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Morgane FOURNIER,
Sandrine LADEVÈZE,
Kevin LE VERGER,
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Robert P. SPEIJER &
Floréal SOLÉ

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On the morphology of the astragalus and calcaneus of the amphicyonids (Carnivora, Mammalia) from the Paleogene of Europe: implications for the ecology of the European bear-dogs

Morgane FOURNIER
Sandrine LADEVÈZE
Kévin LE VERGER
CR2P (CNRS, MNHN, Sorbonne Université),
Département Origines et Évolution, Muséum national d'Histoire naturelle,
case postale 38, 57 rue Cuvier, F-75231 Paris cedex 05 (France)

Valentin FISCHER
Evolution & Diversity Dynamics Lab, Université de Liège (ULiège), Quartier Agora,
Bâtiment B18, Allée du six août, 14, 4000 Liège (Belgium)

Robert P. SPEIJER
KU Leuven, Department of Earth and Environmental Sciences,
Celestijnenlaan 200E, B-3001 Leuven-Heverlee (Belgium)

Floréal SOLÉ
Directorate Earth and History of Life, Palaeobiosphere Evolution Research Unit,
Royal Belgian Institute of Natural Sciences, Rue Vautier 29, B-1000 Brussels (Belgium)

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ABSTRACT
The Paleogene mammals of Europe are rarely known from partial or complete skeletons. As a result, their systematics and ecology are often solely based on dental characters and postcranial remains, when available, are usually neglected. This explains why the locomotion of mammals of the Eocene-Oligocene transition, the "Grande Coupure", is poorly known. The aim of this study is to describe the tarsal bones (astragali and calcanei) and characterize the locomotion of amphicyonid carnivorans, one of the most abundant mammalian predator groups from the Phosphorites du Quercy (France) sites. The identification of taxa and the characterization of both posture and locomotion were carried out using four criteria: relative abundance (in comparison with dental data), morphology, size, and body mass. Seven morphotypes, four among astragali and three among calcanei, are identified as Amphicyonidae and show various postures: plantigrade, semi-digitigrade, and digitigrade. One morphotype of the astragalus and one of the calcaneus are identified as *Cynodictis lacustris* Gervais, 1852, which exhibits a digitigrade posture. The study of postcranial bones, such as tarsals, allows for a better understanding of the ecology of these animals and deserves more interest in future morphological and phylogenetic studies.

KEY WORDS
Caniformia,
Quercy,
France,
Eocene,
Oligocene,
Diet,
Posture,
Locomotion.

RÉSUMÉ
À propos de la morphologie de l'astragale et du calcanéum des amphicyonidés (Carnivora, Mammalia) du Paléogène d'Europe ; implications sur l'écologie des chiens-ours européens.
Les mammifères du Paléogène Européen sont rarement représentés par des squelettes complets et leur systématique est souvent fondée sur des caractères dentaires. Le squelette postcrânien est, en comparaison, délaissé car très fragmentaire, ce qui rend son attribution systématique difficile, voire impossible de prime abord. Cela explique, en particulier, pourquoi la locomotion des faunes mammaliennes de la transition Éocène-Oligocène, nommée « Grande Coupure », est extrêmement peu connue. Le but de cette étude est de décrire et caractériser la locomotion de l'un des plus abondants groupes de prédateurs mammaliens des Phosphorites du Quercy (France), les carnivores amphicyonidés. Le matériel étudié est composé de deux os du tarse, l'astragale et le calcanéum, qui jouent un rôle important dans le mouvement du pied. L'identification des taxons et la caractérisation de la posture et de la locomotion se font selon quatre critères : abondance relative, morphologie, taille et masse corporelle. Sept morphotypes – quatre pour les astragales et trois pour les calcanéums – sont identifiés comme Amphicyonidae ; ils montrent différentes postures : plantigrade, semi-digitigrade et digitigrade. Deux d'entre eux sont identifiés comme appartenant à *Cynodictis lacustris* Gervais, 1852 ; ils présentent une posture digitigrade. L'étude des os postcrâniens permet, au final, de mieux comprendre l'écologie de ces animaux et mérite assurément plus d'attention dans les études ultérieures.

MOTS CLÉS
Caniformia,
Quercy,
France,
Éocène,
Oligocène,
régime alimentaire,
posture,
locomotion.

INTRODUCTION

The "Grande Coupure" is one of the main events that impacted the evolution of European Paleogene mammals (Legendre & Hartenberger 1992). First described by Stehlin (1910), this event corresponds to the transition between the Eocene and the Oligocene in Europe (± 33.9 Ma; Vandenberghe *et al.* 2012). It is characterized by an important decrease in global temperature (Zachos *et al.* 2008), which would have led to the decline of forests that were predominant in the middle Eocene, and resulted in a transition from a rather hot and humid climate to an arid climate (Legendre 1989; Legendre *et al.* 1991; Escarguel *et al.* 2008). These environmental changes, as well as the migration of many mammals from Asia, were probably the main drivers of the profound modifications seen in the European fauna with disappearances within several mammal groups and, conversely, diversification in others (Legendre & Hartenberger 1992).

This faunal turnover is particularly noticeable among carnivorous mammals. Hyaenodonta – an extinct group distributed across Laurasia and Africa – were abundant and diverse during the Eocene in Europe (from 56 to 33.9 Ma; Solé *et al.* 2014, 2015) and declined rapidly during the Oligocene (from 33.9 to 23.03 Ma) (Legendre & Hartenberger 1992). Conversely, the diversity of Carnivora exploded after the Grande Coupure (Legendre *et al.* 1991), resulting in the appearance of various clades of feliformians (e.g., Nimravidae) and caniformians (e.g., Amphicyonidae, Ursoidea, Ailuridae, Musteloidea) (Goswami & Friscia 2010). Carnivora is one of the most diverse placental orders currently recognized, with 281 species (Wilson & Mittermeier 2009).

The Quercy region (southwestern France; Fig. 1) contains many deposits that are crucial to a better understanding of this faunal turnover, with more than 80 distinct mammal faunas, all associated to karstic fissure fillings (Legendre *et al.* 1997). These paleokarst faunas range from the middle Eocene (*c.* 38 Ma) to the early Miocene (*c.* 22 Ma) (Renault *et al.* 1978; Remy *et al.* 1987; Maitre *et al.* 2006; Escarguel *et al.* 2008; Maitre 2014), and include various clades: Marsupialia, Primates, Chiroptera, Rodentia, Artiodactyla, Perissodactyla, and Carnivora (Legendre 1989; Legendre *et al.* 1991; Maitre 2014). The extensive temporal record of these faunas, in addition to the quality and richness of the mammal fossils, makes the Quercy region one of the most important for understanding the evolution of European Paleogene mammals (Legendre & Hartenberger 1992; Escarguel *et al.* 2008). However, from the beginning of the exploitation of the Quercy Phosphorites in the late 1860's until the mid-20th century, the exact sources of the fossils were rarely recorded, and only toponyms were provided (e.g., Caylux, Lamandine, Bach). These localities do not correspond to clearly defined fossiliferous sites but to nearby villages, resulting in occasional mixing of faunas of different ages (Maitre 2014; Pélissié 2015). The fossils collected during that period make up the so-called "old collections" (Rage 2006). However, since 1965, paleontologists have more precisely exploited the rich fissure fillings of this area in order to provide a refined chronology of the deposits (Bonis *et al.* 1973; Remy *et al.* 1987; BiochroM'97 1997a). This has enabled characterisation of the long-term evolution of the regional mammal fauna (Escarguel & Legendre 2006; Escarguel *et al.* 2008).

In the Quercy Phosphorites, dental remains are generally well preserved and are preferentially used for taxonomic identifications. Furthermore, dental remains provide information on diet, as well as body mass (e.g., Coillot *et al.* 2013). Postcranial remains are rarely found in association

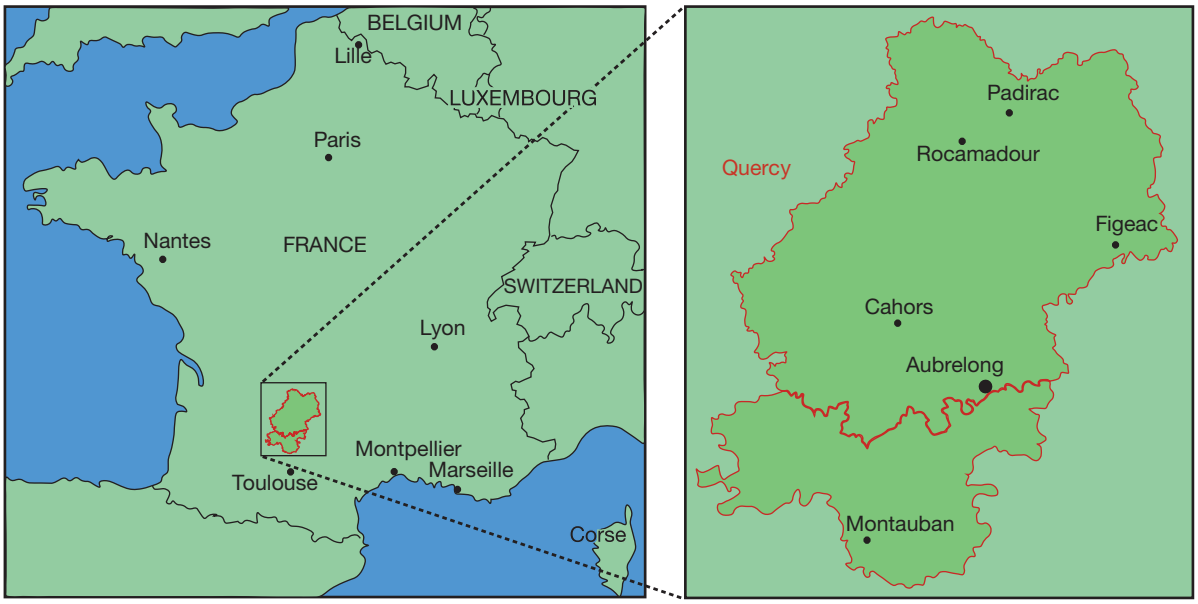


Fig. 1. — Location map of Aubrelong (France; Rupelian, MP21) where the new fossils of *Cynodictis lacustris* were found. The Quercy area is composed of the Lot Department and part of the Tarn-et-Garonne.

with dental remains, and are difficult to associate with certainty to craniodental elements; consequently they have often been neglected. For instance, the predator taxa known from the Quercy Phosphorites were mostly defined on the basis of dental characters, and the postcranial material associated with these taxa is extremely rare (e.g., Peigné 2000; Peigné & Bonis 1999; Bonis 2011). Postcranial bones and dental elements were, however, not subjected to the same selective pressure (see Szalay & Lucas (1996), and, as a result, two taxa can display widely different dental morphotypes but similar locomotor adaptations. The morphology of the postcranial bones of carnivorans are correlated with the type of locomotion, being influenced by habitat (arboreal or terrestrial) and/or by hunting strategies (pursuit or ambush) (Goswami & Friscia 2010). This is particularly the case for the ankle bones and more particularly for astragali and calcanei. Their morphology is strongly correlated with the degree of flexion and inversion-eversion of the foot and thus provides information on the mechanics of the hindlimb (Panciroli *et al.* 2017). Therefore, postcranial material is the best indicator of locomotor and postural habits, which are an essential component for the reconstruction of the ecology (Panciroli *et al.* 2017).

The present study focuses on Amphicyonidae, which are among the most abundant carnivorous mammals in the Quercy deposits (Teilhard de Chardin 1915). They are therefore a key taxon to better understand the Grande Coupure and the evolution of Paleogene faunas. This family of Carnivora, the so-called 'bear-dogs', consists of at least 42 genera and ranges from the Eocene to the Miocene (Goswami & Friscia 2010). The phylogenetic position of Amphicyonidae has long been debated: they were first considered closely related to Canidae (Matthew & Granger 1924; Petter 1966), then placed as the sister group of Ursoidea (Ginsburg 1966; Hough 1948; Hunt 1977; Wyss & Flynn 1993), and more recently as the sister group of Arctoidea (Finarelli 2008; Hunt 1996, 1998), to finally be considered as the sister group of all Caniformia (Tomiya & Tseng 2016).

This study aims to identify isolated ankle bones of Amphicyonidae as accurately as possible, using four criteria: relative abundance, size, body mass, and morphology. The final goal is to characterize the evolution of posture and locomotion of European amphicyonids across the "*Grande Coupure*" in order to reveal a new aspect of this profound turnover.

MATERIAL AND METHODS

Studied specimens

The study material includes 118 tarsal bones: 30 astragali and 88 calcanei; 61 of these fossils come from the Paleontology Collections of the Muséum national d'Histoire naturelle (MNHN, Paris), 28 belong to those of the Université de Liège (ULiege, Belgium) and 29 belong to those of the KU Leuven (KUL, Belgium). These bones are all from the Quercy Phosphorites (southwestern France). Of these, 91 lack locality information or have information that is of no use because it corresponds to undated localities from the Quercy area such as Caylus, Mouillac, Promilhanes, and Bach. The samples were identified in the three collections as "Carnivores" (i.e., Carnivora or Hyaenodonta) without further specification. Only 27 fossils are from a dated locality: Aubrelong (commune de Bach, Lot, France; Oligocene, Rupelian) (Fig. 1); this locality is close to the MP21 reference locality (Soumailles, France) of the MP scale (Gèze 1974; BiochroM'97 1997b; Lange-Badré 1970, 1979 – MP = Mammal Paleogene reference-levels – BiochroM'97 1997b).

Table 1. — List of specimens used for the comparisons.

Family rank	Genus/species	References
Hyaenodontidae	*Hyaenodon* Laizer & Parieu, 1838	Bastl 2012
	Galecyon chronius Zack, 2011	Zack & Rose 2015
	Indohyaenodon raoi Bajpai, Kapur & Thewissen, 2009	Rana *et al.* 2015
Nimravidae	*Hoplophoneus primaevus* (Leidy & Owen, 1851)	Barrett 2016
	Nimravus brachyops (Cope, 1878)	Barrett 2016
Miacidae	*Vulpavus* Marsh, 1871	Heinrich & Rose 1997
Ursidae	*Ursus spelaeus* Rosenmüller, 1794	Santi *et al.* 2005
	Ursus arctos Linnaeus, 1758	Baryshnikov 2015
Ailuridae	*Simocyon batalleri* (Viret, 1929)	Salesa *et al.* 2008
Mustelidae	*Martes sansaniensis* Lartet, 1851	Peigné 2012
	Ischyrictis zibethoides Blainville, 1841	Peigné 2012
	Taxodon sansaniensis Lartet, 1851	Peigné 2012
Amphicyonidae	*Afrocyon ginsburgi* Morales, Pickford, Soria & Fraile, 1998	Morales *et al.* 2016
	Amphicyon major Blainville, 1841	Argot 2010
	Amphicyon galushai Hunt, 2003	Hunt 2009
	Amphicyon lathanicus Ginsburg, Cheneval, Janvier, Pouit & Sen, 2000	Ginsburg 2002
	Amphicyon giganteus Schinz, 1825	Gagnaison *et al.* 2017
	Daphoenodon robustum Peterson, 1910	Hunt 2009
	Cynelos lemanensis Pomel, 1846	Peigné & Heizmann 2003
	Daphoenodon superbus Peterson, 1907	Hunt 2011
	Ysengrinia americana Wortman, 1901	Hunt 2002

Table 2. — Relative abundances (%) of taxa defined on dental specimens, astragali and calcanei according to each collection (ULg, KUL and MNHN). Highlighted in gray, the values discussed in the text. Abbreviation: **n**, number of specimens in the collections.

	m1			Astragali				Calcanei			
Taxa	**Ulg (n=203)**	**KUL (n=58)**	**Total (n=261)**	**Ulg (n=15)**	**KUL (n=14)**	**MNHN (n=54)**	**Total (n=83)**	**Ulg (n=43)**	**KUL (n=36)**	**MNHN (n=85)**	**Total (n=164)**
Hyaenodonta	20	–	10	20	14.29	31.48	21.92	16.28	22.22	17.65	18.72
Miacidae	–	–	–	6.67	–	5.55	4.07	13.95	5.56	7.06	8.86
Basal Aleuroidea	19.02	27.59	23.31	–	–	–	–	–	–	–	–
Amphicyonidae	30.73	31.03	30.88	20	57.14	35.19	42.21	58.14	58.33	49.41	55.28
Ursoidea	16.59	39.66	28.12	–	–	–	–	–	8.33	11.76	6.7
Musteloidea	–	–	–	40	–	9.25	16.42	2.33	–	2.35	1.56
Basal Arctoidea	3.9	1.72	2.81	–	–	–	–	–	–	–	–
Ailuridae	1.46	–	0.73	–	–	–	–	–	–	–	–
Caniformia indet	–	–	–	–	14.29	–	–	4.65	5.55	–	3.4
Nimravidae	8.29	–	4.145	13.3	14.29	16.67	14.76	2.33	–	8.24	3.52
Feliformia indet	–	–	–	–	–	1.85	0.62	2.33	–	3.53	1.95

Systematic identification

Due to the absence of identified carnivoran postcranial elements in the Quercy deposits and the fact that postcranial remains are found isolated from cranial elements, four criteria are used for the identification: morphology, relative abundance, size, and body mass. Postcranial elements of fossil Carnivora from other deposits in France, Eurasia, and North America, as well as extant, closely related species of Carnivora (Table 1), are used for the anatomical comparisons. Our analyses allowed us to identify as accurately as possible the tarsal bones studied (here at the family rank, Amphicyonidae). Due to their substantial postcranial morphological disparity (e.g., Argot 2010; Hunt 2009), Amphicyonidae are not formally characterized by discriminating features from the tarsal bones. We compensate for this by relying heavily on existing anatomical comparisons between Amphicyonidae and other extinct and extant carnivorans (Ginsburg 2002; Peigné & Heizmann 2003; Argot 2010; Hunt 2002, 2009, 2011; Morales *et al.* 2016; Gagnaison *et al.* 2017), from which we were able to deduce general characteristics for each amphicyonid tarsal bone. These are the following: the astragalus displays a medial projection of the head and an asymmetrical trochlea, while the calcaneus has a rounded sustentacular facet and a cuboid facet with a slight tilt in a medioproximal-laterodistal orientation. These feature associations, however, may vary according to the amphicyonid species; for instance *Daphoenodon robustum* (Hunt 2009) and *Amphicyon major* (Argot 2010) display clearly different morphologies.

The relative abundances of the tarsal bones identified were compared to the dental specimens from the ULiege

and KUL collections; these specimens were identified by F.S. and K.L.V. We chose to restrict our comparisons to these two Belgian collections because they have an unusually high abundance of dental and postcranial fossils and, unlike the MNHN, they seem to cover a short period of time, which implies a certain homogeneity (Solé *et al.* in press). The relative abundances are based on the number of specimens (dental material, astragalus, and calcaneus) of each group compared to the total number of specimens in the collection (Table 2).

Size and body mass can make it possible to further specify the identification at the species rank. Body masses of Amphicyonidae were estimated on the basis of dental material using the methods established by Van Valkenburgh (1990) for Carnivoramorpha (Table 3). The masses are calculated according to the following formula: Log10(BM) = [2.97 × Log10(Lm1)] – 2.27; BM = estimated body mass in kg; Lm1 = length of the first lower molar in millimeters. We also estimated the body mass of the taxa represented in our sample of tarsal bones. Body mass was estimated using the astragalus based on Tsubamoto (2014): Log(BM) = [3.125 × Log10(La)] – 0.463; BM = estimated body mass in g; La = maximum length of the astragalus in millimeters (Table 4). Estimations are not yet possible from calcanei.

We use the terminology of recent works about the postcranial anatomy of mammals (e.g., Coillot *et al.* 2013; Argot 2013) and when useful, the corresponding terminology following the Nomina Anatomica Veterinaria (Waibl *et al.* 2005; Schaller 2007) is indicated in parentheses.

Locomotor reconstruction

The locomotor reconstruction is based on direct observations on the specimens together with data from the literature. We distinguish locomotor categories and the following foot postures:

– Plantigrade: the heel (= calcaneus + astragalus) is placed completely flat on the ground during locomotion (Wang 1993; Polly 2010);

– Semi-digitigrade: the heel is occasionally in contact with the substrate at rest, but in motion the animal adopts a more digitigrade position (Polly 2010);

– Digitigrade: the animal stands on the distal ends of the middle metapodials and phalanges; the heel does not come into contact with the ground during locomotion (Wang 1993; Polly 2010).

For the locomotor categories, the following terms are used:

– Terrestrial: spends most time on the ground (Polly & McLeod 2008). A terrestrial animal can be also cursorial;

– Scansorial: spends considerable time on the ground, but is also a good climber (Polly & McLeod 2008);

– Arboreal: spends most of its time in trees (Polly & McLeod 2008);

– Semifossorial: digs frequently for food and protection (Bastl 2012);

– Cursorial: forages over large areas. There are three types of cursorial mammals: 1) runner capable of prolonged trotting, but not fast (e.g., hyenas); 2) fast runner depending upon both speed and stamina (e.g., grey wolf); and 3) sprinters with fast acceleration for short distances (e.g., cheetah) (Taylor 1989).

Moreover, the calcaneal gear ratio helps in determining the posture and locomotion (Polly 2010). It corresponds to the calcaneal proximodistal length divided by the length from the proximal end of the calcaneus to the distal margin of the sustentaculum tali. We calculated the calcaneal gear ratio for each morphotype (Table 5) and compared them with gear ratios in Polly *et al.* (2017).

Table 3. — Comparison of body mass (in kg) estimated on the basis of the lower first molar (Van Valkenburgh 1990) for the amphicyonid genera known in the Paleogene of Europe, with indication of their stratigraphic distribution (MP levels). The body mass of all amphicyonids species are in Appendix 2.

Genus	Body mass	Stratigraphic distribution (MP)
"*Cynodictis*"	4-9	19-21
Cynodictis	5-9	18-23
Symplectocyon	7	21
Goupilictis	13	28-30
Cynelos	23-42	26-30
Haplocyon	29-45	29-30
Pseudocyonopsis	29-73	21-29
Harpagocyon	35	29
Brachycyon	45	26-28
Haplocyonopsis	86	30
Ysengrinia	96	29-30
Crassidia	134	29-30

Table 4. — Estimation of body masses (in kg) of the amphicyonids from Quercy Phosphorites based on astragalus (Tsubamoto 2014). The measurements used for the estimations are in Appendix 1.

Taxon/Morphotype	Estimated body mass
Cynodictis lacustris	1.042-1.843
Morphotype 1	7.846-16.566
Morphotype 2	18.091-21.225
Morphotype 3	0.812-2.783
Morphotype 4	1.806

Table 5. — Calcaneal gear ratio (Polly 2010) estimated for *C. lacustris* and each morphotype.

Taxon/Morphotype	Gear ratio
Morphotype A	1.23
Morphotype B	1.25
Morphotype C	1.18
C. lacustris	1.27

Institutional abbreviations

MNHN.F Palaeontological collection of the Muséum national d'Histoire naturelle;
MNHN.F.Au fossil collection from Aubrelong;
MNHN.F.Qu fossil collection from the Quercy Phosphorites;
KUL.PLV1542 vertebrate fossil collection of KU Leuven;
ULgPA.17.170 collection of Quercy calcanei of the Université de Liège;
ULgPA.17.175 collection of Quercy astragali of the Université de Liège.

SYSTEMATIC PALAEONTOLOGY

CARNIVORAMORPHA Wyss & Flynn, 1993
CARNIVORAFORMES
Flynn, Finarelli & Spaulding, 2010
Order CARNIVORA Bowdich, 1821
Suborder CANIFORMIA Kretzoi, 1943
Family AMPHICYONIDAE Trouessart, 1885
Genus *Cynodictis* Bravard & Pomel, 1850

Cynodictis lacustris Gervais, 1852
(Fig. 2)

HOLOTYPE. — Fragmentary mandible bearing P4 and M1; MNHN.F.Qu unnumbered (Gervais 1852).

NEWLY REFERRED SPECIMENS. — **Astragali**. MNHN.F.Au1076, MNHN.F.Au3169, MNHN.F.Au847, MNHN.F.Au3186I, MNHN.F.Au984, MNHN.F.Au994, unnumbered specimen (astragalus + navicular).
Calcanei. MNHN.F.Au2188, MNHN.F.Au2699, MNHN.F.Au1059*, MNHN.F.Au848, MNHN.F.Au2398, MNHN.F.Au2020, MNHN.F.Au991, MNHN.F.Au2044, MNHN.F.Au2118*, MNHN.F.Au618, MNHN.F.Au822, MNHN.F.Au2209*(10), MNHN.F.Au2705, MNHN.F.Au2703, MNHN.F.Au992, MNHN.F.Au976, MNHN.F.Au2471, MNHN.F.Au845, MNHN.F.Au2391, MNHN.F.Au2018, MNHN.F.Qu9699, MNHN.F.Qu9757.

STRATIGRAPHIC DISTRIBUTION. — MP18-MP21 Priabonian – early Rupelian. It should be noted that some authors suggest that the genus is present up to MP23 (e.g., Kotsakis 1980: 268, 269).

TYPE LOCALITY. — La Débruge (Vaucluse, France).

LOCALITY. — Aubrelong (Lot, France).

AGE LOCALITY. — MP21, early Rupelian.

REMARKS ON NEWLY REFERRED SPECIMENS
These specimens are here identified as Amphicyonidae because of their morphological similarities with European and North American amphicyonids: astragalus with a medial projection of the head and the asymmetry of the trochlea; calcaneus with a rounded shape of the sustentacular facet and a slight tilt in a medioproximal-laterodistal orientation of the cuboid facet. Futhermore, the differences observed with other carnivoran clades found in the Quercy deposits (Table 1) allow us to differentiate the studied bones from these taxa, and to support the assignment to amphicyonids. The specimens are assigned to the species *C. lacustris* because of their geographic localization, small size, and high relative abundance (see Comparison for determination).

ASTRAGALUS (TALUS) DESCRIPTION (FIG. 2A-E)
Dorsal view
The trochlea (*trochlea tali proximalis*) is deeply excavated. Its proximodistal length is greater than its mediolateral length. The axis of elongation of the trochlea is inclined relative to that of the neck. Its medial and lateral lips are of approximately the same proximodistal length and are more or less parallel. The proximal plantar tuberosity is very small or absent. The neck *(collum tali)* is mediolaterally thinner than the head (*caput tali*) and is relatively short. The head is strongly distally convex. It is broad (wider than the mediolateral length of the trochlea) and projected on the medial side. It rises on the neck on the medial side of the astragalus and almost reaches the distal edge of the trochlea.

Ventral view
The ectal facet (*facies articularis calcaneae lateralis*) is proximodistally elongated and more distally distinct than proximally. It is strongly concave and its medial edge curves slightly. The sinus of the tarsus (*sinus tarsi*) is deep. It clearly separates the two facets for the articulation with the calcaneus (*facies articulares calcaneae*). The sustentacular facet (*facies articularis calcaneae medialis*) is quite large and occupies a large portion of the width of the neck. Its medial and distal edges are well marked. It is elongated and extends proximomedially towards the trochlea. The distolateral part of this facet extends to almost reach the head of the astragalus (*caput tali*). It is slightly convex except on its proximomedial extension, where it becomes concave. The foramen in the proximal portion of this sinus is present. The head has a small ventral extension that goes partly back to the sustentacular facet.

Lateral view
A slight depression is formed proximal to the fibular facet (*facies malleolaris lateralis*). The proximomedial edge of the fibular facet forms a nearly right angle with the distal edge. The distal edge is relatively distally convex in the extension of the lateral edge of the trochlea. The ectal facet is well curved.

Distal view
The trochlea is slightly asymmetrical. The head is dorsoventrally flattened, thinner on the medial side, and wider on its lateral side. The axis of elongation of the head is inclined relative to the mediolateral axis of the astragalus. The lateral process is limited in breadth, forming only a slight medially directed tip.

Proximal view
The trochlear foramen is present on some specimens and absent in others. The proximoventral edge of the medial lip of the trochlea forms a slight ventral tip. The plantar tendon groove (for the *flexor digitorum fibularis*) is very weak. It seems to be fused with the proximal prolongation of the trochlea. The trochlea is mediolaterally thinner on its proximal part than on its dorsal part.

CALCANEUS DESCRIPTION (FIG. 2F-J)
Dorsal view
The medial process of the *tuber calcanei* is slightly proximally broader than the lateral process. The sagittal groove is rather marked. The *tuber calcanei* is not very mediolaterally broad but rather proximodistally elongated. The ectal facet (*facies articularis talaris proximalis*) is proximodistally elongated. It

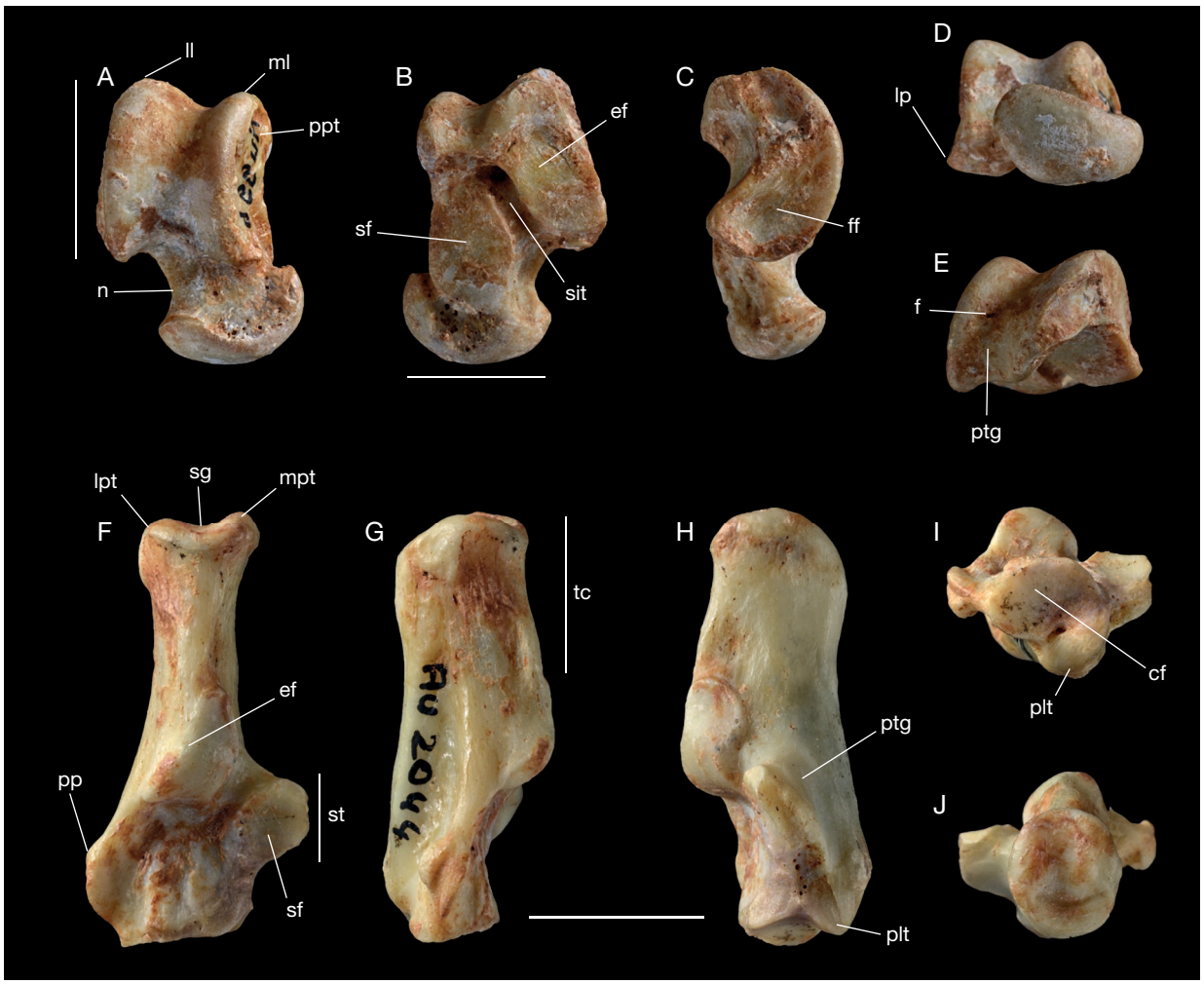


Fig. 2. — Tarsal bones of *Cynodictis lacustris* from Aubrelong (France; Rupelian, MP21): **A**-**E**, MNHN.F.Au994, left astragalus (reversed views); **A**, dorsal view; **B**, ventral view; **C**, lateral view; **D**, distal view; **E**, proximal view; **F**-**J**, MNHN.F.Au2044, right calcaneus; **F**, dorsal view; **G**, lateral view; **H**, medial view; **I**, distal view; **J**, proximal view. Abbreviations: **cf**, cuboid facet; **ef**, ectal facet; **f**, foramen; **ff**, fibular facet; **h**, head; **ll**, lateral lip; **lp**, lateral process; **lpt**, lateral process of tuber; **ml**, medial lip; **mpt**, medial process of tuber; **n**, neck; ppt, proximal plantar tuberosity; **plt**, plantar tubercle; **pp**, peroneal process; **ptg**, plantar tendon groove; **sf**, sustentacular facet; **sg**, sagittal groove; **sit**, sinus of the tarsus; **st**, sustentaculum tali; **tc**, tuber calcanei; **tr**, trochlea. Scale bar: 1 cm.

is strongly convex in the middle and very slightly proximally and distally concave. Its medial and lateral edges are slightly curved. The edges of this facet are rather well marked, except the distal edge, which merges with the body of the calcaneus and therefore is difficult to delimit. The sustentacular facet (*facies articularis talaris distalis*) is slightly elongated in the proximolateral-distomedial direction and extends slightly on the proximal edge of the *sustentaculum tali*. This gives a rather oval shape to this articular surface. The peroneal process is quite broad. The cuboid facet (*facies articularis cuboidea*) is inclined with respect to the mediolateral axis and its lateral edge rises above the body of the calcaneus.

Lateral view

The dorsal and ventral edges of the tuber are very slightly curved; the tuber is dorsoventrally wide. A well marked ridge is formed at the continuity of the peroneal process and join more distally the *tuber calcanei*.

Medial view

The groove for the plantar tendon (*sulcus tendinis musculus flexor digiti lateralis*) is pronounced. The plantar tubercle is distally large, forming a distally oriented tip.

Distal view

The cuboid facet is very slightly concave, quite dorsoventrally thin and mediolaterally elongated. The plantar tubercle is ventrally broad. The edge separating these two structures is not very broad.

Proximal view

The distal part of the *tuber calcanei* has a rather oval surface that is slightly dorsoventrally elongated. A slightly curved groove is ventrally clearly visible.

Comparison

These tarsal elements are all from Aubrelong (France, MP21; except two specimens whose exact locality is unknown).

Cynodictis lacustris differs from Hyaenodonta (e.g., *Hyaenodon* Laizer & Parieu, 1838 from the Eocene of Europe [Bastl 2012] and *Galecyon chronius* Zack, 2011 from the Eocene of North America [Zack & Rose 2015]) in its astragalus morphology which displays an astragalar neck that is less distomedially oriented and mediolaterally thinner; a head that extends less on the medial part of the neck, and a medial edge of the head that is more pronounced (Table 1). Moreover, the plantar tendon groove is less pronounced than the proximal plantar tuberosity and the lateral process is slenderer than in Hyaenodonta. For the calcaneus, the cuboid facet of *C. lacustris* is less inclined than in *Indohyaenodon raoi* Bajpai, Kapur & Thewissen, 2009 (Ypresian, India; Rana *et al.* 2015) and *Galecyon chronius* (Eocene, North America; Zack & Rose 2015).

Compared to Nimravidae, such as *Hoplophoneus primaevus* (Leidy & Owen, 1851) and *Nimravus brachyops* (Cope, 1878) (Oligocene, North America; Barrett 2016), the astragalus of *C. lacustris* has a longer neck and the head extends less on the medial side of the neck. Its calcaneus has a thinner *sustentaculum tali* and a shallower plantar tendon groove than in Nimravidae.

Compared to Miacidae such as *Vulpavus* Marsh, 1871 (Eocene, North America; Heinrich & Rose 1997), the tarsal bones of *C. lacustris* are smaller, the neck of the astragalus is shorter and less medially projected, and the plantar tendon groove is less pronounced and less dorsally extended. Moreover, the *sustentaculum tali* is not as medially broad and proximally located, and the cuboid facet is less inclined.

Cynodictis lacustris differs from Ursoidea (only modern forms because of the lack of ursid tarsal bones from the Paleogene or Miocene in the literature) (Gagnaison *et al.* 2017), such as *Ursus spelaeus* Rosenmüller, 1794 (early Pleistocene of Europe; Santi *et al.* 2005) and *Ursus arctos* Linnaeus, 1758 (Pleistocene of Europe; Baryshnikov 2015): the astragalus of *C. lacustris* is thinner, the neck is much longer, and the trochlea is mediolaterally narrower and is not flattened proximodistally . The *tuber calcanei* is less stockier and mediolaterally thinner. The *sustentaculum tali* is less distally positioned and its sustentacular facet is shorter, more rounded, and not as inclined in the medio-proximal-laterodistal direction.

In comparison with Ailuridae, such as *Simocyon batalleri* (Viret, 1929) (Miocene, Spain; Salesa *et al.* 2008), the astragalus of *C.lacustris* has a shallower trochlea, a shorter and mediolaterally broader neck, and a less flattened head. The *sustentaculum tali* of the calcaneus is proximodistally thinner, the cuboid facet is more inclined and the plantar tendon groove is less marked than in *S. batalleri*.

Compared with mustelids such as *Martes sansaniensis* Lartet, 1851, *Ischyrictis zibethoides* Blainville, 1841, and *Taxodon sansaniensis* Lartet, 1851 (Miocene, Europe; Peigné 2012), the astragalar neck of *C. lacustris* is shorter and less medially projected and the sustentacular facet is mediolaterally broader. The calcaneus of *C. lacustris* has a more inclined cuboid facet and a shorter plantar tubercle than in *M. sansaniensis*. The *sustentaculum tali* is proximodistally and mediolaterally narrower, the *tuber calcanei* is mediolaterally thinner and the peroneal process is proximodistally broader than in *T. sansaniensis*. *Cynodictis lacustris* also exhibits a smaller calcaneus as compared with *I. zibethoides*, with a *sustentaculum tali* that is proximodistally narrower and a thinner medial process of *tuber*.

All the features discussed above allow us to discriminate the Aubrelong amphicyonids from the other carnivorous groups recorded in Aubrelong and the Phosphorites du Quercy analysed in the framework of this study. The studied bones particularly resemble those of the Amphicyonidae, such as the European *Amphicyon major* Blainville, 1841 (Miocene) (Argot 2010) and the North American *Amphicyon galushai* Hunt, 2003 and *Daphoenodon superbus* Peterson, 1907 (Miocene) (Hunt 2009; 2011). In these four species, the head is mediolaterally broad and medially projected, while the trochlea is asymmetrical. Futhermore, the deep and relatively broad thochlea observed in *C. lacustris* is a characteristic of large amphicyonids according Gagnaison *et al.* (2017) as *Amphicyon giganteus* Schinz, 1825. Moreover, some differences are noticeable: for instance, the average length of the *C. lacustris* astragali (14.91 mm) is much less than the length of those of *A. major*, *D. superbus* and *A. galushai* (around 50 mm) and the neck in *C. lacustris* is more elongated than in the other two species. The morphology of the calcaneus of *Cynodictis lacustris* is close to that of *Amphicyon major*. In these two species, the medial process of the *tuber calcanei* is proximally longer than the lateral process, the sustentacular facet is prolonged on its proximal edge, the *tuber calcanei* is quite thick dorsoventrally, and the cuboid facet is inclined with respect to the mediolateral axis. However, the cuboid facet is more inclined and more concave, the peroneal process is less broad and the *sustentaculum tali* is more distally prolonged in *Amphicyon major* than in *Cynodictis lacustris*.

The ratio of tarsal bone length/skull length of *C. lacustris* described here is similar to that of other amphicyonids. For instance, the ratio for *Daphoenodon robustum* Peterson, 1910 ranges between 0.14 to 0.16 for the astragalus and 0.24 to 0.26 for the calcaneus (Hunt 2009). In *C. lacustris*, the ratio for the astragalus ranges from 0.13 to 0.15 and for the calcaneus 0.18 to 0.26. This ratio is also close to that of modern ursids: 0.11 to 0.14 for the astragalus and 0.18 to 0.22 for the calcanueus (Baryshnikov & Boeskorov 2004; Baryshnikov 2015). Moreover, it is different from Hyaenodonta: astragalar ratio 0.09 to 0.11, and calcaneal ratio of 0.13 (Bastl 2012). In *S. batalleri* (Ailuridae), the astragalar ratio is 0.17 and the calcaneal ratio is 0.25. It is close to *C. lacustris* regarding the 1 (Salesa *et al.* 2008). The lack of data in the literature prevents us from calculating ratios for other fossil carnivoran clades.

Furthermore, the use of other criteria, such as relative abundance and size, allow us to be more specific and to attribute these tarsal bones to *Cynodictis lacustris* (Priabonian-Rupelian), primarily because this species is the only amphicyonid recognized based on dental and cranial elements in the Aubrelong locality (K. Le Verger pers. obs.).

Amphicyonidae Gen. indet.

Newly referred specimens. — **Astragali.** Morphotype 1: MNHN.F.Qu9986, MNHN.F.Qu10038, KUL.PLV1542.1, KUL.PLV1542_2, KUL.PLV1542_3, KUL.PLV1542_4. — Morphotype 2: MNHN.F.Qu10231, KUL.PLV1542_5, KUL.PLV1542_6, KUL.PLV1542_7, KUL.PLV1542_8. — Morphotype 3: MNHN.F.Qu9570, MNHN.F.Qu9758, MNHN.F.Qu10369, MNHN.F.Qu10368, MNHN.F.Qu10372, MNHN.F.Qu10371, MNHN.F.Qu10042, MNHN.F.Qu10367, ULgPA.17.175_1, ULgPA.17.175_2, ULgPA.17.175_3. — Morphotype 4: MNHN.F.Qu10039.
Calcanei. Morphotype A: MNHN.F.Qu9845, MNHN.F.Qu10095, MNHN.F.Qu10230, MNHN.F.Qu10237, MNHN.F.Qu10284, MNHN.F.Qu10282, MNHN.F.Qu10344, MNHN.F.Qu10350, MNHN.F.Qu10349, MNHN.F.Qu10347, MNHN.F.Qu10351, ULgPA.17.170_1, ULgPA.17.170_2, ULgPA.17.170_3, ULgPA.17.170_4, ULgPA.17.170_5, ULgPA.17.170_6, ULgPA.17.170_7, ULgPA.17.170_8, ULgPA.17.170_9, ULgPA.17.170_10, ULgPA.17.170_11, ULgPA.17.170_12, ULgPA.17.170_13, ULgPA.17.170_14, ULgPA.17.170_15, ULgPA.17.170_16, ULgPA.17.170_17, ULgPA.17.170_18, ULgPA.17.170_19, KUL.PLV1542_9, KUL.PLV1542_10, KUL.PLV1542_11, KUL.PLV1542_12, KUL.PLV1542_13, KUL.PLV1542_14, KUL.PLV1542_15, KUL.PLV1542_16, KUL.PLV1542_17, KUL.PLV1542_18, KUL.PLV1542_19, KUL.PLV1542_20, KUL.PLV1542_21, KUL.PLV1542_22, KUL.PLV1542_23. — Morphotype B: MNHN.F.Qu10399, MNHN.F.Qu10005, MNHN.F.Qu10003, MNHN.F.Qu9775, MNHN.F.Qu10002, MNHN.F.Qu10381, MNHN.F.Qu10239, MNHN.F.Qu10346, MNHN.F.Qu9987, ULgPA.17.170_20, ULgPA.17.170_21, ULgPA.17.170_22, ULgPA.17.170_23, ULgPA.17.170_24, ULgPA.17.170_25, KUL.PLV1542_24, KUL.PLV1542_25, KUL.PLV1542_26, KUL.PLV1542_27, KUL.PLV1542_28. — Morphotype C: KUL.PLV1542_29.

Stratigraphic distribution. — MP18-MP30; Priabonian-Chattian.

Locality. — Quercy (France), exact locality not indicated.

Remarks on newly referred specimens

These fossils are identified as Amphicyonidae because of their relative abundances, size, morphological similarities with European and North American amphicyonids and with *C. lacustris* described above, together with morphological differences from other carnivoran clades (Table 1). Moreover, relative abundance and body mass criteria support our identifications (see below). Although these bones are similar enough to those of amphicyonids to all be assigned to this family, morphological differences are noticeable between all these different specimens. These differences are perhaps representative of several amphicyonid genera or species, but so far more precise attribution is not possible, for lack of reliable arguments. For these reasons, they remain grouped into several morphotypes in this study, based on morphology and size (see Comparison for more details).

Astragalus descriptions

This set of astragalus morphotypes has the following characteristics. The trochlea is asymmetrical. Its mediolateral length is shorter than its proximodistal length. The axis of elongation of the trochlea is inclined relative to that of the neck. A depression is formed proximal to the fibular facet. The ectal facet is concave, proximodistally elongated and more distally thin. The sinus of the tarsus (*sinus tarsi* – *sensu* Schaller 2007) is deeply excavated. The sustentacular facet rises proximomedially towards the plantar tendon groove (for the *flexor digitorum fibularis*), as well as distolaterally to the head. This head is strongly distally convex and has a ventral extension that reaches back to the sustentacular facet. The head is dorsoventrally flattened, thinner on the medial side and wider on its lateral side. Four morphotypes are recognized among this sample of astragali due to differences in size and morphology.

Morphotype 1
(Fig. 3A-E)

Dorsal view
The trochlea is somewhat shallow. Its medial and lateral edges are more or less parallel to each other and are of different proximodistal lengths, the lateral edge being much shorter than the medial one. The proximal plantar tuberosity is present and slightly broad. The neck is thin, short and more mediolaterally extended than the head. The head is broad and projected on the medial side. It has strongly pronounced edges, rising on the neck at the medial side of the astragalus and reaching the level of the most distal edge of the trochlea.

Ventral view
The medial and lateral edges of the ectal facet have fairly strong curvatures. The foramen at the proximal level of this sinus is visible on some specimens. The sustentacular facet is quite large and occupies a large part of the neck width. It looks almost rhomboidal and its edges are strongly marked. The facet is slightly convex except on its proximomedial extension, where it becomes concave.

Lateral view
The proximomedial edge of the fibular facet forms a nearly right angle with the distal edge. The distal edge is flat, giving the facet a rectangular appearance. The ectal facet is shallow.

Distal view
The head has a groove in the center. The axis of elongation of the head is in the mediolateral axis of the *astragalus*. The lateral process is poorly broad.

Proximal view
The proximoventral part of the medial edge of the trochlea forms a ventral tip. The trochlear foramen is absent. The tendinous plantar groove is strongly excavated, rather mediolaterally thin, inclined with respect to the axis of the trochlea, and very deep.

Morphotype 2
(Fig. 3F-J)

Dorsal view
The trochlea is deeply excavated. The medial and lateral edges are relatively equal. The trochlea extends a little distally on the neck, almost forming a squatting facet. The proximal

plantar tuberosity is weakly broad. The neck is thin and more mediolaterally extended than the head. The neck is longer than that of Morphotype 1. The head is a little projected on the medial side (much less than in Morphotype 1) and its edges are not pronounced. It rises strongly on the medial edge of the neck, up to the level of the distal edge of the medial lip.

Ventral View
The ectal facet has little curvature on its medial and lateral margins. The foramen at the proximal level of this sinus is visible. The sustentacular facet is proximodistally elongated. Its lateral edge is rather marked, contrary to the other edges. The facet is slightly convex except on its proximomedial extension, where it becomes concave.

Lateral view
The edges of the fibular facet are relatively rounded, giving this facet a half-moon shape. The ectal facet is sharply convex.

Distal view
The axis of elongation of the head is inclined relative to the mediolateral axis of the astragalus. The lateral process is weak or absent.

Proximal view
The trochlear foramen is wide. The tendinous plantar groove is weakly excavated and is inclined almost 90° with respect to the axis of the trochlea.

Morphotype 3
(Fig. 3K-O)

Dorsal view
The trochlea is weakly excavated. The medial and lateral lips are of different proximodistal length, the lateral being shorter than the medial. The proximal plantar tuberosity is very slightly broad. The neck is short. In two specimens (MNHN.F.Qu10042 and MNHN.F.Qu10367), the neck is slightly longer than in the others, but these two specimens do not differ enough to represent another morphotype. The head is broad and projected on the medial side. It has more pronounced edges on the lateral side than on the medial one and rises strongly on the medial edge of the neck, reaching the level of the most distal edge of the trochlea.

Ventral View
The medial and lateral edges of the ectal facet are curved (more on the medial than on the lateral edge). A foramen is visible at the proximal level. The sustentacular facet has a rhomboidal area. Its edges are marked. The facet is slightly convex except on its proximomedial extension, where it becomes concave. In two specimens (MNHN.F.Qu10042 and MNHN.F.Qu10367), the sustentacular facet is slightly less elongated and more proximally positioned on the body than in the others.

Lateral view
The edges of the fibular facet are relatively rounded, giving this facet a half-moon look, as in Morphotype 2. The ectal facet is sharply convex.

Distal view
The axis of elongation of the head is slightly inclined with respect to the mediolateral axis of the astragalus. The lateral process is only slightly broad.

Proximal view
The trochlear foramen is absent in some specimens and present in others. The proximoventral edge of the medial lip of the trochlea (*trochlea tali proximalis*) forms a small ventral point. The tendinous plantar groove is present but weakly excavated and is well inclined relative to the axis of the trochlea.

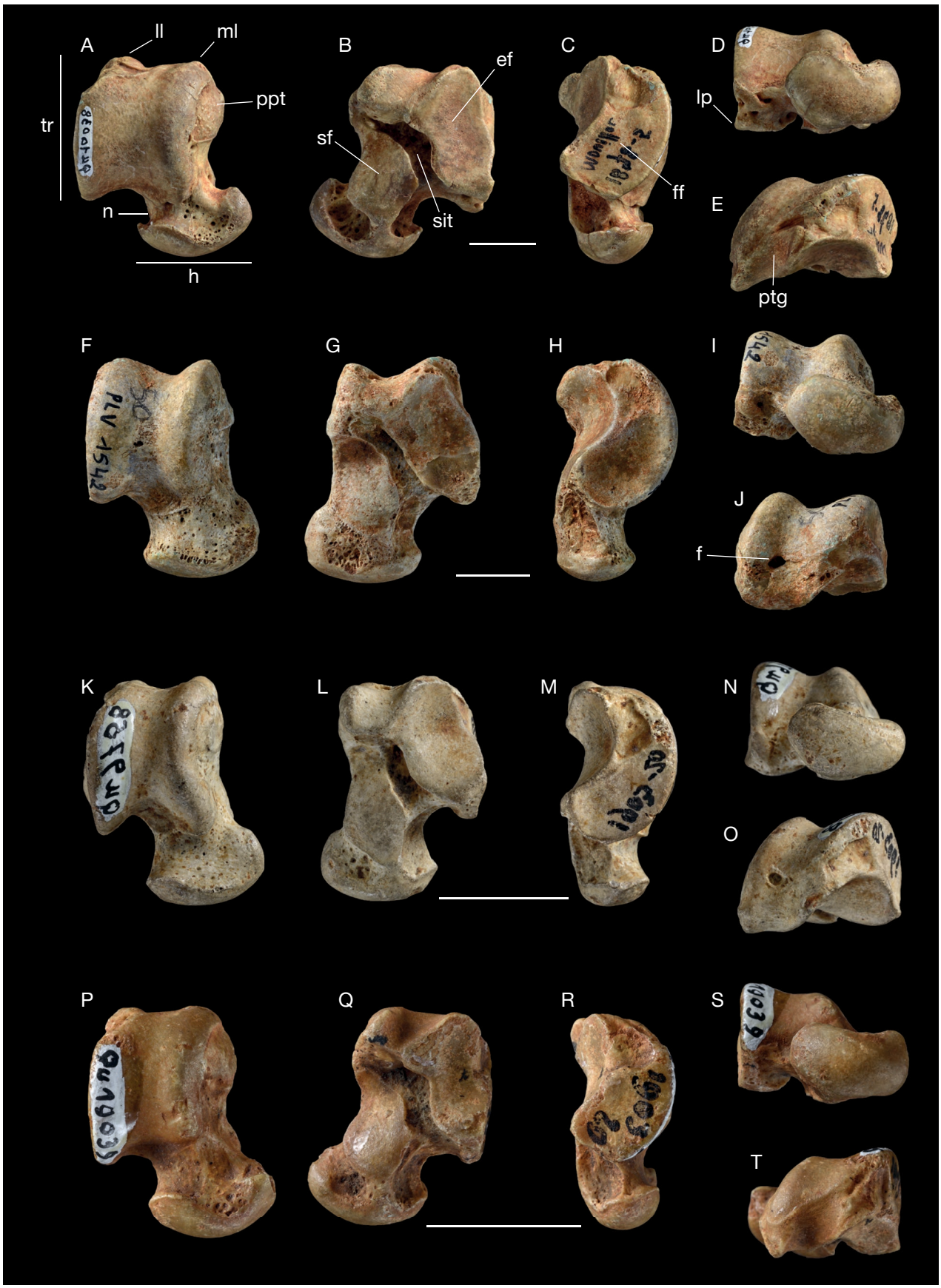
Morphotype 4
(Fig. 3P-T)

Dorsal view
The trochlea is shallow. The medial and lateral lips are more or less parallel to each other, but of different proximodistal lengths, and have a distal edge of the medial lip that is more proximal than the lateral lip. The proximal plantar tuberosity is a little broader than in Morphotype 3. The neck is longer than in Morphotype 3. The head is quite large and a little projected on the medial side. It has more pronounced edges than in Morphotype 3 and extends much less on the neck of the medial side of the *astragalus*. The medial edge of the head is well separated from the distal edge of the medial lip of the trochlea.

Ventral view
The medial and lateral edges of the ectal facet have a strong curvature. The sustentacular facet has a rhomboidal area. Its edges are well pronounced. This facet is slightly convex except on its proximomedial extension, where it becomes concave.

Lateral view
The proximomedial edge of the fibular facet is less rounded than in Morphotype 3 and therefore displays a somewhat rectangular shape. The ectal facet is sharply convex.

Fig. 3. — Astragali of undetermined amphicyonids from the Quercy (France; Priabonian-Chattian, MP18-MP30): **A**-**E**, Morphotype 1, MNHN.F.Qu10038, left astragalus (reversed views): **A**, dorsal view; **B**, ventral view; **C**, lateral view; **D**, distal view; **E**, proximal view; **F**-**J**, Morphotype 2, KUL.PLV1542_8, right astragalus: **F**, dorsal view; **G**, ventral view; **H**, lateral view; **I**, distal view; **J**, proximal view; **K**-**O**, Morphotype 3, MNHN.F.Qu9758, left astragalus (reversed views); **K**, dorsal view; **L**, ventral view; **M**, lateral view; **N**, distal view; **O**, proximal view; **P**-**T**, Morphotype 4, MNHN.F.Qu10039, right astragalus: **P**, dorsal view; **Q**, ventral view;



R, lateral view; **S**, distal view; **T**, proximal view. Abbreviations: **ef**, ectal facet; **f**, foramen; **ff**, fibular facet; **h**, head; **ll**, lateral lip; **lp**, lateral process; **ml**, medial lip; **n**, neck; **ppt**, proximal plantar tuberosity; **ptg**, plantar tendon groove; **sf**, sustentacular facet; **sit**, sinus of the tarsus; **tr**, trochlea. Scale bar: 1 cm.

Distal view
The axis of elongation of the head is along the mediolateral axis of the astragalus. The lateral process is very little broad.

Proximal view
The trochlear foramen is absent. The proximoventral edge of the medial lip of the trochlea forms a ventral tip. The plantar tendon groove is well marked, very inclined relative to the axis of the trochlea, and well excavated.

Calcaneus descriptions
For all morphotypes, the medial process of the *tuber calcanei* is proximally longer than the lateral process. A groove on the proximal surface of the *tuber calcanei*, positioned rather ventrally, is clearly visible. The cuboid facet is larger mediolaterally than proximodistally. Three different morphotypes have been determined based on differences in size and morphology.

Morphotype A
(Fig. 4A-E)

Dorsal view
The sagittal groove is rather marked. The proximal part of the *tuber calcanei* is rather mediolaterally wide. It is rather proximodistally elongated, as is the ectal facet. This facet is highly convex. Its edges are rather well pronounced, except the distal one, which merges with the body of the calcaneus (and therefore is difficult to delimit). The sustentacular facet is well-rounded, very slightly concave, and extends on the proximal edge of the *sustentaculum tali*. The peroneal process is quite broad and its proximal edge is well-defined. The cuboid facet is inclined with respect to the mediolateral axis and its lateral edge rises slightly on the body of the calcaneus. This articular surface is strongly concave.

Lateral view
The dorsal and ventral edges of the *tuber calcanei* are slightly concave. A cavity – probably for the insertion of the lateral collateral ligament – is clearly visible proximal to the ectal facet.

Medial view
The tendinous plantar groove is well excavated. The *sustentaculum tali* is dorsoventrally quite thick, even more so than in *Cynodictis lacustris* and Morphotype B. The plantar tubercle does not form a distally directed tip as seen in *Cynodictis lacustris*.

Distal view
The plantar tubercle is ventrally broad. The edge separating the plantar tubercule and the cuboid facet is more visible than in *Cynodictis lacustris*.

Proximal view
The proximal part of the *tuber calcanei* has a sub-spherical surface. The groove is slightly more pronounced than in *Cynodictis lacustris*.

Morphotype B
(Fig. 4F-J)

Dorsal view
The sagittal groove is rather visible. The *tuber calcanei* is proximodistally quite elongated. The ectal facet is more inclined relative to the proximodistal axis than in other morphotypes, as well as in *Cynodictis lacustris*. It is strongly convex in the middle and very slightly concave in its proximal part. The edges of this facet are rather well pronounced, except the distal edge, which merges with the body of the calcaneus and is therefore difficult to delimit. The sustentacular facet is rounded and extends slightly on the proximal edge of the *sustentaculum tali*. It is placed more proximal on the body of the calcaneus than in the other two calcaneal morphotypes. The peroneal process and its proximal and distal edges are quite well defined. The cuboid facet is inclined with respect to the mediolateral axis and its lateral edge rises over the body of the calcaneus. The plantar tubercle is distally very long and clearly visible in dorsal view. It is longer than that of *Cynodictis lacustris*.

Lateral view
The dorsal and ventral edges of the *tuber calcanei* are very slightly concave. The cavity, proximal to the ectal facet, is deep and positioned higher on the tuber than in Morphotype A.

Medial view
The tendinous plantar groove is quite excavated.

Distal view
The cuboid facet is smaller than in Morphotype A. The plantar tubercle is ventrally quite broad. The edge separating these two structures is not very clear.

Proximal view
The proximal part of the *tuber calcanei* has a rather oval surface that is slightly dorsoventrally elongated.

Morphotype C
(Fig. 4K-O)

Dorsal view
The sagittal groove is poorly defined. The *tuber calcanei* is proximodistally quite elongated. The ectal facet is convex in the middle and very slightly concave in its proximal part. The edges of this facet are rather clear, except the distal edge, which merges with the body of the calcaneus (and is therefore difficult to delimit). The *sustentaculum tali* has a rounded articular surface, as in Morphotypes A and B, and extends slightly on the proximal edge. The peroneal process is not broad and merged with the ridge extending up on the *tuber calcanei*. The cuboid facet is concave and inclined with respect to the mediolateral axis, but its lateral edge does not extend up the body of the calcaneus as seen in Morphotypes A and B.

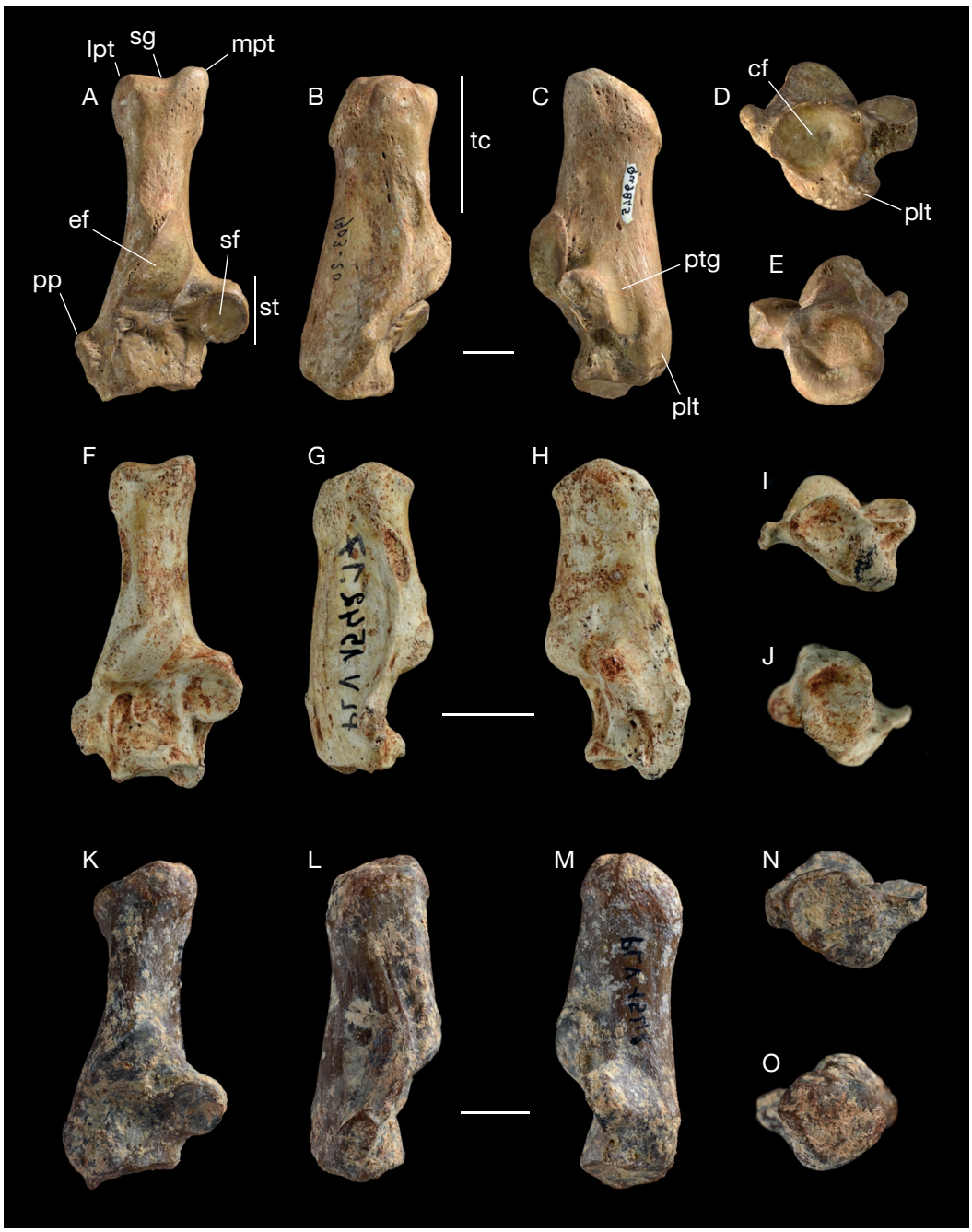


Fig. 4. — Calcanei of undetermined amphicyonids from the Quercy (France; Priabonian-Chattian, MP18-MP30): **A**-**E**, Morphotype A, MNHN.F.Qu9845, left calcaneus (reversed views): **A**, dorsal view; **B**, lateral view; **C**, medial view; **D**, distal view; **E**, proximal view; **F**-**J**, Morphotype B, KUL.PLV1542_28, left calcaneus (reversed views); **F**, dorsal view; **G**, lateral view; **H**, medial view; **I**, distal view; **J**, proximal view; **K**-**O**, Morphotype C, KUL.PLV1542_29, left calcaneus (reversed views): **K**, dorsal view; **L**, lateral view; **M**, medial view; **N**, distal view; **O**, proximal view. Abbreviations: **cf**, cuboid facet; **ef**, ectal facet; **lpt**, lateral process of tuber; **mpt**, medial process of tuber; **pp**, peroneal process; **plt**, plantar tubercle; **ptg**, tendinous plantar groove; **sg**, sagittal groove; **sf**, sustentacular facet; **st**, sustentaculum tali; **tc**, tuber calcanei. Scale bar: 1 cm.

Lateral view
The dorsal and plantar edges of the *tuber calcanei* are very slightly concave. The cavity, which is proximal to the ectal facet, is not very deep.

Medial view
The tendinous plantar groove is not very marked. The *sustentaculum tali* is dorsoventrally quite thick, as in Morphotype A.

Distal view
The plantar tubercle is ventrally well broad.

Proximal View
The edges of the proximal part of the *tuber calcanei* are quite irregular.

Comparison

These morphotypes exhibit morphological differences from tarsal bones of Hyaenodonta, such as *G. chronius* (Zack & Rose 2015) and *Hyaenodon* (Bastl 2012). The neck of the *astragalus* is mediolaterally thinner and the medial edge of the head is more pronounced in these morphotypes. The plantar tendon groove is less pronounced, the proximal plantar tuberosity and the lateral processes are slenderer. The calcaneus of the morphotypes has a much less inclined cuboid facet than in *I. raoi* (Rana *et al.* 2015) and *G. chronius* (Zack & Rose 2015).

In comparison with Nimravidae, such as *H. primaevus* and *N. brachyops* (Barrett 2016), all astragalus morphotypes have a longer neck and the head extends less on the medial side of this neck. The calcanei have a thinner *sustentaculum tali* and a shallower plantar tendon groove than in Nimravidae.

Compared to Miacidae such as *Vulpavus* (Heinrich & Rose 1997), the tarsal bones of the morphotypes are smaller, and the four astragalar morphotypes have a shorter neck, which is less medially projected, and a less pronounced plantar tendon groove, which is less dorsally extended. Moreover, the *sustentaculum tali* is medially thinner and not as distally positioned as in *Vulpavus*.

These morphotypes are also very different from those of Ursoidea such as *Ursus spelaeus* (Santi *et al.* 2005) and *Ursus arctos* (Baryshnikov 2015). They have less robust tarsal bones, the neck of the astragalus is much longer and the trochlea is mediolaterally thinner. The *tuber calcanei* is mediolaterally narrower, the *sustentaculum tali* is less distally positioned and its sustentacular facet is more rounded, not as elongated, and not inclined in the medioproximal-laterodistal direction as observed in ursoids.

Compared to the ailurid *Simocyon batalleri* (Salesa *et al.* 2008), the morphotypes have a less flattened astragalar head, and a mediolaterally broader sustentacular facet. The sustentaculum tali is proximodistally thinner, the peroneal process is mediolaterally and proximodistally thinner and the plantar tendon groove is less marked than in *S. batalleri.*

Compared to mustelids such as *M. sansaniensis*, *I. zibethoides* and *T. sansaniensis* (Peigné 2012), the astragalar neck of the morphotypes is shorter and less medially projected, and he sustentacular facet is mediolaterally broader. The calcaneus morphotypes are larger with a more rounded *sustentaculum tali*.

All these differences exclude an assignment of the bones to Hyaenodonta, Nimravidae, Miacidae, Ursidae, Ailuridae or Mustelidae and indicate a close relationship to amphicyonids. The astragalus of Morphotypes 1, 3, and 4 is very similar to that generally observed in Amphicyonidae such as *Amphicyon major* (Argot 2010), *Amphicyon galushai* (Hunt 2009), and the North American *Ysengrinia americana* Wortman, 1901 (Oligo-Miocene) (Hunt 2002). The head is relatively projected on the medial side of the *astragalus* and quite broad; the trochlea is asymmetrical and its mediolateral width is greater than its proximodistal length. Futhermore, Morphotype 1 displays a relatively large trochlea, just as Morphotype 2, which also features a deep trochlear articulation. These characteristics are present in large amphicyonids such as *Amphicyon giganteus* (Miocene of Europe and Africa; Gagnaison *et al.* 2017). Despite these morphological similarities, these three morphotypes display some differences from these amphicyonids (i.e., *A. major*, *A. galushai*, and *Y. americana*). The neck of Morphotype 1 is mediolaterally thinner and proximodistally shorter, and the fibular facet is dorsoventrally thicker than in Morphotypes 3 and 4. Moreover, Morphotype 1 is taller than the two others. The neck of Morphotype 3 is proximodistally longer and the head edges are less marked than in the others. In Morphotype 4, the distal edge of the trochlea medial lip is more proximal than the lateral lip and the plantar tendon groove is more marked. Morphotype 2 is assigned to Amphicyonidae because of its strong resemblance to the amphicyonid *Daphoenodon robustum* (North America, Miocene) (Hunt 2009). Indeed, the shape of the trochlea, relatively well excavated, the elongated neck, and the shape of the head, which is not mediolaterally wide in comparison to the width of the neck, are observed in *Daphoenodon robustum*.

The morphology of the calcaneus Morphotype A is closely similar to that of *Amphicyon galushai* (Hunt 2009), which also has a broad tubercle on its proximal part that is much thinner on its distal part. Moreover, the sustentacular facet is rounded and distally placed. Morphotype B is similar to the specimen of *Daphoenodon robustum* illustrated in Hunt (2009). The *sustentaculum tali* is more proximally located than in the other morphotypes. The plantar tubercle is ventrally and distally long, forming a tip at the cuboid facet. Morphotype C is morphologically similar to the calcaneus of the European *Amphicyon lathanicus* Ginsburg, Cheneval, Janvier, Pouit & Sen, 2000 (Miocene) (Ginsburg 2002). The *sustentaculum tali* is distally located, the cuboid facet is inclined with respect to the mediolateral axis and is distally strongly concave. Its morphology is also strongly similar to that of *Cynelos lemanensis* Pomel, 1846 (Peigné & Heizmann 2003), *Afrocyon ginsburgi* Morales, Pickford, Soria & Fraile, 1998 (Morales *et al.* 2016) and *Amphicyon longiramus* White, 1942 (Olsen 1960). The four amphicyonids share the following features: the peroneal process is poorly broad, the *sustentaculum tali* is distally positioned and the cuboid facet is concave. Moreover, the sustentacular facet is rounded in both *C. lemanensis* and Morphotype C. At the opposite side, the sagittal groove is more defined and the tuber *calcanei* is distally a little thinner in *C. lemanensis*. Relative abundance and body mass (see below) support the attribution of these morphotypes to amphicyonids, but they cannot be further assigned to infra-familial ranks.

Relative abundances

In almost all collections studied here, amphicyonids are by far the most abundant group (Table 2). This is also true for the dental specimens of this carnivoran group in the ULiege collection, with 30.73%. Amphicyonids are not the most abundant carnivorans in the KUL collection, but still represent 31.03% of the assemblage, making it the second most abundant group in this collection after Ursoidea (39.66%). The high relative abundance of amphicyonid tarsal bones is thus congruent with the high relative abundance of amphicyonids based on dental remains.

Body mass estimation

The body mass estimated for *Cynodictis lacustris* based on its astragalus (1 to 2 kg; Table 4) is lower than the values obtained from dental material (*c.* 5 kg; Table 3). For the European amphicyonids, the body mass estimated from the lower first molar varies between 4 and 134 kg (Table 3). This range is very broad and is greater than the values obtained for the four astragalar morphotypes. Morphotypes 1 and 2 fall within this range, but Morphotypes 3 and 4 are just outside this range with values below 3 kg; one can note that the latter case is similar to that of *C. lacustris* (Table 4).

Among the amphicyonids recorded in the Paleogene of Europe (Table 3), body masses between 5 and 10 kg correspond to the genera *Cynodictis*, *Symplectocyon* Springhorn, 1979, and "*Cynodictis*" (*C. exilis* Teilhard de Chardin, 1915 and "*C.*" *palmidens* Teilhard de Chardin, 1915). Therefore, Morphotypes 3 and 4 might correspond to these genera.

Morphotype 1 groups heavier specimens (between 8 and 17 kg based on astragalus; Table 4). Because it seems that the body masses estimated from the astragalus are lower than those estimated from the m1, Morphotype 1 could correspond to the smallest species of *Cynelos*, *Cynelos rugosidens* Schlosser, 1899 or *Cynelos crassidens* Filhol, 1876 (≈ 23-24 kg). Some specimens could also correspond to the Oligocene amphicyonid *Goupilictis* Ginsburg, 1969 (13 kg).

Finally, Morphotype 2 could also include specimens that correspond to the genus *Cynelos* Jourdan, 1862. It may also include representatives of the genera *Pseudocyonopsis* Kuss, 1965 and *Haplocyon* Schlosser, 1901 (Table 3).

Interestingly these new tarsal bones indicate significant differences in body mass within the same family (Table 4), as does the dental material (Table 3). Furthermore, there are no specimens that may correspond to the largest European amphicyonids *Brachycyon* Filhol, 1872, *Harpagocyon* Springhorn, 1977, *Ysengrinia* Ginsburg, 1965, *Haplocyonopsis* Bonis, 1973, and *Crassidia* Heizmann & Kordikova, 2000. It is worth noting that these genera are only known in the Chattian (MP26-MP30). Thus, the astragali studied here might come from Priabonian and Rupelian localities, except if some belong to *Goupilictis*.

Locomotion

Posture and locomotion significantly affect the morphology of the tarsal bones (Szalay & Decker 1974; Jenkins & McClearn 1984; Taylor 1989). The crurotarsal joint, where the tibia and astragalus are in contact, is the main axis of flexion of the foot. The posture is therefore related to the morphology of this articulation (Wang 1993). The calcaneus, which articulates with the astragalus, also has an important role in the movement of the hindlimb because of the insertion of the *m. gastrocnemius* and *m. soleus*. They attach to its distal end via the achilles tendon, which constitutes the main lever of plantar flexion (Barone 2000). Among the Carnivora, two postures are recognized: plantigrady and digitigrady. Some authors define an intermediate state present in many extant Mustelidae and Viverridae: semi-digitigrady (Wang 1993; Polly 2008).

Table 6. — Comparison of postures estimated on the basis of the *astragalus* and *calcaneus*.

Taxa/Morphotype	Posture	Locomotion
Cynodictis lacustris	Digitigrade	Cursorial ?
Morphotype 1	Plantigrade	–
Morphotype 2	Semidigitigrade	–
Morphotype 3	Plantigrade	–
Morphotype 4	Plantigrade	–
Morphotype A	Plantigrade	Terrestrial ?
Morphotype B	Semidigitigrade	Terrestrial ?
Morphotype C	Plantigrade	–

It appears that the absence of the trochlear foramen and a tendinous groove in digitigrade predators allows the tibia to rotate over the entire surface of the trochlea and thus to have a greater amplitude of flexion-extension (Wang 1993). According to Ginsburg (1961), an elongated astragalus is associated with digitigrade locomotion. Carrano (1997) remarked that the orientation of the astragalus head is a distinctive element between digitigrade and plantigrade postures: the head is oriented in the same direction as the body in dorsal view in a plantigrade mammal, whereas in a digitigrade mammal, it is inclined relative to the direction of the body of the *astragalus*. According to Polly (2008), in a digitigrade animal the calcaneal ectal facet is sharply convex, the peroneal process is small, the *sustentaculum tali* is more proximally and posteriorly positioned, and the astragalar ectal facet is sharply curved. In plantigrade animals: the calcaneal ectal facet is rounded, the peroneal process is long, the *sutentaculum tali* is larger and distally positioned, the astragalar neck is narrow, and the astragalar ectal facet is shallow. Finally, the presence of large and flat facets on these two bones causes a reduction of intertarsal mobility (Polly 2008).

All the postures and locomotion hypothesized for the sample presented herein are listed in Table 6. Morphotype 1 has a plantar tendinous groove, and the head is not inclined towards the mediolateral axis. The ectal facet is shallow, as for *Ailurus fulgens* Cuvier, 1825 (Ailuridae) and *Bassaricyon gabbii* Allen, 1876 (Procyonidae), two plantigrade species (Polly 2008). It has a narrow neck and an ectal facet that is shallow. These characters suggest that Morphotype 1 corresponds to a plantigrade animal. Morphotype 2 has a longer neck than in Morphotype 1, and a head that is slightly inclined towards the mediolateral axis. The neck is also larger and the ectal facet is sharply curved, as observed in *Canis lupus* Linnaeus, 1758 (Canidae), *Felis catus* Linnaeus, 1758, *Leptailurus serval* (Schreber, 1776), and *Lynx rufus* (Schreber, 1777) (Felidae), which are all digitigrade (Polly 2008). Morphotype 2 therefore better corresponds to a digitigrade animal. Moreover, it strongly resembles the astragalus of the North American amphicyonid *Daphoenodon robustum*, which was considered a digitigrade animal capable of powerful propulsive force (Hunt 2009). However, Morphotype 2 has a tendinous groove, which is placed fairly ventrally on the trochlea and weakly excavated. Flexion-extension should therefore have moderate amplitude, but more than a plantigrade animal with a strongly defined

tendinous groove. *Daphoenodon robustum* does not appear to have a tendinous groove (Hunt 2009 does not mention this structure, which is also not visible on the illustrations). Because of this morphology, Morphotype 2 is probably better characterized as a semi-digitigrade animal. Morphotypes 3 and 4 have a head that is oriented on the mediolateral axis as well as a plantar tendon groove, like in the plantigrade species used in Carrano's (1997) analyses and *Procyon lotor* Linnaeus, 1758 (Procyonidae) (Wang 1993). The neck is long and narrow and the ectal facet is well curved (deeper in Morphotype 3 than in Morphotype 4), as in *B. gabbii* and *A. fulgens*, which are plantigrade mammals (Polly 2008). Morphotypes 3 and 4 are therefore interpreted as plantigrade, but the latter displays a larger range of movements enabled by a less deep trochlear surface.

Morphotypes A and C have a rounded *sutentaculum tali* that is rather distal; this structure is even more distal in Morphotype C, as observed in *A. fulgens* and *B. gabbii*, which are plantigrade (Polly 2008). This would therefore be characteristic of a plantigrade animal. However, in Morphotype C, the peroneal process is poorly broad, which seems to be a digitigrade feature (e.g., *L. serval*; Polly 2008). The gear ratio for morphotype A is 1.23 (Table 5), which is similar to that of *Vulpes velox* (Say, 1823) (Canidae; digitigrade, terrestrial), *Spilogale gracilis* (Linnaeus, 1758) (Mephitidae; plantigrade, terrestrial), *Taxidea taxus* (Schreber, 1777) (Mustelidae; plantigrade, semifossorial), and *Nasua narica* (Linnaeus, 1766) (Procyonidae; plantigrade, scansorial) (Polly 2010; Polly *et al.* 2017). The gear ratio for Morphotype C (1.18; Table 5) is similar to that of *Tremarctos ornatus* (Cuvier, 1825) (Ursidae; Plantigrade, scansorial), *Potos flavus* (Schreber, 1774) (Procyonidae; plantigrade, arboreal) and *Galictis vittata* (Schreber, 1776) (Mustelidae; plantigrade, semi-fossorial) (Yensen & Tarifa 2003; Polly 2010; Polly *et al.* 2017). Morphotypes A and C may therefore correspond to plantigrade amphicyonids. Morphotype B has a more proximal *sustentaculum tali*, as in *F. catus* and *L. rufus* (Polly 2008). In addition, its morphology is close to that of the calcaneus of *Daphoenodon robustum*, which is digitigrade as indicated above (Hunt 2009). It also resembles the specimen of the Miocene digitigrade *Plithocyon ursinus* Cope, 1875 in North America (Paleontological Collection of MNHN), which also has a proximal *sustentaculum tali* and a distally long plantar tubercle. On the other hand, the peroneal process is well broad and the sustentaculum tali is located a little more dorsally, which seem to be plantigrade features (e.g., *A. fulgens*; Polly 2008). Even if the *sustentaculum tali* is more proximal than the other morphotypes, it is still far distal relative to extant digitigrade carnivorans (e.g., *F. catus*; Polly 2008). The gear ratio for Morphotype B is 1.25 (Table 5), which is close to *P. lotor* (semi-digitigrade, scansorial), *Martes americana* (Turton, 1806) (Mustelidae; plantigrade, scansorial) and *Conepatus chinga* (Molina, 1782) (Mephitidae; semi-digitigrade, terrestrial) (Polly 2010; Polly *et al.* 2017). Morphotype B would therefore rather be a semi-digitigrade and terrestrial or scansorial animal, but probably not cursorial (gear ratio less than 1.22).

The head of the astragalus of *Cynodictis lacustris* is inclined with respect to the mediolateral axis and the tendinous groove seems to merge with the trochlea, as in the digitigrade *Urocyon cinereoargenteus* (Schreber, 1775) (Wang 1993). However, the neck is quite short and the astragalar ectal facet is well curved, as in *F. catus* and *L. rufus* which are digitigrade and scansorial. In addition, the *sustentaculum tali* of the *calcaneus* is not placed very distally, as can be observed in a digitigrade animal (e.g., *C. lupus*; Polly *et al.* 2017). The gear ratio is 1.27 for *C. lacustris* (Table 5), which is similar to *Vulpes vulpes* (Linnaeus, 1758) (Canidae; digitigrade, terrestrial), *Canis latrans* Say, 1823 (Canidae; digitigrade, terrestrial), *Canis rufus* Audubon & Bachman, 1851 (Canidae; digitigrade, terrestrial), and *Panthera onca* Linnaeus, 1758 (Felidae; digitigrade, scansorial) (Polly *et al.* 2017). The canid species (i.e., *Canis* Linnaeus, 1758 and *Vulpes* Frisch, 1775) are all cursorial (Polly *et al.* 2017). Therefore, *Cynodictis lacustris* can be considered as digitigrade and cursorial.

Interpretations are more contentious regarding locomotion. Based on the model of Polly & MacLeod (2008), the calcaneus of *Cynodictis* morphology is intermediate between the terrestrial and the scansorial morphologies. Morphotypes A and C are between the arboreal and terrestrial morphologies. But the specimens used for the implementation of this model are all extant animals and, in the case of plantigrady, the majority of the specimens are arboreal. Therefore, Polly & MacLeod's (2008) model links plantigrady and arborality. While it is true that arboreal animals are often plantigrades (Taylor 1989; Panciroli *et al.* 2017), plantigrades are not necessarily arboreal (Wang 1993). Morphotypes A and C do not exhibit a large *sustentaculum tali*, in contrast to arboreal animals. Therefore, Morphotypes A and C may represent terrestrial predators.

CONCLUSIONS

This work describes for the fist time the tarsal bones of carnivoran mammals from the Quercy Phosphorites (Eocene, France). Based on morphology, relative abundances, size, and estimated body mass, we refer numerous astragali and calcanei to Amphicyonidae, some of which are assigned to *Cynodictis lacustris*. However, the absence of previously identified carnivoran tarsal bones from the Quercy, as well as the lack of exact locality information of the old Quercy collections precludes a finer identification of the seven morphotypes we describe.

Isolated postcranial bones are rarely described for European amphicyonids. Neither Eocene nor Oligocene tarsals have as yet been described from European localities. This work demonstrates that it is possible to identify these bones, some even at the species level.

The morphological diversity of the tarsal bones of this study confirms that European amphicyonids from the Paleogene displayed a wide diversity in their locomotion and posture, as is seen in the American amphicyonids. Three main postures are here identified, although the boundary between them is sometimes tenuous: plantigrade (Morphotypes 1, 3,

4, A and C), semi-plantigrade (Morphotype 2 and B), and digitigrade (*Cynodictis lacustris*). Including postcranial bones other than these two tarsal bones would surely help to better determine the posture, locomotion, and hunting strategies (e.g., pursuit, ambush).

At least one amphicyonid survived the "Grande Coupure": the digitigrade and potential runner *Cynodictis lacustris*. Nonetheless, and in the absence of accurate age information of the fossiliferous deposits, it remains impossible to reconstruct the evolution of amphicyonid locomotion on either side of this important turnover.

Finally, of potential interest in the taxonomic determination of carnivoran postcranial bones is their use for phylogenetic analyses, mostly because they are likely to provide phylogenetic signals different from those provided by the dentition. Improving our knowledge of the phylogeny of Amphicyonidae is crucial to reconstruct this radiation.

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APPENDICES

Appendix 1. — Measurements, in mm, of astragali used for the estimation of body mass. For each morphotype, only the values of the smallest and biggest specimens are provided.

Taxon/Morphotype	Specimen number	Proximodistal lenght (mm)
Cynodictis lacustris	MNHN.F.Au1076	13
	MNHN.F.Au847	15.6
Morphotype 1	MNHN.F.Qu9986	24.8
	MNHN.F.Qu10038	31.5
Morphotype 2	MNHN.F.Qu10231	32.4
	KUL.PLV1542.50	34.1
Morphotype 3	MNHN.F.Qu10371	12
	MNHN.F.Qu10042	17.8
Morphotype 4	MNHN.F.Qu10039	15.5

Appendix 2. — Body mass (in kg and g) estimated on the basis of dental material for the amphicyonid species known in the Paleogene of Europe, with indication of their stratigraphic distribution (MP levels). Only the species with accurate stratigraphic records are considered. Estimations realized in the framework of the Brain Pioneer BR/175/PI/CARNAGES of the Federal Science Policy Office of Belgium (BELSPO).

Species	Bodymass kg	Bodymass g	FAD (MP)	LAD (MP)
"Amphictis" nana	1.15	1150	28	28
Amphictis ambigua	5.89	5890	28	28
Amphictis milloquensis	4.72	4720	29	29
Amphictis borbonica	3.91	3910	29	29
Amphictis schlosseri	5.16	5160	30	30
Cynodictis intermedius	6.65	6650	18	18
Cynodictis lacustris	5.16	5160	18	18
"Cynodictis" compressidens	3.79	3790	19	19
"Cynodictis" palmidens	8.61	8610	21	21
Symplectocyon praecursor	7.28	7280	21	21
Pseudocyonopsis antiquus	29.19	29190	21	23
Cynodictis ferox	8.61	8610	23	23
Cynelos rugosidens vireti	23.4	23400	26	26
Brachycyon gaudryi	45.39	45390	26	28
Pseudocyonopsis ambiguus	54.26	54260	26	28
Pseudocyonopsis landesquei	72.62	72620	26	29
Cynelos lemanensis	42.26	42260	27	30
Cynelos crassidens	24.23	24230	28	29
Goupilictis minor	12.77	12770	28	30
Harpagocyon inusitatus	35.33	35330	29	29
Crassidia intermedia	133.54	133540	29	30
Haplocyon crucians	45.39	45390	29	30
Haplocyon dombrowskii	40.09	40090	29	30
Haplocyon elegans	28.77	28770	29	30
Ysengrinia tolosana	95.75	95750	29	30
Haplocyonopsis crassidens	85.89	85890	30	30