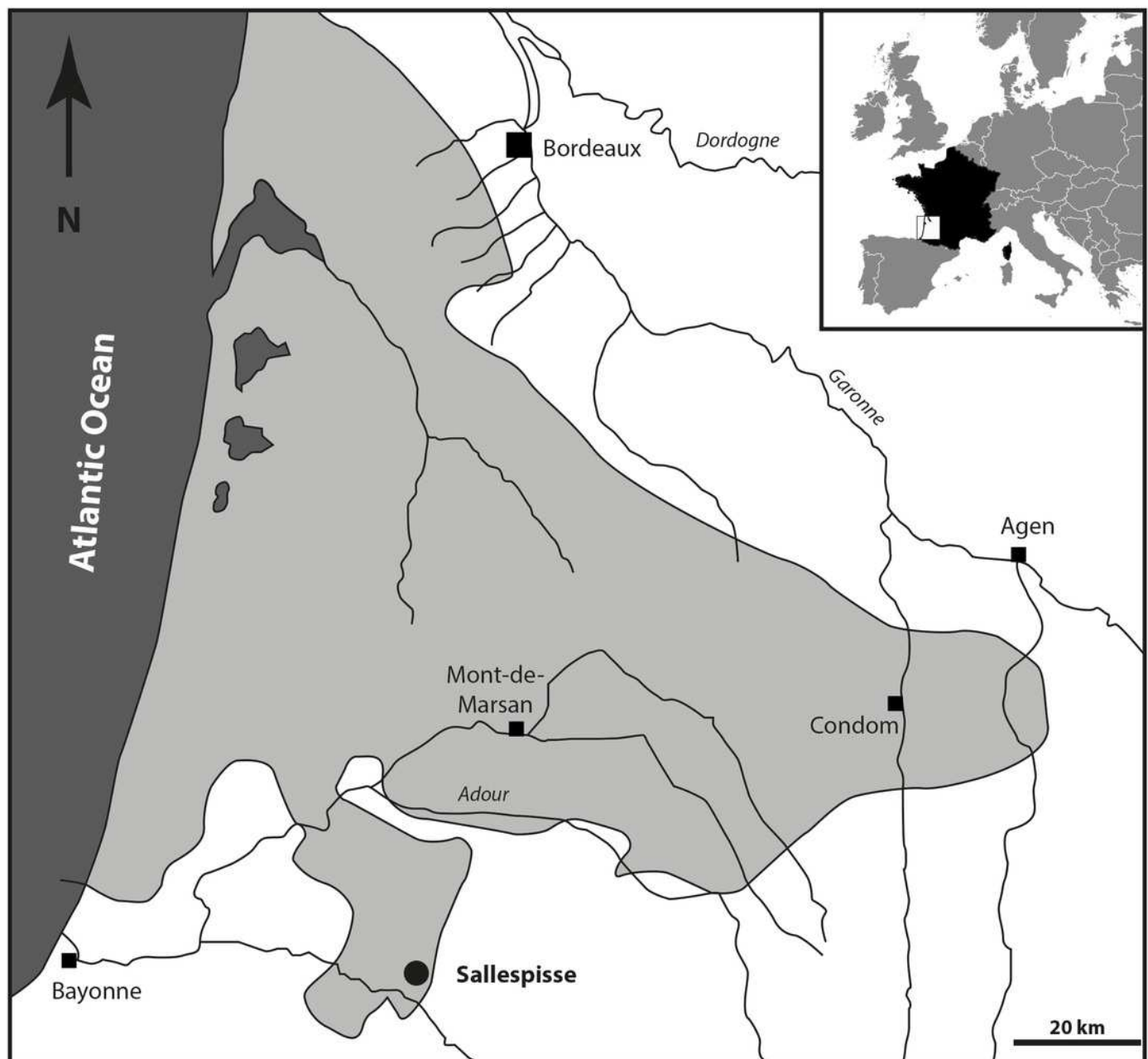


Figure 2

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

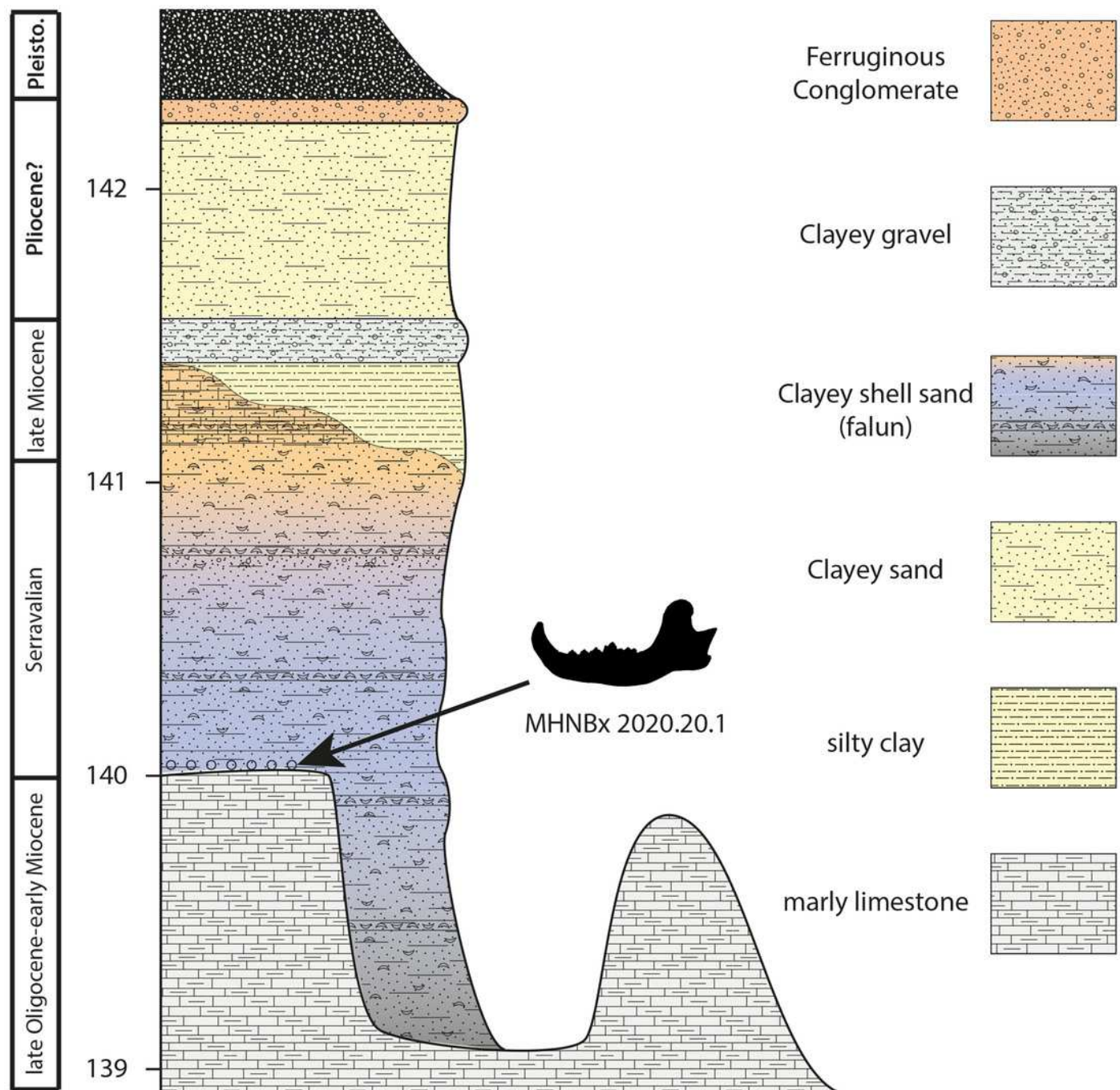


Figure 3

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

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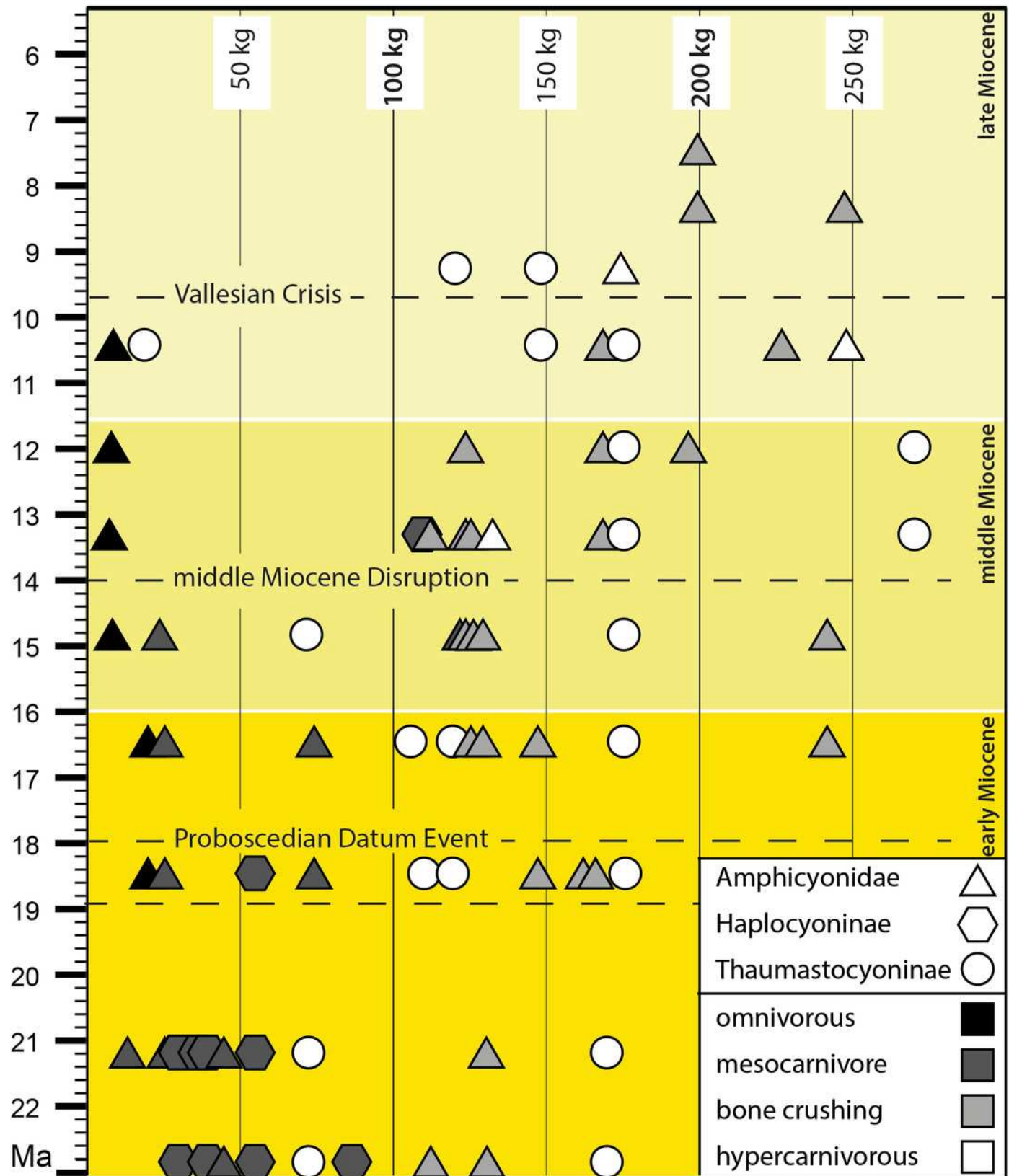


Table 1(on next page)

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*

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

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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

- 1 **Table 2.** Several measurements of the teeth and mandible of the holotype (MHNbX
- 2 2020.20.1) of *Tartarocyon cazanavei* nov. gen. & sp. from Sallespisse (MN7/8). MD:
- 3 Mandible height.
- 4

Table 3 (on next page)

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

table 4.7)

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

Mean

- 1 **Table 3.** Ratios estimated based on premolars and molars for several amphicyonines
- 2 and thaumastocyonines known in the Miocene of Europe. Grey font:
- 3 Thaumastocyonina; white font: Amphicyoninae.
- 4

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). *: body mass and diet based on Viranta (1996).

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

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

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

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(on next page)

Number of taxa by MN levels 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

1 **Table 5.** Number of taxa by MN levels in totality and based on diet after Table 4.

2