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

First revision

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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 sized 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 unique morphology of its p4, unknown in this clade, allows the erection of the new genus *Tartarocyon cazanavei* nov. gen. & sp. This taxon may be derived from a *Cynelos*-type amphicyonine. The description of this new taxon 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 sized 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 unique morphology of its p4, unknown in this clade, allows the erection of the new genus *Tartarocyon cazanavei* nov. gen. & sp. This taxon may be derived from a *Cynelos*-type amphicyonine . The description of

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

Introduction

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

The last transgression in the 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 shelly sandy deposits named “Faluns bleus” (Delbos, 1848), also known as Blue Faluns of Orthez (Lesport, Cluzaud & Verhecken, 2015). This formation attracted scientists early in paleontological history.

In 1833, the naturalist Dufour made an excursion in this area (Dufour, 1836) and gave indications to his palaeontologist friend Grateloup who soon after published new fossil gastropod species (Grateloup, 1835; 1845-1847). Since then, numerous authors have 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 (thanatocenoses) may represent a nearshore environment in a subtropical to tropical climate. In 1993, JFL and Philippe Renard 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 specimen belongs to an Amphicyonidae (Carnivora, Caniformia).

The Amphicyonidae, which are colloquially referred to as "bear-dogs", represent 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 included numerous species during the early and middle Miocene in Europe (Viranta, 1996), but went extinct before the end of the Miocene, the last European amphicyonids being known from the late Tortonian (*Amphicyon pannonicus*; Kretzoi, 1985; Viranta, 1996). Miocene amphicyonids are characterized by the presence of a pronounced, trenchant dentition (Morlo et al., 2020; Morales et al., 2021).

Three subfamilies of Amphicyonidae are recognized in the Miocene of Europe: the Haplocyoninae, the Thaumastocyoninae, and the Amphicyoninae, which are supposedly paraphyletic (Morales et al., 2021). The typical haplocyonines (*Haplocyon*, *Haplocyonoides*, and *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). Based on phylogenetic analysis, Jiangzuo et al. (2021), proposed to include in the Haplocyoninae the genera *Sarcocyon*, *Gobicyon*, and *Aktaucyon*. Among these genera, only *Gobicyon* is known from Europe (*G. serbiae* in MN6; Pavlovic & Thenius, 1959; Ginsburg, 1999; Jiangzuo et al., 2018). The Thaumastocyoninae groups the genera *Thaumastocyon*, *Ysengrinia*, *Tomocyon*, *Crassidia*, *Agnotherium*, *Ammitocyon*, and possibly *Amphicyonopsis* (Morales et al., 2019; 2021a,b; Morlo et al., 2020). 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 included in this subfamily (Morales et al., 2019; 2021a,b). Whatsoever, Morales et al. (2021b) created two new tribes (Pseudarctini and Magericyonini) to clarify systematics of Miocene amphicyonines. Amphicyonini groups the genera *Amphicyon*, *Cynelos*, *Euroamphicyon*, *Heizmannocyon*, *Megamphicyon*, and *Paludocyon*. Pseudarctini groups the genera *Ictiocyon*, *Dehmicyon*, and *Pseudarctos*. Magericyonini comprises the hypercarnivorous genus *Magericyon* and with some doubt *Pseudocyon*.

European Miocene amphicyonids were also ecologically diverse: taxa ranged in body mass 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 a few taxa recorded during MN9-MN12 (Viranta, 1996). The amphicyonids may have suffered from the Vallesian Crisis, with only rare and specialized taxa known in the late Vallesian and early Turolian in some parts of Central Europe (Agustí, Cabrera & Garcés, 2013; Viranta, 1996). Therefore, the description of this new Amphicyonidae from Serravallian of Southwestern Europe 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 of 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 similarity in the taxonomic composition of the fauna and the sedimentological content allowed previous authors to consider all these localities as synchronous and they were grouped under the locality name of Sallespisse (Daguin, 1948). Nevertheless, very small differences in proportions within the different mollusc communities are observed, indicating small local environmental differences (Degrange-Touzin, 1895). The most common gastropod families 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 common 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 (e.g. *Theoxodus*) may indicate sediments of continental origin.

The locality of Crousquillière (Figure 1), misspelled in Lesport, Cluzaud & Verhecken, 2015 as La Croustillère, is located on the Carré farm property (also known as Carrey) owned 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 was poorly exploited for its fossiliferous contains before the 1990s. 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 studied outcrop measures 3.5m. It is composed from base to top of:

- Molasse deposits observed represent more than 10 meters all 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 dated between the middle Eocene and the Burdigalian in this area (Karnay, 1997). Being at the very end of this sequence may indicate an age 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 a variation of colour and sedimentation from base to top. The basal transition between the molasse 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 was found in this layer. New remains (an isolated molar and an astragalus) of a ruminant and cetaceans 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. *Pelecyora*, *Procardium*, *Megacardita*, *Hexaplex*, *Conus*). This level is sealed with a few centimetres of 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

oxidating conditions. This Formation clearly corresponds to the Faluns de Sallespisse (Karnay, 1997). The age of these deposits is discussed below.

- 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 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 the la Crousquillière (in Sallespisse) locality. The age of the Falun deposits in Orthez area have been interpreted many times variously as 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 permits constraining 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 encompasses 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 have led to a revaluation of the age of the Faluns deposits from Sallespisse and Orthez 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 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 donated 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 from the open access article Mennecart et al. (accepted).

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The dental nomenclature of premolars follows Ginsburg (1999). The measurements, taken by calipers, have an accuracy of 0.1 mm.

Body Mass. We used the equation of Van Valkenburgh (1990) for all Carnivora irrespective of familiar assignment in order to estimate the body mass of some amphicyonids including ~~*Tartarocyon cazanavei* nov. gen. & sp.~~: $\mathrm{Log}^{10}(\mathrm{BM}) = [2{,}97 \times \mathrm{Log}^{10}(\mathrm{Lm1})] - 2{,}27$; 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

Order CARNIVORA Bowdich, 1821

Suborder CANIFORMIA Kretzoi, 1943

Family Amphicyonidae Trouessart, 1885

Tribe Amphicyonini 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 Pyrenees, 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 with the excavation during many years.

Diagnosis. Large size Amphicyoninae possessing a complete dental formula. The taxon is characterized by the following features: long diastemata between the premolars, low p2 and p3, absent anterior accessory cuspid on p4, large and individualized distal accessory cuspid on p4, and unreduced m2 and m3. The taxon differs from all the European amphicyonids from the Miocene by the individualization of the distal accessory cuspid from the main cuspid on p4 and the extreme reduction of the distal shelf and cingulid.

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 and nearly horizontally oriented; it is high and extends posteriorly up to the distal root of 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 foramen 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 toothrow. 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 of large size. Its root extends in the mandible to 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 of these teeth. The main cuspid is low and located mesially, which results in an asymmetric morphology in lateral view. Mesial to the main cuspid, the lingual cingulid is thicker, but no individualized anterior cuspid 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 short distal cingulid, but no cuspid is present. The p4 is distinctly longer and mediolaterally wider than the p2 and p3. However, the main cuspid remains low. The tooth is less asymmetric, the apex of the main cuspid being more mesiodistally centered. No real anterior accessory cuspid is present mesial to the main cuspid. A distal accessory cuspid is present: it is mostly individualized from the main cuspid. The distal accessory cuspid is mediolaterally centered. The distal cingulid is thin on the labial and lingual parts and is almost completely absent at the distal part; it does not form a distal shelf. 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 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 main cuspid) and short. Like the typical haplocyonines, the premolars of *Gobicyon serbiae* (MN6) differ from those of MHNBx 2020.20.1 in being tall and short. Moreover, the p2 and p3 of *G. serbiae* possesses an individualized and large distal accessory cuspid. Additionally, typical haplocyonines and *Gobicyon* have a short toothrow lacking diastemata. These amphicyonids are thus relatively short-snouted compared to the taxon from Sallespisse.

All the thaumastocyonines differ from MHNBx 2020.20.1 in having relatively 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 main cuspid is noticeably lower than the p4 main cuspid). The p4 of MHNBx 2020.20.1 also shares with the thaumastocyonines the presence of a strong distal accessory cuspid (Figure 4); the youngest thaumastocyonines (*e.g., Agnotherium*, *Ammitocyon*) shares with the p4 of MHNBx 2020.20.1 the reduced distal shelf and cingulid (Figure 4). However, the p4 of the thaumastocyonines differs from that of MHNBx 2020.20.1 in having a leaning backward p4 main cuspid (Figure 4). The youngest thaumastocyonines – *Ammitocyon* and *Agnotherium* – moreover, 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 lacking 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.

Three amphicyonines are regarded to be separate from those recorded in the Miocene: *Ictiocyon*, *Dehmicyon*, and *Pseudarctos* (Ginsburg, 1992; Morales et al., 2021b). They are all included among Pseudarctini (Morales et al., 2021b). These small amphicyonids are short-snouted (i.e., short diastemata between the premolars) and the p2 and p3 are distinctly taller than on MHNBx 2020.20.1. Moreover, the distal accessory cuspid on p4 is reduced to lost in *Dehmicyon*, *Ictiocyon*, and *Pseudarctos* (Ginsburg, 1992; Morales et al., 20~~32~~b) (Figure 4

The hypercarnivorous *Magericyon* (Peigné et al., 2008), which belongs to the tribe Magericyonini (Morales et al., 2021b) differs from MHNBx 2020.20.1 in the absence of p2, in having a single-rooted p3, a p4 relatively shorter compared to the m1 (Table 3) and in the absence of a distal cuspid on p4 (Figure 4). The genus *Pseudocyon* is probably close to *Magericyon* according to Morales et al. (2021b). MHNBx 2020.20.1 is similar to the species of *Pseudocyon* in the presence of very long diastemata between the premolars and of low p2, p3. However, the p4 is relatively mesiodistally shorter (compared to the m1) in the *Pseudocyon* species than in MHNBx 2020.20.1; moreover, the distal part of the p4 of *Pseudocyon* is widened compared to that of the p4 of MHNBx 2020.20.1 (Figure 4).

The Miocene Amphicyonini *Cynelos*, *Amphicyon*, *Megamphicyon*, *Euroamphicyon*, *Paludocyon*, and *Heizmannocyon* 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 is even absent in hypercarnivorous amphicyonids; Table 3) (Kuss, 1965; Peigné & Heizmann, 2003; Viranta, 1996). Despite sharing a characteristically slender ramus of the mandible, the p4 of MHNBx 2020.20.1 differs from that of the *Cynelos* species by the absence of an anterior accessory cuspid (even if this structure is not individualized in *Cynelos*) and a much more reduced distal shelf (Figure 4). The case of *Cynelos* is interesting because its p4 does not display a widening of its distal part; in this regard, its p4 is similar to that of MHNBx 2020.20.1 in occlusal view (Figure 4). MHNBx 2020.20.1 shares with the species of *Paludocyon*, *Amphicyon*, *Heizmannocyon*, *Megamphicyon*, and *Pseudocyon* the reduction of the anterior accessory cuspid compared to *Cynelos*. However, the distal shelf of the p4 is more developed in these amphicyonines than in MHNBx 2020.20.1 and none of the above-mentioned species has a p4 that displays a distal accessory cuspid separated from the main cuspid as it is on the p4 of MHNBx 2020.20.1. Moreover, these amphicyonine genera (see *Megamphicyon carnutense* and *Paludocyon bohemicus* in Morales et al., 2021b) possess a p4 that is characterized by a widening of the distal part. Additionally, the mandible of *Amphicyon* and *Megamphicyon* appears more massive than that of MHNBx 2020.20.1 (Kuss, 1965; Peigné & Heizmann, 2003; Viranta, 1996, Figure 4).

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 has 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. One can imagine that the taxon from Rimbez could also be closely related to the taxon from Sallespisse.

To conclude, the fossil from Sallespisse shows striking similarities with *Cynelos* (i.e., presence of long diastemata between the premolars, unreduced premolars and m3, low p2 and p3, no widening of the distal part of the p4. The general morphology of the p4 remain relatively stable within the Amphicyoninae, until now, having a distal accessory cuspid more or less individualized and a distal shelf present (Figure 4). MHNBx 2020.20.1 present a unique morphology among the Amphicyoninae in having an individualized distal accessory cuspid on p4 and a distal shelf extremely reduced, extending the morphology range of the p4 in this subfamily (Figure 4). 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 diagnostic 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, 2021a,b) 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 of *Tartarocyon cazanavei* nov. gen. & sp. did not provide statistically significant results, adding noise to the topology forming politomies, 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, which possess tall and short premolars without diastemata. *Tartarocyon cazanavei* nov. gen. & sp. also does not belong to the Thaumastocyoninae, this family having reduced premolars and postcarnassial molars (Table 3). The youngest thaumastocyonine species, from the middle and late Miocene, are further characterized by the absence of m3 and of p1, p2, and p3, and a leaning

~~backward main cuspid on p4 (Figure 4, Table 3) (Morales et al., 2019; 2021; Morlo et al., 2020).~~ A reduction of premolar size is also observed in amphicyonines; this is a common trend in European amphicyonids. However, as seen on Table 3, the premolar and molar ratios show that the premolars (except the p4) and postcarnassial molars tend to reduce more among the thaumastocyonines than in the amphicyonines amphicyonini *Megamphicyon*, *Cynelos* and *Amphicyon* (Table 3). The values estimated for *Tartarocyon* nov. gen. are similar to those of *Cynelos*, *Megamphicyon*, and *Amphicyon* (Table 3). Moreover, diastemata are still present between the premolars in these amphicyonines as in *Tartarocyon cazanavei* nov. gen. & sp. Interestingly, the ratio between the p4 and the m1 is greater in the thaumastocyonines (except for *Ysengrinia depereti*, Table 3) than in *Megamphicyon*, *Amphicyon*, and *Tartarocyon* nov. gen.

The case of *Magericyon* is puzzling. This amphicyonid differs from the contemporaneous thaumastocyonines by the presence of an 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). In contrast, its shoulder anatomy is relatively primitive and generalized, being similar to that of *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). Morales et al. (2021b) highlighted the originality of *Magericyon* in including this genus among the tribe Magericyonini. They also included, but with some doubt, the genus *Pseudocyon* in this tribe. One can note that this amphicyonine also has a reduced p4 compared to the m1 (Table 3).

It appears that *Tartarocyon cazanavei* nov. gen. & sp. is morphologically similar to *Cynelos*, *Amphicyon*, and *Megamphicyon* in having premolars and postcarnassial molars that are only slightly reduced in length. However, one can note that the anterior accessory cuspid 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 its reduced p2, p3, and p4 (Table 3). This feature is shared with *Amphicyon*, *Paludocyon*, and *Megamphicyon*. However, *Tartarocyon cazanavei* nov. gen. & sp. recalls *Cynelos* in having a p4 that does not show a widening of its distal part; at the opposite, *Amphicyon*, *Paludocyon*, and *Megamphicyon* have p4 that is characterized by a widening of the distal part. Despite these similarities, *Tartarocyon cazanavei* nov. gen. & sp. differs from *Cynelos* and *Amphicyon* in the large and individualised distal cuspid that is positioned distally on the p4; moreover, the distal shelf and distal cingulid is more reduced in *Tartarocyon cazanavei* nov. gen. & sp. than in *Cynelos* and *Amphicyon*. As a consequence, we think that *Tartarocyon cazanavei* nov. gen. & sp. is derived from a *Cynelos*-type amphicyonine.

Cynelos and *Amphicyon* are Amphicyonini known from the early Miocene (Ginsburg, 1999). *Tartarocyon* nov. gen. seems to be more derived than *Cynelos* but more basal than *Amphicyon*. *Tartarocyon cazanavei* nov. gen. & sp. followed a distinct evolutionary path from the other amphicyonids due to geographic isolation, as shown by its unusual p4 morphology.

Ecology of *Tartarocyon cazanavei* nov. gen. & sp. The 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 species of *Cynelos*, which range from 13 to 86 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), *Megamphicyon carnutense* (182 kg), and *Tomocyon grivense* (190 kg) (Viranta, 1996, Table 4). Amphicyonids that are significantly 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 ecology: omnivores, mesocarnivores, bone-crusher mesocarnivores, and hypercarnivores. The presence of the four premolars as well as the presence of large m2 and m3 (relative to the m1) indicate that *Tartarocyon cazanavei* nov. gen. & sp. was not a hypercarnivore. ~~Indeed, hypercarnivorous amphicyonids such as *Magericyon castellanus*, *Pseudocyon caucasicus*, *Thaumastocyon* spp. and *Agnotherium* spp. are characterized by a 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 high mass of *Tartarocyon cazanavei* nov. gen. & sp. contrasts with those of the omnivorous amphicyonids *Pseudarctos bavaricus* and *Ictiocyon socialis*, which were the smallest amphicyonids in the Miocene of Europe together with the mesocarnivorous *Dehmicyon schlosseri* (Viranta, 1996; Morales et al., 2021). Moreover, the Pseudarctini *P. bavaricus*, *D. schlosseri*, and *I. socialis* are characterized by high-crowned teeth with blunt cuspids 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 5).

The evolution of European amphicyonids during the Miocene. Viranta (1996) carried out 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 the Miocene of Europe until MN3, reveals a similar specific diversity during the entire lower Miocene with 9 to 12 contemporaneous Amphicyonidae species in Europe (Table 5). The diversity seen in MN4 and MN5 is thus due to a diversification of the remaining amphicyonids (Amphicyoninae and Thaumastocyoninae) with a maximum of 11 species as already evidenced by Viranta (1996).

Moreover, contrary to Viranta (1996), the diversity of the Amphicyoninae and Thaumastocyoninae is already observed in MN3 (11 species; Figure 6; Table 5). For instance, the locality of Tuchořice (Czech Republic) yielded one thaumastocyonine (Morales et al., 2019) and three amphicyonines (two Amphicyonini and one Pseudarctini; Morales et al., 2021b). At the European level, the amphicyonids were clearly taxonomically and ecologically diverse in MN3 (Figure 6; Table 5), as illustrated by the presence of the small omnivore *Ictiocyon*, the mesocarnivores *Cynelos* and *Dehmicyon*, the hypercanivore *Peignecyon*, and the large bone-crusher mesocarnivores *Pseudocyon*, *Amphicyon*, *Megamphicyon*, and *Janvierocyon*.

The diversification of the Amphicyoninae and Thaumastocyoninae must be questioned because it was 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 developed, with wet and closed environments in France and Germany during the Orleanian (Costeur, 2005; Costeur & Legendre, 2008). Due to these environmental restructuring and the competition from the newcomers, nearly 60% of the ungulate fauna was replaced during that time (Scherler et al., 2013). The restructuring of the community and of the environment may have been fatal to the Haplocyoninae but favored the Amphicyoninae and Thaumastocyoninae.

The amphicyonids remained diverse during MN5 (9 species), MN6 (10 species), MN7/8 (7 species), and MN9 (8 species) (Table 5). The bone-crushing mesocarnivorous amphicyonids are taxonomically well-diversified in MN6 (5 species) and MN7/8 (4 species including *Tartarocyon* nov. gen.). On the other hand, mesocarnivorous amphicyonids are unknown in Europe after MN6. Additionally, no amphicyonid between 50 kg and 100 kg is known after MN5 (Figure 6). The disappearance of the mesocarnivorous amphicyonids and of amphicyonids of 50-100 kg is related to the disappearance of *Cynelos* from Europe (Figure 6; Table 5). One can, however, 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 mass 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 and is only known from 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 Climatic Transition (Steinthorsdottir et al., 2021), which results for instance in an increase in 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 – except the case of the monospecific omnivorous *Pseudarctos*. However, the taxonomic diversity of the bone-crushing mesocarnivores starts to decrease after MN5, as exemplified by the presence of only three taxa during MN9 (Figure 6; Table 5). In contrast, hypercarnivorous amphicyonids were still taxonomically diverse in MN9 with 4 species. Viranta (1996) estimated that the decline of the Amphicyonidae started in MN7/8 and considered that MN9 marked the probable disappearance of amphicyonids in Western Europe. However, the recent descriptions of the amphicyonids *Mager~~e~~cyon anceps* (Magericyonini; Peigné et al., 2008), *Ammitocyon kainos* (Thaumastocyoninae; Morales et al., 2021a) in MN9 and MN10 Spanish localities, and *Tartarocyon* nov. gen. have greatly changed our perception of the latest amphicyonid evolution (Figure 6; Table 5). Indeed, the amphicyonids, notably the Thaumastocyonines, were still diversified in MN7/8 (7 species) and MN9 (8 species) although less than in MN6.

The amphicyonid community changed considerably from MN9 to MN11 (Figure 6). The omnivorous amphicyonid *Pseudarctos*, which was also the smallest and only omnivorous amphicyonid at that time (and last representative of the Pseudarctini), disappeared from Europe (last record in MN9) (Figure 6; Table 5). As a consequence, the European amphicyonids are only represented by large to very large forms of at least 100 kg body mass during MN10 and even 200 kg during MN11 (Figure 6). 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 decreased in comparison to MN9 (Figure 6; Table 5). This modification of the amphicyonid fauna between MN 9 and MN10 could be related to the

Vallesian Crisis. This crisis coincided with the early/late Vallesian boundary (at 9.7 Ma) (Figure 6). At first 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 expansion 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 small sized predators.

Because Viranta (1996) extensively discussed the possible explanations for the decline of the amphicyonids (e.g., extinction of potential prey, competition), we will not develop these discussions herein. Agustí, Cabrera & Garcès (2013) noted that the amphicyonids were 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 very large forms that display bone-crushing mesocarnivorous dentition (Viranta, 1996; Figure 6). However, as mentioned above, 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 across 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 of a mass below 150 kg is 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 restructuring of the mammalian communities. Regarding the other amphicyonids (i.e., bone-crushing mesocarnivorous and hypercarnivorous), the Vallesian crisis seem to have had a profound effect (decrease in 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 from the French locality Sallespisse (12.8-12.0 Ma, France). It differs morphologically from the Thaumastocyoninae and Haplocyoninae. It seems that this amphicyonid is a part of the radiation of a group of amphicyonines during the Miocene after MN3 (as exemplified by the genera *Pseudocyon*, *Cynelos*, *Amphicyon*, and *Magericyon*); it probably derived from a *Cynelos*-type amphicyonine.

Tartarocyon nov. gen., moreover, illustrates the diversity of the amphicyonids in Europe: during MN7/8 amphicyonids were diversified in both the body mass and diet. However, the ecological and diversity reduction 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.

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 l'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* I(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., 2021a. *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.

Morales J., Fejfar O., Heizmann E., Wagner J., Valenciano A., Abella, J., 2021b. The Amphicyoninae (Amphicyonidae, Carnivora, Mammalia) of the early Miocene from Tuchořice, the Czech Republic. *Fossil Imprint* 77, 126–144.

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.

Steinthorsdottir M., Coxall H.K., de Boer A.M., Huber M., Barbolini N., Bradshaw C.D., Burls N.J., Feakins S.J., Gasson E., Henderiks J., Holbourn A.E., Kiel S., Kohn M.J., Knorr G., Kürschner W.M., Lear C.H., Liebrand D., Lunt D.J., Mörs T., Pearson P.N., Pound M.J., Stoll H., Strömberg C.A.E., 2021. The Miocene: The future of the past. Paleoceanography and Paleoclimatology, 36, e2020PA004037.

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.

Figures

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

Figure 2. Sedimentological succession of the Sallespisse outcrop with the location of 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, lingual, and labial views. Scale bar is 5 cm.

Figure 4. Mandib~~u~~le and p4 comparison for several European amphycionids. The red circle indicates the p4 position on the mandible. Modified from Dehm 1950, Kuss 1965, Bergounioux & Crouzel 1973, Viranta 1996, Peigné & Heizmann 2003, Peigné et al. 2008, Nagel et al. 2009, Morales et al. 2021 NMB TD1162 (*Heizmannocyon steinheimensis*), NMB SO4377 (*Megamphicyon giganteus*). The scale bare is 5 cm for the mandibles. The p4 are not to scale.

Figure 5. Reconstruction of *Tartarocyon cazanavei* nov. gen. & sp. feeding on a stranded dolphin along the Serravallian sea. We know only few on the inland environmental conditions where *Tartarocyon* lived. T~~hen, t~~his illustration combines all

the data from the site la Crousquillière in Sallespisse including the intertidal dark deposits, the abundance of the molluscs, and the mandibule of Tartarocyon in the high-tide line. Drawing by Denny Navarra.

Figure 6. Body mass and diet distribution of the amphicyonids during the Miocene biozones. The horizontal dashed lines refer 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.

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

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.

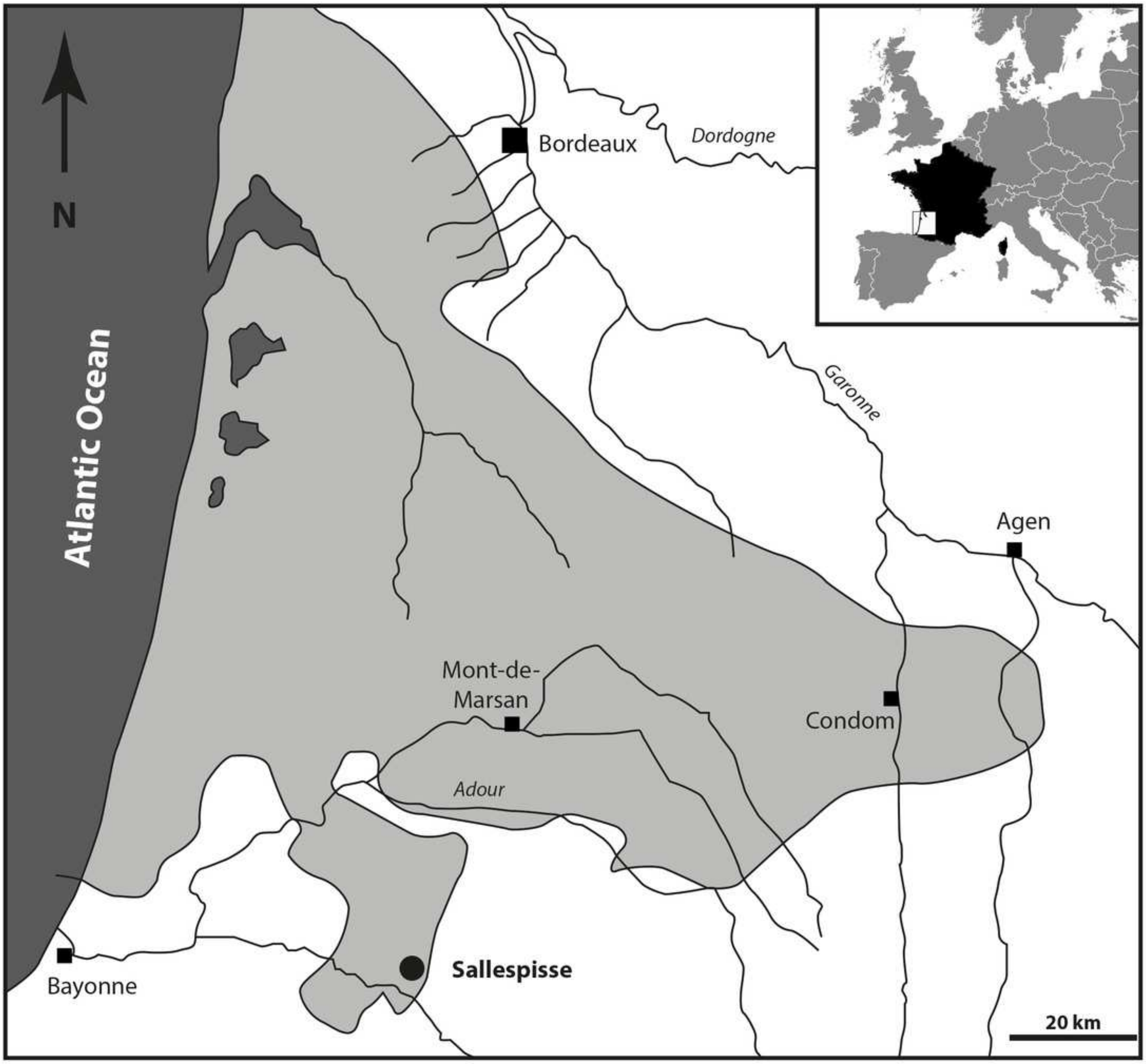


Figure 2

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

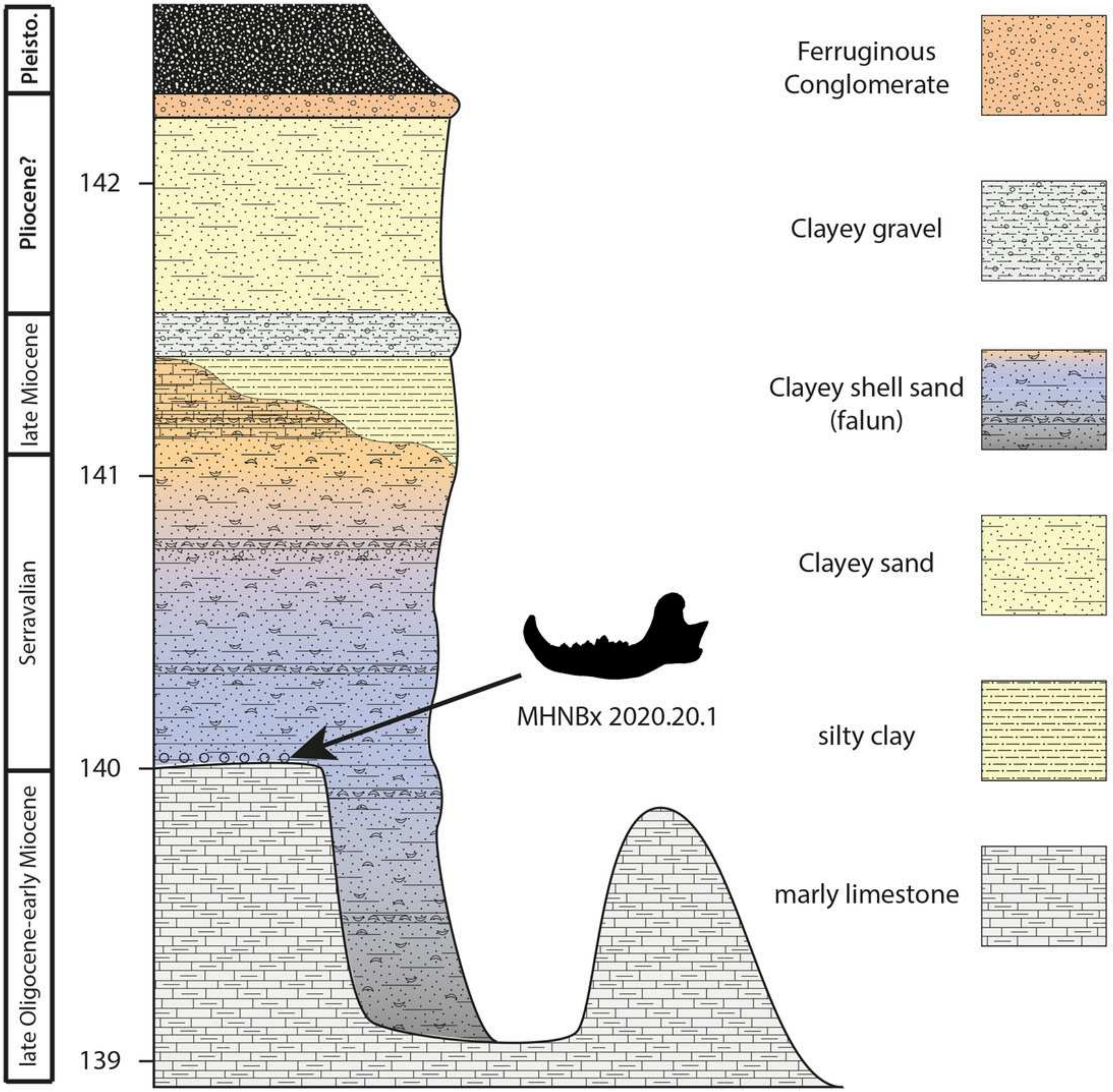


Figure 3

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.


5 cm

Figure 4

Mandibule and p4 comparison for several European amphycionids.

The red circle indicates the p4 position on the mandible. Modified from Dehm 1950, Kuss 1965, Bergounioux & Crouzel 1973, Viranta 1996, Peigné & Heizmann 2003, Peigné et al. 2008, Nagel et al. 2009, Morales et al. 2021.NMB TD1162 (*Heizmannocyon steinheimensis*), NMB SO4377 (*Megamphicyon giganteus*). The scale bare is 5 cm for the mandibles. The p4 are not to scale.

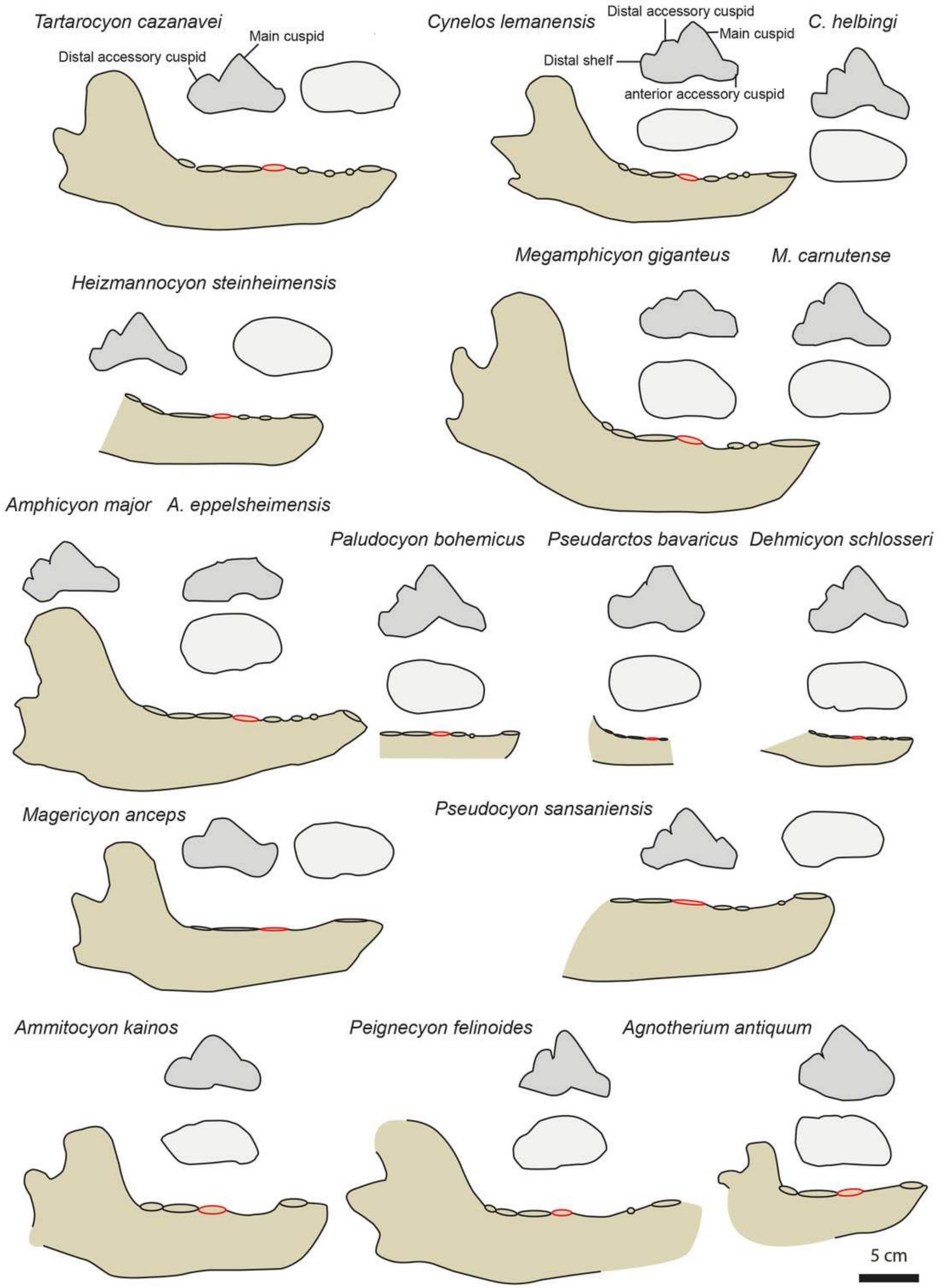

Tartarocyon cazanavei
Main cuspid
Distal accessory cuspid
Cynelos lemanensis
Distal accessory cuspid
Main cuspid
Distal shelf
anterior accessory cuspid
C. helbingi
Heizmannocyon steinheimensis
Megamphicyon giganteus
M. carnutense
Amphicyon major
A. eppelsheimensis
Paludocyon bohemicus
Pseudarctos bavaricus
Dehmicyon schlosseri
Magericyon anceps
Pseudocyon sansaniensis
Ammitocyon kainos
Peignecyon felinoides
Agnotherium antiquum
5 cm

Figure 5

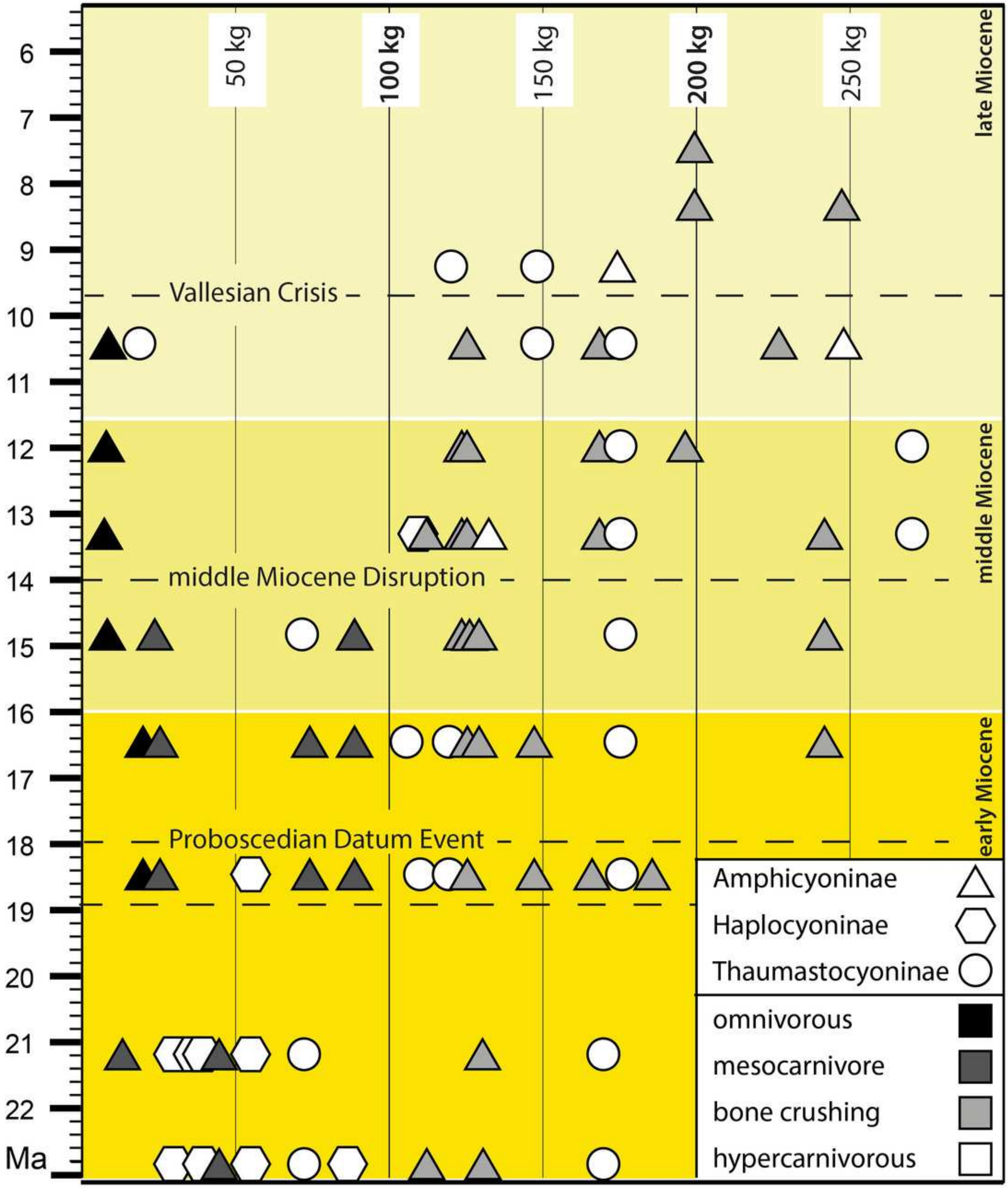
Reconstruction of *Tartarocyon cazanavei* nov. gen. & sp. feeding on a stranded dolphin along the Serravallian sea.

We know only few on the inland environmental conditions where *Tartarocyon* lived. Then, this illustration combines all the data from the site la Crousquillière in Sallespisse including the intertidal dark deposits, the abundance of the molluscs, and the mandibule of Tartarocyon in the high-tide line. Drawing by Denny Navarra.

Figure 6

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

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


6
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20
21
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
Amphicyoninae
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 from the Miocene of Europe.

Grey: Thaumastocyoninae; white: 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	-
Megamphicyon carnutense Fs 6953	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
Dehmicyon schlosseri BSP 13562	MN3-MN5	0.37	0.48	0.61	0.59	0.37
Paludocyon bohemicus *NM-PV 11723*	MN3-MN5	0.43	0.49	0.59	0.65	0.37
Pseudocyon sansaniensis	MN3-MN9	0.28	0.29	0.51	0.6	-

MNHN.F.Sa207						
Tomocyon grivense UCBL-FSL 213797	MN3-MN9	-	-	-	0.6	-
Megamphicyon giganteus Specimen from Vienna & Basel SO6521 (Hunt 2003, table 4.7)	MN4-MN6	0.3	0.42	0.58	0.71	-
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 &*	MN9-MN10	No p2	No p3	0.62	0.37	No m3

MNHM Epp 117-2017						
Ammitocyon kainos BAT-3’08 604	MN10	No p2	No p3	0.71	0.54	No m3
Magericyon anceps Mean	MN10	No p2	0.15	0.38	0.54	-

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(on next page)

List of Amphicyonidae known from 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, table 4), **: estimation based on the alveoli of the m1.

Family-subfamily	Tribe	Taxon	Stratigraphic distribution	Body mass (in kg)	Diet
Amphicyoninae	Amphicyonini	*Amphicyon astrei*	MN1	112	Bone-crushing mesocarnivores
		A. laugnacensis	MN1-MN2	130 (est.)	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*
		Euroamphicyon olisiponensis	MN3-MN4	147*	Bone-crushing mesocarnivores*
		Heizmannocyon steinheimensis	MN5-MN7/8	123*	Bone-crushing mesocarnivores*
		Janvierocyon pontignensis	MN3	162	Bone-crushing mesocarnivores
		Megamphicyon carnutense	MN3	182	Bone-crushing mesocarnivores
		M. giganteus	MN4-MN6	157-317*	Bone-crushing mesocarnivores*
		Paludocyon	MN3-MN5	86	Mesocarnivores

		bohemicus			
		Tartarocyon cazanavei	MN7/8	195**	Bone-crushing mesocarnivores
	Magerocyonini	*Magericyon castellanus*	MN9	246	Hypercarnivores*
		M. anceps	MN10	171	Hypercarnivores
		Pseudocyon sansaniensis	MN3-MN9	126*	Bone-crushing mesocarnivores*
		P. caucasicus	MN6	130*	Hypercarnivores*
		P. styriacus	MN6	118*	Bone-crushing mesocarnivores*
	Pseudarctini	*Dehmicyon schlosseri*	MN3-MN5	23	Mesocarnivores*
		Ictiocyon socialis	MN3-MN4	21	Omnivorous*
		Pseudarctos bavaricus	MN5-MN9	9*	Omnivorous*
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	MN1-MN2	72	Hypercarnivores*

	gerandiana			
	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

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 level in totality and based on diet, after Table 4.

MN level	Omnivores	Mesocarnivores	Bone-crushing mesocarnivores	Hypercarnivores	Totality
MN1		1	2	6	9
MN2		2	1	6	9
MN3	1	3	4	4	12
MN4	1	4	3	3	11
MN5	1	2	4	2	9
MN6	1	0	5	3	10
MN7/8	1		4	2	7
MN9	1		3	4	8
MN10			0	3	3
MN11			2		2
MN12			1		1

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