



# Paleoneurology of Artiodactyla, an Overview of the Evolution of the Artiodactyl Brain

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## Chapter 13 #. Paleoneurology of Artiodactyla, an overview of the evolution of the artiodactyl brain

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**Abstract:** This chapter presents a detailed review of works published on Artiodactyla endocasts and provides a comprehensive examination of artiodactyl brain evolutionary history, including Cetacea, from the early Eocene (c.a. 45 Ma) onwards. Artiodactyl endocasts have been actively studied from the second half of the 19<sup>th</sup> century to the 1970's. These works on natural or artificial endocasts widely took place outside the frame of phylogenetic concerns. We compile here the data available, including recent works using  $\mu$ CT-scan imagery techniques, and place them in a phylogenetic framework. We also provide new additional data regarding paleogene representatives of North American extinct clades (*Homacodon*, *Helohyus*, *Leptauchenia*, *Agriochoerus*), endemic European clade (*Mouillacitherium*, *Dichobune*), and Suoidea (*Palaeochoerus*) to complete the picture. The brain of modern artiodactyls is remarkable by the expansion and by the folding of the neopallium. We highlight the diversity of neopallium patterns at the Artiodactyla scale and their convergent nature on the last 45 millions years and show that encephalization increases with time, but with different modes between terrestrial and fully aquatic taxa (i.e. Cetacea). Each clade shows a mosaic pattern of derived and plesiomorphic features that now has to be put in perspective with both the history and the ecology of taxa.

**Keywords:** endocast, Neopallium, Cetacea, operculization

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*Content:*

### 1. Systematic and Phylogenetic context

The name "artiodactyl" (Owen 1848) comes from the ancient Greek *άρτιος*, pair, and *δάκτυλος*, finger, and unites ungulate mammals that have an even number of digits and paraxonian limbs (i.e. the axis of the limb is between digits III and IV; Thewissen and Hussain 1990; Luckett and Hong 1998). They are generally characterized by a "double pulley" astragalus with a distal trochlea and a large articular surface for the cuboid (Schaeffer 1947, Thewissen and Hussain 1990; Martinez and Sudre 1995; Rose 1996; Luckett and Hong 1998; Thewissen and Madar 1999; Geisler 2001; Gingerich et al. 2001; Thewissen et al. 2001b; Geisler et al. 2007), and a trilobed lower deciduous fourth premolar (e.g., Luckett and Hong 1998; Geisler et al. 2007).

Behind the name "artiodactyl" lies one of the greatest mammalian evolutionary successes. Indeed, artiodactyls occupy today the second rank in terms of family diversity after rodents, and rank third in terms of generic and specific diversity (Burgin et al. 2018), overtaken there by chiropterans.

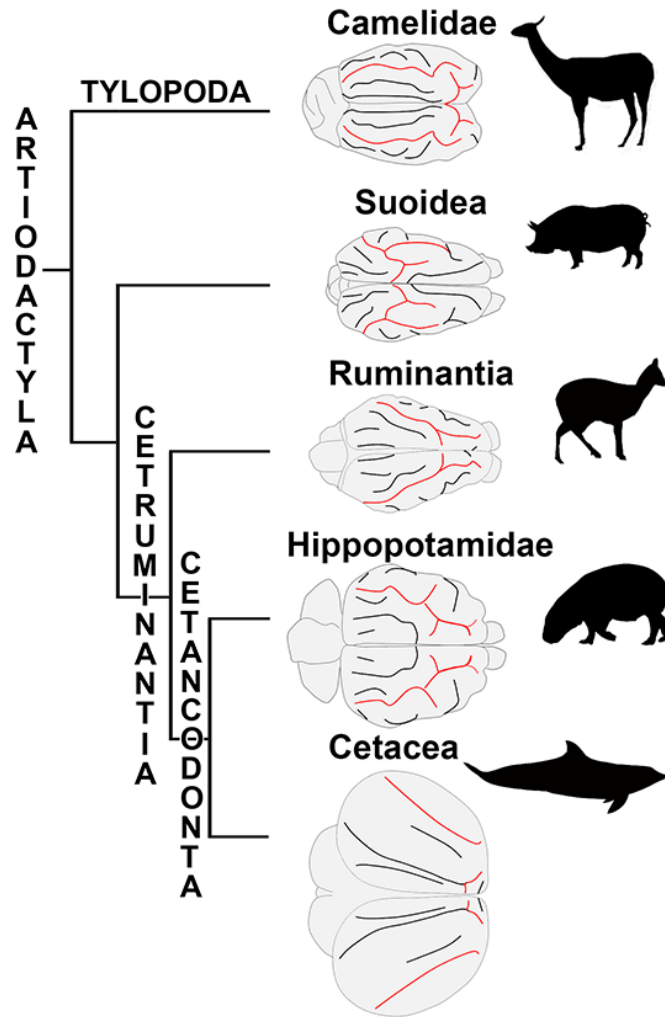
Artiodactyla today encompass five major crown groups: the tylopods (Tylopoda Illiger, 1811), the suoids (Suoidea Gray, 1821 sensu Gentry and Hooker 1988), the ruminants (Ruminantia Scopoli, 1777), the hippopotamoids (Hippopotamoidea Gray, 1821 sensu Gentry and Hooker 1988), and the cetaceans (Cetacea Brisson, 1762).

Artiodactyls appeared quite abruptly in the fossil record ca. 55.8 Ma ago in the Holarctic, followed by an intense adaptive radiation in the early-middle Eocene (50-45 Ma; Theodor et al. 2007, Rose et al. 2012, Boivin et al. 2018). Past generic diversity is at least seven times larger than today's, with more than 40 extinct families and nearly 950 fossil genera recognized (Janis et al. 1998; Uhen 1998; Williams 1998; Uhen 2007; Prothero and Foss 2007; Gingerich 2010; Marx et al. 2016).

Despite a major breakthrough in Artiodactyla phylogenetic relationships made through molecular analyses, that is, the identification of the close affinities between hippopotamids and cetaceans (e.g., Miyamoto and Goodman 1986; Irwin et al. 1991; Montgelar et al. 1997; Hassanin et al. 2012), basal relationships of the group remain largely unresolved and the origin of modern clades is still problematic when morphological characters are considered (e.g., O'Leary and Gatesy 2008; Geisler and Theodor 2009). According to most recent phylogenetic analyses, Tylopoda would be the first modern artiodactyl group to differentiate, followed by Suoidea; Ruminantia shares a close relationship with the Cetancodonta clade gathering hippos and cetaceans (Arnason *et al.* 2000, 2002, Hassanin et al. 2012; Gatesy et al. 2016). Total-evidence analyses, combining morphological and molecular characters, have been performed in the 2000s in order to enhance resolution of the early radiation and clarify the relationship of extinct artiodactyl groups relative to modern ones, although with unsuccessful results (e.g., Geisler and Uhen 2005; O'Leary and Gatesy 2008; Geisler and Theodor 2009; Spaulding et al. 2009). Since 2009, no new comprehensive contribution to artiodactyl phylogeny based on morphological characters including all four modern families and fossils has been published, and major questions remain about the placement of extinct taxa in the artiodactyl phylogenetic tree. The huge diversity of artiodactyls is perceptible in their brain pattern. Modern representatives show a wide array of brain morphologies (Fig.1), including some of the biggest and most convoluted mammalian brains (Welker 1990) in those of delphinid cetaceans (e.g., *Tursiops truncatus*), where brain size expressed as a function of the body mass ('encephalization quotient = EQ', Jerison 1970) ranks second after that of humans (Marino 1998, 2002).

## 2. Historical background

It is worth noting that the first definition of the endocranial cast was provided by Cuvier (1822) after an observation based on a natural endocast of an artiodactyl, *Anoplotherium commune*, from Montmatre gypsum. He wrote: "... it was moulded in the cavity of the skull; and as this cavity itself in the living animal was moulded on the brain, the clay necessarily represents the true shape of the latter..." Like many other mammalian groups, the first descriptions of artiodactyl endocranial casts mainly date from the second half of the 19<sup>th</sup> century and are based on natural endocasts. Among them are included those of European cainotheriids (Gratiolet 1858) and ruminants (Gaudry 1873), North American oreodontids (Leidy 1869; Bruce 1883), and North African archaeocete whales (Gervais 1871). Descriptions of these endocranial features are directly related to the discovery and scientific exploitation of major fossil outcrops that yielded abundant and well-preserved remains in a taphonomic context that allowed for natural preservation of casts of the endocranial cavity. Thus, the historical knowledge of endocranial anatomy is much contrasted depending on the taxonomic group and the geological period considered.



**Figure 1** – Phylogenetic relationships and general neocortical pattern of modern artiodactyl groups. Suprasylvia and connected sulci (coronal and ansate sulci) are highlighted in red. Not to scale.

The brain of modern artiodactyls is remarkable by the expansion and by the folding of the neopallium. Modern artiodactyl groups are all highly gyrencephalic (Kazu et al. 2014) and differ in their neocortical pattern (Fig. 1), and most of the early works on fossil artiodactyl endocranial casts pay special attention to the foldings of the neopallium and their identification. Detailed identification of the different sulci of the neopallium of artiodactyls was established during the end of the 19<sup>th</sup> century (Krueg 1878) and the first half of the 20<sup>th</sup> century based on the study of embryologic/ontogenetic series by Anthony and Grzybowski (1931, 1934, 1936) for suids (*Sus scrofa*) and domestic bovids (sheep *Ovis aries*, and cow *Bos taurus*), and by Friant (1937, 1940) for hippopotamids. The study of artiodactyl endocasts during the 19<sup>th</sup> and 20<sup>th</sup> centuries can be divided into two approaches: qualitative studies focusing on anatomy from the second half of 19<sup>th</sup> century until the 1970's (see for instance the chapter of Dechaseaux 1961 in the “*Traité de Paléontologie*” tome 6 of Piveteau for a remarkable summary of the knowledge of artiodactyl endocasts in the 1960's), and quantitative focusing on the increase of brain size through time that mainly developed in the 1980's (e.g., Jerison 1970, 1973; Radinsky 1987). Most of these observations were performed in a systematic framework separating artiodactyls in two categories on the basis of tooth morphology: Bunodontia (pigs, hippos and extinct relatives) and Selenodontia (ruminants – including camelids – and extinct relatives). The lack of a clear phylogenetic context (or basically the lack of phylogenetic concepts for earliest

works) has limited the scope of the thorough, highly detailed, first observations performed on artiodactyl endocasts (see next section 2.1).

Endocranial studies did not progress much until the democratization of CT-scan investigations due to the small number of natural endocranial casts available (and the limitation of their taxonomic attribution if not associated with dental remains) and to the often destructive nature of preparation of plaster/silicone endocasts. Yet descriptions of fossil artiodactyl endocasts based on virtual intracranial investigations and 3D reconstructions of the internal mould of the cranial cavity remain scarce and are only available for early representatives of the group (Oreodontoidea, Macrini 2009; *Diacodexis*, Orliac and Gillissen 2012), for early Hippopotamoidea (Thiery and Ducrocq 2015), for Cetacea and their closest relative (Raoellidae, Orliac and Thewissen 2021; Remingtonocetidae, Bajpail et al. 2011; crown Cetacea, Marino et al. 2003; Racicot and Rowe 2014; Boessenecker et al. 2017), and for crown Ruminantia (Cervidae, Fontoura et al. 2020).

## 2.1. Documentation of artiodactyl endocasts in the fossil record

### 2.1.1. Endocranial morphology of extinct Artiodactyla clades

**The endocast of *Diacodexis*, earliest Artiodactyla** - The oldest known artiodactyl endocasts described in the literature belong to the genus *Diacodexis* and originate from the Early Eocene of North America (*Diacodexis ilicis*, earliest Wasatchian, ca. 55 Ma; Orliac and Gilissen 2012, 3D reconstruction of the virtual endocast) and from the early Middle Eocene of Pakistan (*Diacodexis pakistanensis*, ca. 48 Ma; Sigogneau-Russel and Russel 1983, partial composite reconstruction based on nine skull fragments). The presence of a simple neopalleal pattern in *Diacodexis*, shared by other early artiodactyls, allowed for proposing a reconstruction of the ancestral neopalleal pattern for Artiodactyla.

**Endemic European artiodactyls (EEA)** - Several extinct artiodactyl genera and families (including Cebochoeridae, Mixtotheridae, Robiacinidae, Cainotheriidae, Choeropotamidae, Anoplotheriidae, Xiphodontidae, and Amphimerycidae) are geographically restricted to Europe. They derive from several endemic radiations that took place during the late early and middle Eocene when Europe was geographically isolated from other land masses in a general context of high sea level (Prothero 1994). Phylogenetic relationships among the basal families of artiodactyls remain unclear and greatly differ between analyses (e.g., Geisler et al. 2007; Luccisano et al. 2020; Weppe et al. 2020a, b). Endocasts of European endemic artiodactyls were among the first mammalian endocasts to be studied (Cuvier 1822; Gratiolet 1859). Most of them have been described based on exceptionally well-preserved fossil material from the early Miocene lacustrine deposits of Saint-Gérard-le-Puy (Allier department, France), and from Paleogene karstic infillings from the Quercy Phosphorite Formation (Southwestern France). Among the first taxa described were the cainotheriids, considered then to be early ruminant representatives (Gratiolet 1859; Milne Edwards 1864; Gervais 1873; Hürzeler 1936). The endocast of *Cainotherium* was extensively studied by Anthony and Friant (1938) who concluded that it represented the primitive pattern of the ruminant brain. Dechaseaux (1961, 1968, 1969a, b, 1970, 1973) described then in great detail the endocranial casts of a variety of European endemic artiodactyls (*Tapirulus*, *Mouillacitherium*, *Cebochoerus*, *Dichobune*, *Dacrytherium*, *Cainotherium*, *Oxacron*, *Diplobune*, *Amphimeryx*, *Pseudamphimeryx*, *Mixtotherium*), and the general trends in neocortical fissuration patterns in Artiodactyla. These works from the second half of the 20<sup>th</sup> century benefitted from the identification of cortical patterns established by Anthony and Grzybowski (1931, 1934, 1936) and from the sharp



reflections on external brain features by the works of Friant (1937, 1939, 1940), together with a more integrative evolutionary context (e.g., Dobzhansky 1937; Mayr 1942; Huxley 1942; Simpson 1944; Stebbins 1950).

**Oreodontoidea** - Among the earliest works on artiodactyl endocranial casts are the studies on oreodontoids from North America. Oreodontoidea include two families, Agriochoeridae and Merycoidodontidae, they include a wide variety of subfamilies documented from the middle Eocene to the middle Miocene. The phylogenetic relationships of, and within, Oreodontoidea are still unclear (Ludke 2007; Stevens and Steven 2007). Natural endocasts of multiple oreodontoid taxa are particularly well described in the literature of the second half of the 19<sup>th</sup> century and the first half of the 20<sup>th</sup> (Gratiolet 1859; Leidy 1869; Bruce 1883; Scott 1899; Moodie 1916, 1922; Black 1920; Thorpe 1931, 1937; Friant 1939, 1948). Most of these natural endocasts came from the Oligocene White River fauna of the Western U.S. (Scott and Jepsen 1940), and the Eocene of West Texas (Wilson 1971). Among the taxa described or mentioned are the agriochoerid *Protoreodon* (Macrini 2009) and the merycoidodontids *Merycoidodon* (Gratiolet 1859; Bruce 1883; Black 1920; Friant 1948; Leidy 1959), *Eporeodon* (Marsh 1886; Thorpe 1931), *Merycochoerus* (Moodie 1915, 1922), *Promerycochoerus* (Thorpe 1931), and *Leptauchenia* (originally described as *Cyclopidius* Cope 1878; Prothero and Sanchez 2008). Among these descriptive works, the incredible preservation of a specimen and the thorough description of the smallest details of its brain allowed Black (1920:fig.23-24) to propose a restoration of the “*Oreodon*” brain (in fact rather derived *Merycoidodon* species) with unrivalled precision. Black noticed the strikingly complex cerebellum contrasting with the small and relatively simply arranged neopallium and questioned, as early as the beginning of the 20<sup>th</sup> century, the possible independent evolution of these parts of the brain. Black (1920) and Moodie (1916, 1922) noticed the association of ruminant and “suilline” characters in merycoidodontid brains and qualified them as “pig-like ruminants.” Oreodontid brain features were then discussed in a wider comparative frame by Friant (1939) and Dechaseaux (1961, 1969a). More recently, the endocranial cast of *Bathygenys reevesi* was described by Macrini (2009) based on  $\mu$ CT-scan data, together with a general discussion about morphological diversity within Merycoidodontidae.

### 2.1.2. Endocasts of modern artiodactyl groups

**Tylopoda** – The evolution of brain morphology in Tylopoda is documented mainly by camelids from the Eocene to the Miocene; whose origin is the Holarctic zone of North America. In geochronological order, the camelid brain is represented by endocasts of *Protylopus* (Eocene), *Eotylopus* (Eocene), *Poebrotherium* (early and late Oligocene), and lastly, *Protolabis* (late Miocene) and *Procamelus* (late Miocene). As the earliest known member of Camelidae, the brain of *Protylopus* (ca. 40 Ma) is considered the precursor to the modern camelid brain. The Oligocene camelid brain is known from two specimens: *Poebrotherium wilsoni* of the early Oligocene, and the relatively larger *Poebrotherium labiatum* in the late Oligocene (Bruce 1883; Cope 1886; Jerison 1971). Edinger (1966) briefly described the basic pattern of evolution from these earlier forms to the late Miocene, the latter stage represented by two endocasts of *Procamelus*. The smaller of the two, first recognized as *Procamelus occidentalis* (see Cope 1877a, b), was later re-assigned to the genus *Protolabis* (Jerison 1971). The larger endocast, which remains as *Procamelus*, was referred to as a late Pliocene form by many researchers (Edinger 1966; Jerison 1971; Repérant 1971a, b; Kruska 1982). Recent investigations have clarified, as previously considered by Jerison (1971), that this is actually a Miocene *Procamelus* (ca. 12-10 Ma) (Balcarcel et al. unpublished data). The major trends in neocortical evolution, spanning the Eocene to late Miocene, were described by Repérant (1970, 1971a). Recently,

newly described endocasts including that of *Camelops hesternus* (artificial), a giant camelid, and one of what is likely a “*Palaeolama*” (natural), highlight the degree of brain complexity reached during the Pleistocene (Balcarcel et al. unpublished data).

**Suoidae** – The external features of the brain of *Sus scrofa*, the domestic pig, are well known and described in detail (e.g., Saikali et al. 2010), including its developmental aspects (Krueg 1878; Anthony and Grzybowski 1931). This is not the case for other modern suid genera, which have only been partly documented (Anthony and Grzybowski 1931). The external morphology of the brain of modern Tayassuidae is also described in very few works (Krueg 1878; Allanson 1971; Saraiva 2017). To our knowledge, there is no documentation of a fossil suoid endocast in the literature.

**Ruminantia** – The general morphology of the brain of ruminant artiodactyls and the evolution of brain features has been described and discussed by Friant (1939), and subsequently augmented by Dechaseaux (1961). These works largely build on the studies of embryologic/ontogenetic series in domestic bovids (sheep *Ovis aries*, and cow *Bos taurus*) by Anthony and Grzybowski (1934, 1936). Several endocranial casts (natural or plaster) of fossil ruminants from the Quaternary and the Neogene are described and figured in the literature, and the morphological features are generally described in great detail. Among the first descriptions are those of *Gazella deperdita* (Bovidae), described Gaudry (1873) from the late Miocene deposits of Mont Luberon (France), and *Samotherium* (Giraffidae), described by Black (1915) from the late Miocene of the Samos Island. The endocranial morphology of extinct Bovidae was further documented by natural and silicone endocasts of the Plio-Pleistocene insular bovid *Myotragus* (Dechaseaux 1961:fig. 16, 1962; Köhler and Moyá Solá 2004; Palombo et al. 2008) and of the Pliocene ovine *Megalovis* (Dechaseaux 1961). The endocast of the cervoid Palaeomerycidae *Aletomeryx* was described from the late Miocene of Nebraska (Lull 1920; Friant 1939; Dechaseaux 1961) and the endocranial morphology of the fossil stem Cervidae *Dicrocerus* and *Megaceros* is known from the middle Miocene and the Pliocene of France (Dechaseaux 1961). More recently the small *Candiacervus* from the Plio-Pleistocene of the Mediterranean islands (Angeleti 1980; Palombo et al. 2007, 2008), and the late Pleistocene *Antifer ensenadensis* from southern Brazil (Fontoura et al. 2020) further documented the brain morphology of extinct cervids. The earliest ruminant endocranial casts described in the literature are, to our knowledge, that of *Dremotherium* (unknown family) and *Amphitragulus?* (unknown family) from the late Oligocene-early Miocene deposits of Saint-Gérard-le-Puy (Sigogneau 1968; Dechaseaux 1961, 1969).

**Hippopotamoidea** – A first illustration and very brief mention of a fossil hippopotamid endocast (artificial) was made by Friant (1940:fig.4). To our knowledge, studies of fossil Hippopotamidae endocasts in the literature are limited to *Hippopotamus protamphibius* from the Pleistocene of Ethiopia (uncertain locality from Omo valley), *H. madagascariensis* and *H. lemerlei* from the ?late Pleistocene to Holocene of Madagascar, and *H. minor* from the Pleistocene of Cyprus (Anthony 1948). The latter notice the thickness of the dura mater preventing access to most of the cerebellar structures, and the presence of a large “K lobe”, characteristic of the brain of Hippopotaminae (see section 3.1.3). This work on natural and artificial plaster endocasts was then integrated by Dechaseaux (1961) in her discussions of adaptation to amphibiosis in hippopotamuses. The fossil record of Hippopotamidae only goes back to the Oligocene (ca. 30 Ma, Lihoreau et al. 2015) whereas hippopotamoids (i.e. “Anthracotheriidae”) appear in the fossil record in Asia during the middle Eocene (Lihoreau and Ducrocq 2007). The endocranial morphology of Hippopotamoidea is still poorly documented. Only two “anthracotheriid” taxa are described in the literature, a representative of

the Microbunodontinae *Microbunodon minimum* and of a more derived Botriodontinae *Merycopotamus medioximus* (Thiery and Ducrocq 2015). Description of the endocast of *M. minimum* (late Oligocene from La Milloque, France) relies on a virtual reconstruction of the endocranial cavity of a well-preserved specimen, allowing a precise description of the external brain features of this small-sized animal. The external features of the brain of *M. medioximus* are only partly documented from a partial natural cranial endocast from Potwar Plateau, Pakistan, dated from the late Miocene (Lihoreau et al. 2004). Given the scarcity of available data, the evolutionary history of brain features of hippopotamoids remains widely undocumented.

**Cetacea** – The first descriptions of cetacean endocasts are, to our knowledge, by Gervais who described plaster endocasts of extant Mysticeti (Gervais 1871), a partial braincase referred to the Eocene basilosaurid *Zeuglodon cetoides* (Watchita river, Louisiana, U.S.), and one of the Miocene delphinid *Glyphidelphis sulcatus* (Hérault, France, now referred to as *Schizodelphis sulcatus*) (Gervais 1874). Natural endocranial casts of basilosaurids, fully aquatic archaeocetes sister taxa to Neoceti, have been described based on *Dorudon* by Smith (1903), Andrews (1906), and Stromer (1903), and Dart (1923) who provided an extensive description of Zeuglodontidae endocasts. These works on basilosaurids were integrated with those of Edinger (1955) and Dechaseaux (1961). Following the concerns of Marple (1949) about the interpretation of fossil cetacean endocasts, Breathnach (1955) revised the brain/endocast shape correspondence for a sample of modern cetaceans and concluded that regarding the cerebellar region of odontocetes and the brain of mysticetes in general, the endocranial cast is “little less than a poor and misleading caricature” (Breathnach 1955:541). The earliest evolutionary history of the cetacean brain is only partly documented back to the early middle Eocene by early diverging, non-fully aquatic archaeocetes, pakicetids (Nummela et al. 2006; Kishida et al. 2015), protocetids (*Indocetus* sp., cf. *I. ramani*, Bajpai et al. 1996), and remingtonocetids (Bajpai et al. 2011; Kishida et al. 2015). The endocranial morphology of *Indohyus* belonging to the Raoellidae, the sister taxon to Cetacea, recently provided some additional insights into the onset of cetacean brain characteristics (Orliac and Thewissen 2021). The endocranial morphology of Neoceti, the clade gathering modern cetaceans, is still partially documented relative to their diversity. Odontocetes are the best documented and include records of Xenorophidae (*Albertocetus* from early Oligocene, South Carolina, Boessenecker et al. 2017, and *Xenorophus* from late Oligocene North Carolina, Marino et al. 2003), Eurhinodelphinidae (*Xiphiacetus* sp. described as *Eurhinodelphis morrissi* by Marino et al. 2003, Middle Miocene of Maryland), Eoplatanistidae (Pilleri and Gühr 1982, from Italy, originally referred to *Schizodelphis*, transferred to *Eoplatanista* by Muizon 1988), Delphinidae (Globicephalinae Boessenecker et al. 2015), Phocoenidae (Racicot and Rowe 2014), and several records of indeterminate odontocetes. These include “*Squalodon*” from the Oligocene of New Zealand (Marples 1949; specimen C.34.7; see Fordyce 1978 for systematic reassessment), “*Prosqualodon davidi*” by Dart (1923) from the Miocene of Tasmania, and a specimen from the middle Miocene of Poland (Stefaniak 1993, originally referred to as Delphinidae indet.). Bisconti et al. (2020) recently restudied the natural endocast of an early Miocene Odontocete from Piedmont, Italy, previously studied by Dal Piaz (1905), Parona (1923) and Pilleri and Gühr (1982). Natural endocasts of extinct mysticetes are very scantily documented in the fossil record, which is, to our knowledge, limited to the cetotherids *Cetotherium* (Strobel 1881:pl1, fig2) and *Imerocetus* (Mchedlidze, 1988), to *Pinocetus polonicus* (middle Miocene of Poland; Czyżewska, 1988, originally placed in the Cetotheriidae but recently found outside this clade by Marx et al. 2019), to the Llanocetidae *Llanocetus denticrenatus* (Mitchell 1989) from the latest Eocene of Seymour Island (see Fordyce and Marx 2018 for familial referral), and to *Willungacetus* from the early Oligocene of South Australia (Pledge 2005, placed in Mysticeti



indet. by Fitzgerald 2010). Few endocasts of extant cetaceans are also available in the literature, via physical endocasts (e.g., *Balaenoptera rostrata*, *Balaena mysticetes*, *Megaptera novaeangliae* by Gervais 1871; sperm-whale *Physeter microcephalus* by Flower 1867; foetal fin-whale, common porpoise *Phocaena phocaena* by Breathnach 1955; *Balaenoptera musculus* by Dechaseaux 1961), or digital reconstructions (e.g., Phocoenidae by Racicot and Colbert 2013; narwhal *Monodon monoceros* and beluga *Delphinapterus leucas* by Racicot et al. 2018).

## 2.2 Problematics

As exposed above, endocasts of artiodactyls have been actively described and studied from the second half of the 19<sup>th</sup> century to the 1970's. These works widely take place outside the frame of phylogenetic concerns, or in a paradigm mainly splitting Artiodactyla in two/three groups based on their dental morphology (bunodont/selenodont/bunoselenodont), and, naturally, separating cetaceans from artiodactyls. The phylogenetic context has drastically evolved since the end of the 20<sup>th</sup> and the beginning of the 21<sup>st</sup> centuries, and the relationships between modern artiodactyl groups are now pretty consensual. Integrating Cetacea within a broader definition for Artiodactyla is now necessary, as is the clarification of the evolutionary history of brain structures within this new phylogenetic context. In the meantime, phylogenetic relationships at the order scale including fossil taxa remains highly debated and no consensus has yet been reached today. Major artiodactyl groups can be differentiated by their endocast morphology (Dechaseaux 1969; Macrini 2009), and inclusion of endocranial characters will certainly bring a source of relevant characters to define clades and clarify basal relationships within Artiodactyla. Gathering an increasing corpus of data for artiodactyl endocasts is now crucial to address these evolutionary issues. Indeed, documentation of endocranial morphology of the various artiodactyl groups remains scant compared to their amazing diversity. Most data regarding endocranial morphology of artiodactyls derives from natural and artificial endocasts and the number of available virtual models remains limited so that quantitative parameters such as relative volume of the different components (e.g., olfactory bulb, cerebrum, and cerebellum) or relative neocortical surface cannot currently be discussed at the order scale, hampering a quantitative assessment of brain evolution in the group.

Among major questions that are currently investigated is to what extent ecological specialisation has shaped the neocortical pattern and different components of the artiodactyl brain. The general overview of published endocasts suggests a complicated pattern of evolutionary history of the different structures with decoupling of evolutionary stages between cerebrum and cerebellum; each clade shows a mosaic pattern of derived and plesiomorphic features that has to be put in perspective with both the history and the ecology of taxa. Artiodactyla therefore appears to be a perfect group for a case study of brain evolution and its associated drivers because of their broad temporal and spatial repartition, and their incredible diversity within mammals, including a wide array of body masses and ecological specialisations (e.g., terrestrial and aquatic).

Domestication is also a crucial aspect of the evolution of the artiodactyl brain. Artiodactyls comprise an impressive proportion of today's domestic livestock, including suids, camelids, and a wide variety of ruminants (cervids, bovids). Each group represents a model for exploring morphological changes to the brain in correlation with the domestic niche: selection for tameness, environmental and dietary alterations, and life cycle changes (Zeder 2012). Brain size differences have already been noted between many wild and domestic mammals, particularly in artiodactyls (Kruska 1988), but neuroanatomical differences are less known. This is currently an area of great scientific interest, as behavioral and cognitive abilities are increasingly being inferred from brain morphology (e.g., Balcarcel et al. 2021, Hetch et al. 2019).

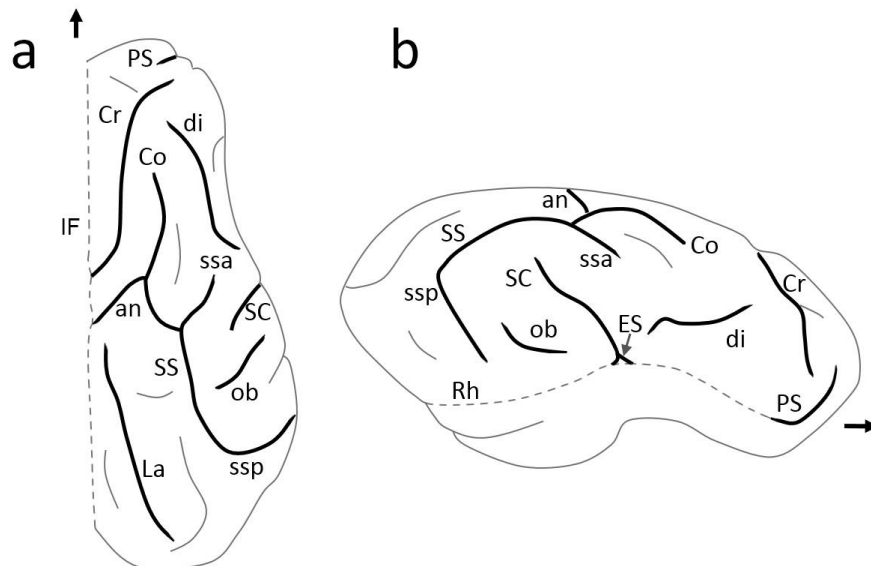
In this chapter, we provide a first step to discussing brain morphology and evolutionary history at the Artiodactyla scale, including Cetacea, based on a first compilation of available data and including recent, yet still very scant, 3D models deriving from  $\mu$ CT-scan acquisitions.

### 3. Overview of general and comparative anatomy

#### 3.1 Characterization of cranial endocast morphology

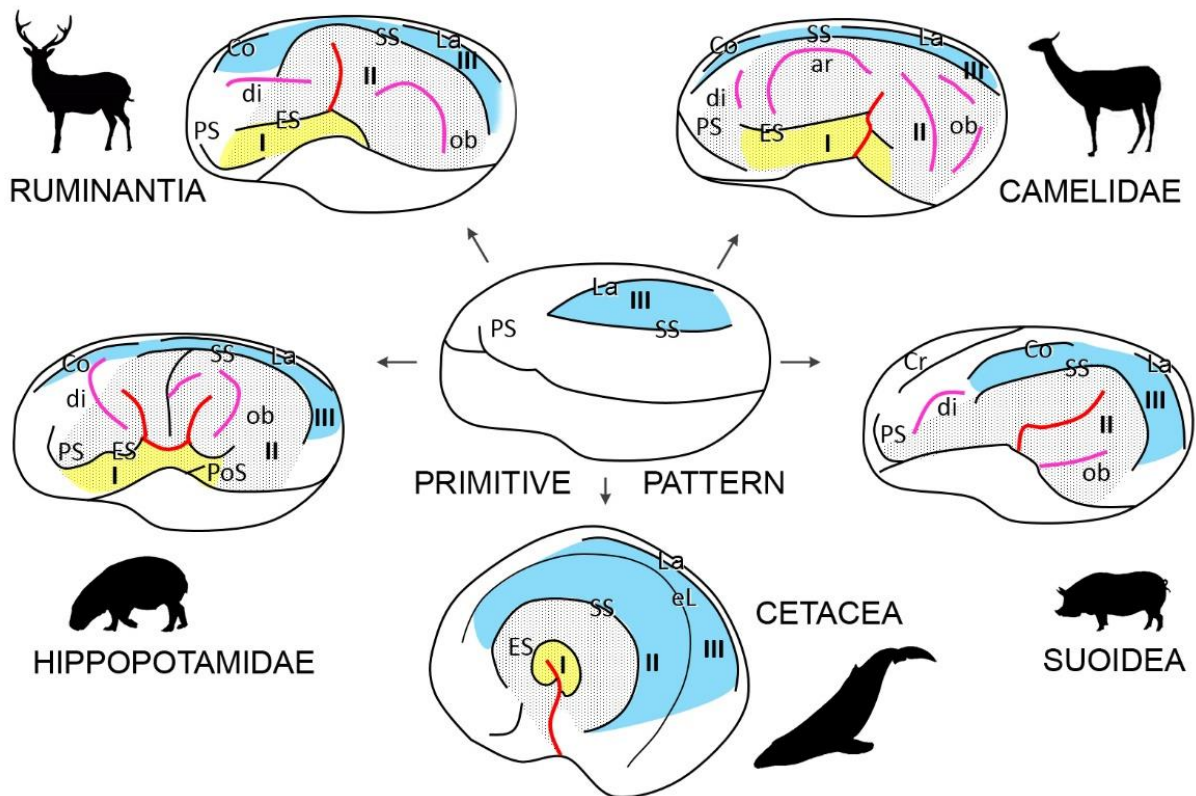
##### 3.1.1. Overview of modern artiodactyl brain morphology, primary identification of structures

Modern Artiodactyla are characterized by an important extension of their neopallium that covers most of the cerebral surface and extends posteriorly over the midbrain, partially hiding the cerebellum. If terrestrial groups mostly differ by the sulcal pattern of their neopallium, Cetacea stand as an exception with a highly morphologically divergent brain, with, among others, drastic reduction or lack of olfactory bulbs, very strong telencephalic flexure, and special cortical characteristics (i.e., simple cortical organization, Glezer et al. 1988; Morgane et al. 1988; Glezer et al. 1988, 1993; Raghanti et al. 2019). Due to these unique features, Cetacea have always been studied outside the Artiodactyla framework. The literature relating to the study of gyrencephaly abounds with diverse and often contradictory nomenclatures. We principally use here the revised nomenclature of Repérant (1971b), mainly built on the work of Smith (1902) and Anthony and Grzybowski (1930) and based on various homology criteria (topographical, morphological, anatomical, histological, ontological, phylogenetic). We add here some other support to homology based on the morphological intermediate criteria as defined by Repérant (1971b). The main neocortical sulci of Artiodactyla observed on endocasts (i.e., exposed on the external aspect of the brain) are, from the rhinal fissure on the ventral margin of the neopallium (delimiting the paleopallium from the neopallium, Smith 1902) to the interhemispheric fissure (at the sagittal plane): the ectosylvia, the suprasylvia, the coronal and the lateral (Figs 1, 2).



**Figure 2** – Dorsal (A) and lateral (B) views of the right cerebral hemisphere of the domestic pig (*Sus scrofa*) illustrating the sulcal nomenclature used in this chapter. Arrow points anteriorwards. Abbreviations: an, ansate sulcus; Co, coronal sulcus; Cr cruciate sulcus; di, diagonal sulcus; ES, ectosylvia; IF, interhemispheric fissure; La lateral sulcus; Ob, oblique sulcus; PS, presylvia; Rh, rhinal fissure; SC, sylvian complex; SS, suprasylvia; SSa suprasylvia anterior; SSp suprasylvia posterior. The inter-hemispheric and the rhinal fissures are in dotted lines.

The cruciate and the splenial sulci, originating from the internal aspect of the neopallium at the interhemispheric fissure, are also exposed on the dorsal surface of the hemispheres in some taxa (see section 3.1.3). There are also typical secondary grooves: the diagonal sulcus (“*sillon γ*” of Anthony and Grzybowski 1931, 1934, 1936; Friant 1939; Anthony 1961, Dechaseaux, 1961), the arcuate sulcus (“*sillon α*” of Friant 1952 – observed in Camelidae), and the oblique sulcus (“*sillon β*” of Anthony and Grzybowski 1936; Friant 1939; Sigogneau 1959; Anthony 1961; Dechaseaux 1961, 1969, 1973). In all modern artiodactyls, the pseudosylvia, observed in gyrencephalic mammal groups such as carnivorans (Smith 1902) is very small or lacking (Repérant 1971b). If the homology of the various artiodactyl sulci has been discussed based on the primitive carnivoran pattern (as exemplified by the dog; e.g., Krueg 1878; Smith 1902), it has never been discussed at the Artiodactyla scale based on a global comparison of extant and extinct taxa.



**Figure 3** – Lateral left view of the cerebral hemisphere of crown Artiodactyla, compared to the primitive pattern (highlighted in central position), showing the operculization of the central territory of the neopallium (yellow, gyrus I). Abbreviations: ar, arched sulcus; Co, coronal; Cr Cruciate; di, diagonal; eL, ectolateral; L lateral; ob, oblique; PS, presylvia; SS, suprasylvia; I-III refers to the neopallial gyri. The sylvian complex, sulci resulting from the operculization, is highlighted in red, diagonal and oblique sulci are highlighted in pink, arcuate is highlighted in orange; yellow, gyrus I; blue, gyrus III; grey sanded area and grey corresponds to the central area.

A hallmark of the complexity of the brain of artiodactyls is the operculization, often incomplete, of the central area (the region delimited by the rhinals, the suprasylvia and the presylvia sulci) of the neopallium. It consists of an invagination of a more or less large surface of neopallium, localized between the rhinal and the ectosylvia and recognized as the gyrus arcuatus I (yellow area on Fig. 3) based on topographical similarities with the carnivoran neocortical pattern (see Repérant 1971b for considerations on homologies). The sylvian complex resulting from this operculization has various orientation depending of artiodactyl clades (Fig. 3). Modern representatives show different patterns, recognizable from each other, and with different degrees of operculization (Fig. 3). It is, for example, almost complete to

complete in suoids (Anthony and Grzybowski, 1931), while the gyrus arcuatus I remains variously exposed in hippopotamids (Friant 1939, 1940), camelids (Repérant 1971b), cetaceans (Hof and Van der Gucht 2007; Knopf et al. 2016), and ruminants (Anthony and Grzybowski, 1934, 1936; Friant 1939). Operculization is related to the expansion of the surface of the neopallium, the part of the brain dedicated to higher cognitive functions. As such, this phenomenon has been central to the study of artiodactyl endocasts and to the evolutionary history of their brains. The endocranial cast only gives access to the external structures of the brain, providing no clues as to the internal folds of the neopallium. This partial access to the morphology of the brain sometimes makes it difficult to identify first steps of operculization based on extinct taxa. Most works on the brain cavity of artiodactyls have focused mainly on the morphology of the neopallium, while studies on the cerebellum are scarce. Modern artiodactyls exhibit a complicated cerebellum with highly convoluted and folded vermis and hemispheres (e.g., Suidae, domestic pig *Sus scrofa*, Saikali et al. 2010; Hippopotamidae, common hippopotamus *Hippopotamus amphibius*, Garrod 1880; Camelidae, Repérant 1971b), but most of these delicate foldings are generally not visible on endocasts. Given the particular attention devoted to the study of the artiodactyl neopallium in the literature and the paucity of data available concerning the cerebellum, this chapter focuses essentially on the former.

### 3.1.2. Endocranial morphology of extinct Artiodactyla clades

**Earliest artiodactyls / primitive pattern** - The endocranial morphology of earliest artiodactyls is documented by the early and early middle Eocene *Diacodexis* (Sigogneau-Russel and Russel 1983; Orliac and Gilissen 2012), *Homacodon* (Fig. 4A-C; Orliac, in press) and *Helohyus* (Fig. 4D-F; Orliac, in press).

**Olfactory bulbs.** These are only documented from the specimen of *Diacodexis ilicis* (Orliac and Gilissen 2012) and from fragmentary specimens of *Diacodexis pakistanensis* (Sigogneau-Russel and Russel 1983). This genus exhibits very large olfactory bulbs (13% of the total endocast volume), so far the largest observed in Artiodactyla (Tab. 1).

**Cerebral hemispheres.** In *Diacodexis*, *Homacodon* and *Helohyus*, the extension of the neopallium on the surface of the cerebral hemispheres is reduced (43-44% of the surface of the cerebral hemisphere) and the paleopallium is visible in dorsal view. The ventral extension is weak and the caudal part of the cerebrum does not abut the cerebellum, letting a wide portion of the midbrain dorsally exposed (Fig. 4A-F). Their groove pattern is very simple with two deep sulci, the suprasylvia and the lateral sulcus (closer to the interhemispheric fissure), converging in their anterior-most part and delimiting an almond-shape gyrus III. A small groove interpreted as the presylvia is also observed merging to the anterior segment of the rhinal fissure in the anterior most portion of the neopallium. The pyriform lobes are large. *Diacodexis* and *Homacodon* also show large olfactory tubercles. The lateral aspect of *Helohyus* endocast cannot be described due to deformations (Fig. 4F).

It is worth to note that in earliest artiodactyls the orbitotemporal canal lies ventral to the rhinal fissure and is not a hallmark of the paleopallium/neopallium limit like it is the case in Primates (Microsyopidae, Silcox et al. 2010; although in some cases it is suggested dorsally, Proprimates, Gingerich and Gunnell 2005) and rodents (Ischyromyidae, Bertrand and Silcox 2016).

**Midbrain exposure.** The midbrain is widely exposed in *Diacodexis*, *Homacodon* and *Helohyus*. Midbrain exposure is observed in few other early artiodactyls (Figs 4, 5), but it is clearly wider in early and middle Eocene taxa (see also *Indohyus*).

**Cerebellum.** Fine morphological details of the cerebellum are not visible on the endocasts, but all three taxa show a rather wide vermis compared to paramedian lobes. On *Diacodexis* (Orliac and Gilissen 2012) and *Helohyus* (Fig. 4D-F), the fissure prima can be identified on the dorsal aspect of the vermis, its position makes the paleocerebellum (lobus rostralis) widely exposed



on the anterior part of the vermis. The lobus caudalis bears few fissures, and the fissure secunda is identifiable as a deep groove on the vermis endocast.

**Endemic European artiodactyls (EEA)** - Endocranial casts of EEA are documented from the late Eocene until the late Oligocene, most of them known from Quercy localities or from Saint-Gérard-le-Puy and described by Dechaseaux (1961, 1969a,b, 1973). They show a wide array of morphologies reflecting the radiation of the group in the “Island Europe” context.

Olfactory bulbs: *Cebochoerus*, *Dichobune*, *Mouillacitherium* as well as *Anoplotherium* present a rather similar relative size of the olfactory bulb with values comprised between 5.7 and 7.5 % (Tab. 1). These values are smaller than what is observed in *Diacodexis* (13.8%). Among EEA, the cainotherid *Caenomeryx* exhibits the smallest olfactory bulbs, representing less than 4% of the total volume of the endocast (Tab. 1). In all these taxa, olfactory bulbs are joined on most of their length and separated from the anterior margin of the neopallium by a short circular fissure.

	Specimen	Cerebrum surface (mm <sup>2</sup> )	Neopallium surface (mm <sup>2</sup> )	% neocortical surface	Endocranial volume (cm <sup>3</sup> )	Olfactory bulbs volume (cm <sup>3</sup> )	% olfactory bulbs volume
<i>Diacodexis ilicis</i>	AMNH 16141	944.02	404.34	42.8	4.70	0.65	13.8
<i>Homacodon vagans</i>	AMNH 12695	1384.93	613.82	44.3	#	#	#
<i>Mouillacitherium elegans</i> <sup>EEA</sup>	UM ACQ 6625	1313.55	567.14	43.2	8.77	0.51	5.8
<i>Dichobune leporina</i> <sup>EEA</sup>	MNHN QU16586	2503.02	1107.44	44.2	7.41	0.57	7.7
<i>Cebochoerus</i> sp. <sup>EEA</sup>	MNHN QU17151	#	#	#	17.20	1.20	7.0
<i>Caenomeryx filholi</i> <sup>EEA</sup>	UM PDS 2570	4033.04	2674.96	66.3	8.19	0.30	3.6
<i>Anoplotherium</i> sp. <sup>EEA</sup>	MNHN. no number	7173.92	4419.56	61.6	416.09	31.18	7.5
<i>Bathygenys reevesi</i>	TMM 40209-198	#	#	#	14.37	0.46	3.2
<i>Agriochcerus</i> sp.	AMNH 95330	2967.02	1606.20	54.1	33.00	1.64	5.0
<i>Leptauchenia</i> sp.	AMNH 45508	1748.33	909.04	52.0	13.73	0.75	5.5
<i>Palaeochcerus</i> sp.	MHNT_2014_0_3075	4450.78	2462.48	55.3	#	#	#
<i>Tayassu pecari</i>	UM V 79	7744.90	5748.38	74.2	94.86	3.08	3.3
<i>Sus scrofa</i>	TMM M 454	8568.78	6535.22	76.3	130.59	4.88	3.7
<i>Microbunodon minimum</i>	UP LM1967MA300	151057.00	95121.60	63.0	#	#	#
<i>Hippopotamus madagascariensis</i>	MNHT-Pal-2012-0-218-1	19054.84	13445.16	70.6	486.90	14.01	2.9
<i>Hippopotamus amphibius</i>	AF RG 78	#	#	#	782.21	24.03	3.1
<i>Choeropsis liberiensis</i>	**	13400.30	9389.46	70.1	359.32	7.73	2.2
<i>Leptomeryx</i> sp.	AMNH 53596	2208.72	1249.59	56.6	17.25	0.89	5.15
<i>Moschiola memmina</i>	UM V 68	2037.02	1252.84	61.5	14.06	0.54	3.86
<i>Moschus chrysogaster</i>	UM N 401	4829.50	3244.68	67.2	51.03	1.58	3.1
<i>Tragelaphus scriptus</i>	AF RG35620	11648.02	9125.36	78.3	169.79	4.28	2.52

**Table 1** – Measurements of the area and volume of the artiodactyls (Endemic European artiodactyls -EEA-; and crown artiodactyls) discussed in the text. The cerebrum surface was measured using the tag tool of MorphoDig (Lebrun 2018) \*\* volumes for *Choeropsis liberiensis* correspond to the mean value of four specimens (AF RG 77-51-M1. 31723. 35715. 35716); missing data are indicated by a #. Institution abbreviations: AMNH, American Museum of Natural History; MNHN, Muséum National d’Histoire Naturelle, Paris; MHNT, Muséum d’Histoire Naturelle de Toulouse; AF, Africa Museum, Tervuren; UM, Université de Montpellier; UP, Université de Poitiers; TMM, Texas Memorial Museum.

Cerebral hemispheres: The EEA show a great disparity of neocortical folding pattern, with a very simple pattern (two sulci delimiting the almond shapes gyrus) observed in *Cebochoeridae*



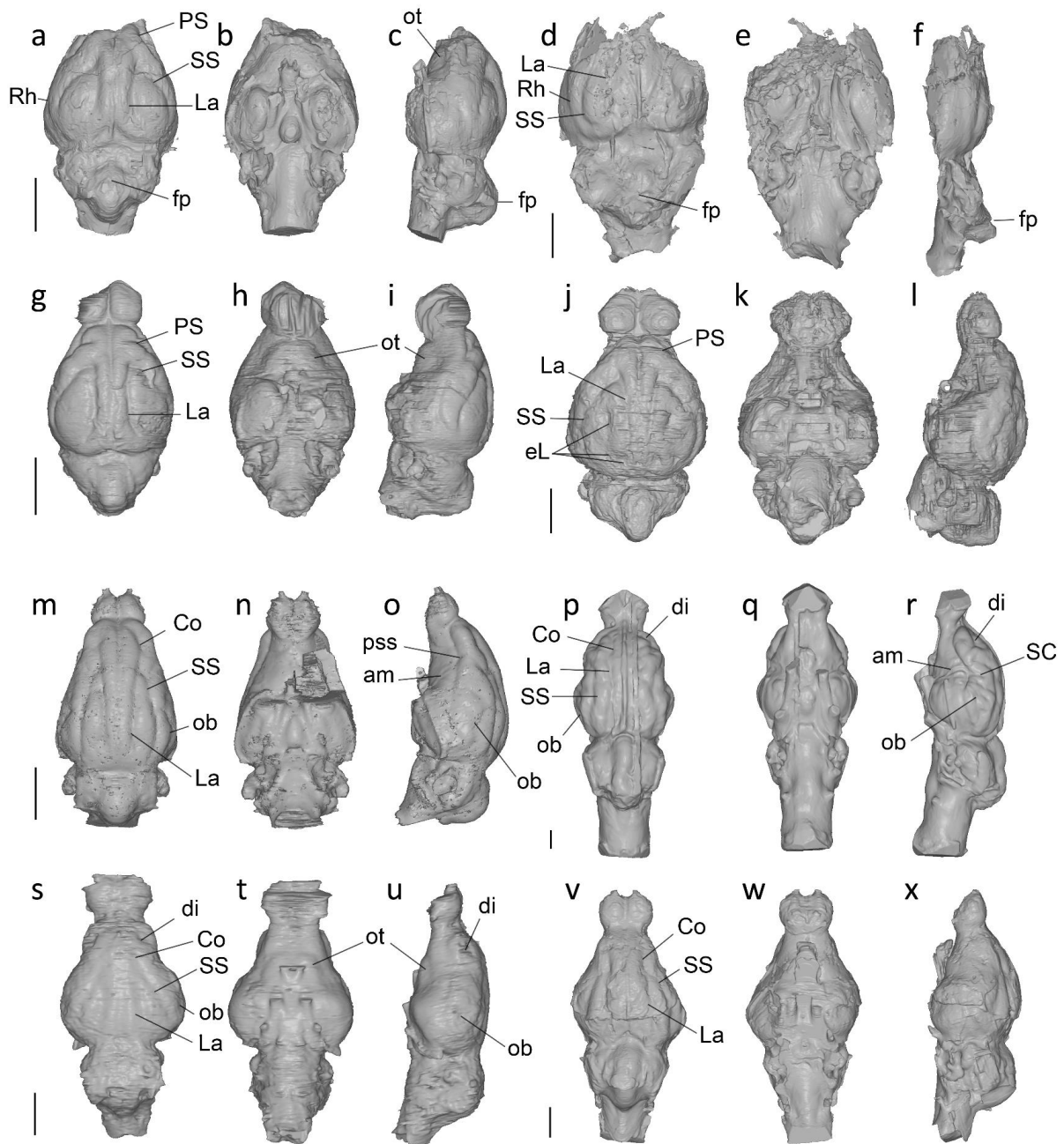
(Dechaseaux 1969a:fig.13) and in *Mouillacitherium* (Figs 4 G-I; Orliac, in press), and more complicated ones found in other groups documented. The dichobunoid *Dichobune* shows a slightly more complex pattern, with a long presylvia widely visible on the dorsal aspect and three accessory sulci notching the gyrus III (entolaterals, Figs 4 J-L; Orliac, in press). Cainotheriidae also present additional sulci, with a long coronal sulcus linked to both the lateral sulcus and the suprasylvia, and a diagonal sulcus, sometimes branched. The cainotheriids taxa analyzed *Caenomeryx filholi* (Fig. 4M-O; Orliac in press), and *Cainotherium* (Anthony and Friant 1938; Friant 1939; Dechaseaux 1969a:fig.12) shows a small sulcus linking the rhinal fissure, here interpreted as a pseudosylvia, and most probably had partial operculization of the central area, highlighted by the pathway of the middle meningeal artery, partly hidden by the gyrus II (Dechaseaux 1961, 1969a; Fig. 4O). Anoplotherioidea exhibit another type of folding pattern. The dacrytherid *Dacrytherium* (Dechaseau 1969a:fig.2) is very close to the cainotherioid plan, with elongated lateral sulcus, suprasylvia and coronal sulcus, and also a small oblique sulcus. Anoplotheriidae exhibit more elongated, parallel sulci, and a coronal sulcus preferentially linked to the lateral sulcus. *Anoplotherium* presents a complex folding pattern of the neopallium with additional ramifications (Fig. 4 PR); an additional sulcus located anterior to the coronal sulcus (“sulcus  $\gamma$ ” of Dechaseaux 1969a) would correspond to a diagonal sulcus according to the nomenclature of Repérant (1971b). *Anoplotherium* shows a clear operculization of the central area, with a deep sylvian complex. The oblique sulcus is sinuous and ramified. The extension of the neopallium on the surface of the cerebral hemispheres of *Dichobune* and *Mouillacitherium* is similar to *Diacodexis* and *Homacodon* (ca. 43%, see Tab. 1), but the paleopallium is not visible in dorsal view for the former (Fig. 4G, J). The relative sizes of the neopallium of the Oligocene taxa *Caenomeryx* and *Anoplotherium* is larger than that of other EEA and exceeds 60% (see Tab. 1).

**Midbrain exposure:** Midbrain exposure varies greatly depending on taxa. Although the exposure is smaller than in early Eocene taxa, the midbrain is exposed in *Cebochoerus* and colliculi are even visible (Dechaseaux 1969a:fig.13). Despite a relatively simple folding pattern and general weak extension of the neopallium, the midbrain exposure is small in *Dichobune* (Fig. 4G) and *Mouillacitherium* (Fig. 4J), *Tapirulus* (Dechaseaux 1969:fig.12) and *Mixtotherium* (Dechaseaux 1973:fig.3), smaller than in *Diacodexis*, *Homacodon* and *Helohyus*. The midbrain is not exposed in Cainotheriidae (*Caenomeryx*; Fig. 4M) and Anoplotheriidae (*Anoplotherium*; Fig. 4P).

**Cerebellum:** Just like in other groups, the cerebellum of EEA has received little attention in the literature. They differ by the folding pattern, size and shape of their vermis (Fig. 4). Compared to the size of the cerebrum, the cerebellum is relatively large in Anoplotherioidea where the anterior extension of the vermis reaches that of the cerebellar hemispheres (Dechaseaux 1969:figs.2,6,10; Fig. 4P). It is relatively smaller in other EEA taxa such as cainotheriids, *Mouillacitherium* or *Dichobune*. In these taxa, the cerebellar hemispheres extend anteriorly to the anterior margin of the vermis, like in early Eocene taxa (Fig. 4G, J, M).

**Oreodontoidea** - Endocranial casts of oreodontoids are best illustrated in the literature by the late Eocene oreodontine *Bathygenys reevesi* (Macrini 2009), and by natural endocasts of the early Oligocene merycoidodontine *Merycoidodon culbertsoni* (Leidy 1869:pl. 14, fig. 11; Black 1920:fig. 18: specimen IV; Moodie 1922:fig. 22) and middle Eocene *Merycoidodon gracilis* (Dechaseaux 1961:fig.10). We complete here the picture with 3D models of the leptachenine merycoidodontid *Leptauchenia* sp. from Washington County, South Dakota (AMNH-FAM 45508; Fig. 4S-U) and of the agriochoerid *Agriochoerus* sp. from Sage Creeck, Chadron Mont. (AMNH- FAM-95330, Late Eocene; Fig. 4V-X) (see Orliac and Gilissen 2012:fig.3).

**Olfactory bulbs:** Olfactory bulbs are proportionally smaller than in early artiodactyls described above (values comprised 3.2-5.5%, Tab. 1), but larger than in crown Artiodactyla.



**Figure 4** – Endocast morphology of extinct artiodactyl clades. A-C, *Homacodon vagans* (AMNH 12695); D-F, *?Helohyus* (AMNH 13079); G-I, *Mouillacitherium elegans* (UM ACQ 6625); J-L, *Dichobune leporina* (MNHN.F.QU16586); M-O, *Caenomeryx filholi* (UM PDS 2570); P-R, *Anoplotherium* sp. (3D surface of plaster cast illustrated by Dechaseaux 1969:fig.6); S-T, *Leptauchenia* sp. (AMNH 45508); V-X, *Agriochoerus* sp. (AMNH 95330). 3D models are available in Orliac (in press). Illustrations in dorsal (A, D, G, J, M, P, S, V), ventral (B, E, H, K, N, Q, T, W), and lateral (C, F, I, L, O, R, U, X) views. Scale bars = 1cm

Unfortunately, most of the oreodontoid specimens are natural endocasts and the volume of the olfactory bulbs is not provided in their original description.

**Cerebral hemispheres.** Oreodontoids described in the literature present different degrees of neopallium sulcal complexity, from few sulci arranged in a rectilinear disposition, without ramifications, to complex, ramified, sulci and an operculization of the central area. The simplest pattern illustrated is described in *Bathygenys* which only presents a suprasylvia prolonged by a coronal sulcus, and a lateral sulcus delimiting a gyrus III (Macrini 2009:fig.3). A more complex

pattern is observed in *Merycoidodon culbertsoni* and *Miniochoerus gracilis* from the middle Oligocene. An ectolateral sulcus divides the gyrus III in *Mi. gracilis* (Dechaseaux 1961:fig. 10). *Me. culbertsoni* (Black 1920:fig.18) presents several ramifications branching on the suprasylvia, including a small sulcus x, originating from the suprasylvia and joining the interhemispheric cleft, and an oblique sulcus located on the lateral margin, posterior to the sylvian complex. We agree with the conclusions of Friant (1939, 1948) and Dechaseaux (1961) that the gyrus I is operculized in those species. Yet, there is no indication of operculization of the central area in *Bathygenys* (see Macrini 2009). A noticeable variability of the neocortical pattern has been described in the literature in *Merycoidon* and *Bathygenys* (Macrini 2009). The virtual endocranial cast of *Leptauchenia* reveals a rather simple cortical pattern with two main sulci, a long oblique suprasylvia/coronal and a small lateral sulcus delimiting a closed gyrus III, and two accessory sulci, an oblique and a diagonal (Fig. 4S-U). There is no indication of operculization. The endocranial morphology of Agriochoeridae is here documented by *Agriochoerus* (Fig. 4V-X). It shows a simple sulcal pattern with only a suprasylvia, a coronal sulcus and a lateral sulcus delimiting a closed gyrus III, without accessory sulcus. It is worth noting that in this taxon, the coronal sulcus is in line with the lateral sulcus and not with the suprasylvia. The extension of the neopallium on the surface of the cerebral hemispheres in *Leptauchenia* and *Agriochoerus* is more important than in *Diacodexis* and *Homacodon* and exceeds 50% (Tab. 1). The pyriform lobes and the olfactory tubercles are proportionally smaller in oreodontids than in *Diacodexis* (Orliac and Gilissen 2012:fig.1c,fig.2d) and *Homacodon* (Fig. 4A).

**Midbrain exposure:** The posterior development of the neopallium and the transverse sinus cover the midbrain in oreodontoid endocasts.

**Cerebellum:** All oreodontoid taxa show a wide vermis compared to the cerebellar hemispheres. Black (1920:fig.9-10) illustrated an incredibly well preserved cerebellum of an oreodont from middle Oligocene of the White River group, South Dakota. The different lobules and crura can be identified in great detail. The fissura prima lies rather anteriorly, especially compared to *Bathygenys*, and the exposition of the lobus rostralis on the anterior part of the vermis is reduced compared to *Diacodexis* and *Helohyus*. Details of the vermis structures cannot be observed on the endocasts of *Leptauchenia* and *Agriochoerus* (see Fig.4).

The endocranial casts of oreodontoids show a diversity of shape and folding pattern. Our sample is restricted to the Late Eocene/Early Oligocene and it would be very interesting to document endocranial casts of all Merycoidodontidae subfamilies and more recent taxa.

### 3.1.3 – Endocranial morphology of crown Artiodactyla clades

**Tylopoda** - Endocranial casts of the Camelidae are known from the late Eocene to the late Pleistocene. At least one endocast is known from each epoch in this timespan, allowing the observation of a tremendous brain size increase in this lineage (Edinger 1966; Jerison 1971, 2007). Basic qualitative descriptions for this group were made by Edinger (1966).

**Olfactory bulbs:** Descriptions of relative sizes of different brain regions, particularly of the anterior region and olfactory bulbs, are largely lacking for this group. These structures are missing from the known *Protylopus* endocast. However, if its brain proportions parallel those of Oligocene camelids, olfactory bulbs would have been about 8mm in length (Edinger 1966).

**Cerebral hemispheres:** Detailed descriptions of gyrification patterns across multiple fossil taxa and modern camelids were made by Repérant (1970, 1971a, b). The late Eocene *Protylopus* brain is more complex than that of earliest artiodactyls and bears three longitudinal sulci: a corono-suprasylvian sulcus prolonged medially by a short ansate sulcus, a lateral sulcus and an entolateral sulcus (Repérant 1971a). By the Oligocene, in *Poebrotherium*, the suprasylvian sulcus moved toward the midline and developed a descending branch at its anterior end. Lateral and entolateral sulci get close to the sagittal plane as new sulci, ectolateral and the sylvian

complex, began to form and move dorsally from the lateral edges of the brain. At this time, the presylvian sulcus is faintly visible in the anterior brain, and the appearance of sulcus “*oblique I*” begins to define the oblique posterior brain. Operculization is observed in *Poebrotherium* where a long ectosylvia and a short sylvian complex occur (Repérant 1971a:fig.2). More sulci developed by the early Pliocene in *Procamelus*, when we observe the greatest expansion of the forebrain. The suprasylvian becomes more complex as its anterior portion couples with the ansate and coronal sulci, forming a branching pattern. All longitudinal sulci continue to move closer to the sagittal plane, as outer sulci develop further, and the rhinal fissure has moved further down the lateral edges of the brain (Repérant 1971a). Operculization is more extended. The main distinction in camelid brain evolution is the pattern of gradual introversion of posterior longitudinal sulci into the sagittal plane, and simultaneous eversion of sulci from the frontal region (Repérant 1971a).

**Cerebellum:** Enlargement of the cerebral hemispheres was paralleled by enlargement of the cerebellum, whereas the vermis becomes less dominant (Edinger 1966). Fine details of cerebellar surface anatomy are scarce in this clade.

**Suoidea** - As mentioned above there is, to our knowledge, no endocast of fossil suoid described in the literature. We document here the endocranial cast of *Palaeochoerus* sp. from an unknown locality in Quercy, France (ancient collections from the Museum d’Histoire Naturelle of Toulouse; MHNT PAL2014.0.3075.1; Fig. 5A-C). Given the biochronological repartition of this taxon in Quercy, it is most likely of late Oligocene age. Phylogenetic analyses (Orliac et al. 2010; Orliac 2012) support a basal position of Palaeochoeridae, before the split between Suidae and Tayassuidae.

**Olfactory bulbs:** The palaeochoerid specimen consists of a partial braincase and unfortunately does not preserve the olfactory bulbs. The small portion preserved indicated that they were of decent size, separated from the cerebral hemispheres by a short circular fissure.

**Cerebral hemispheres:** The neopallium sulcal complexity of *Palaeochoerus* sp. already strongly recalls that of modern suoids (Fig. 5A-C). The lateral sulcus is rather short and close to the interhemispheric fissure, the suprasylvia is prolonged anteriorly by an anterior branch and medially by an ansate sulcus that joins a long coronal sulcus. The later extends anteriorly and bifurcates in its anterior-most portion. On the lateral aspect of the neopallium, there is a clear sylvian complex that forms an open area, letting part of the gyrus I be exposed. There is a short deep oblique sulcus. Contrary to the domestic pig, *Sus scrofa*, there is no trace of a cruciate sulcus (we follow here the identification of Anthony and Grzybowski 1931, and Barone and Bortolami 2004, that the anterior most sulcus in *Sus scrofa* is the anterior prolongation of the splenial; for alternative interpretation see Krueg 1878). The neopallial pattern of *Palaeochoerus* is closer to that of Tayassuidae that do not seem to present a dorsal exposure of the anterior portion of the splenial sulcus (Saraiva 2017:figs.2,5). The neopallium is widely expanded on the cerebral hemisphere and covers 55% of it, a slightly inferior value compared to *Tayassu* (Tab. 1).

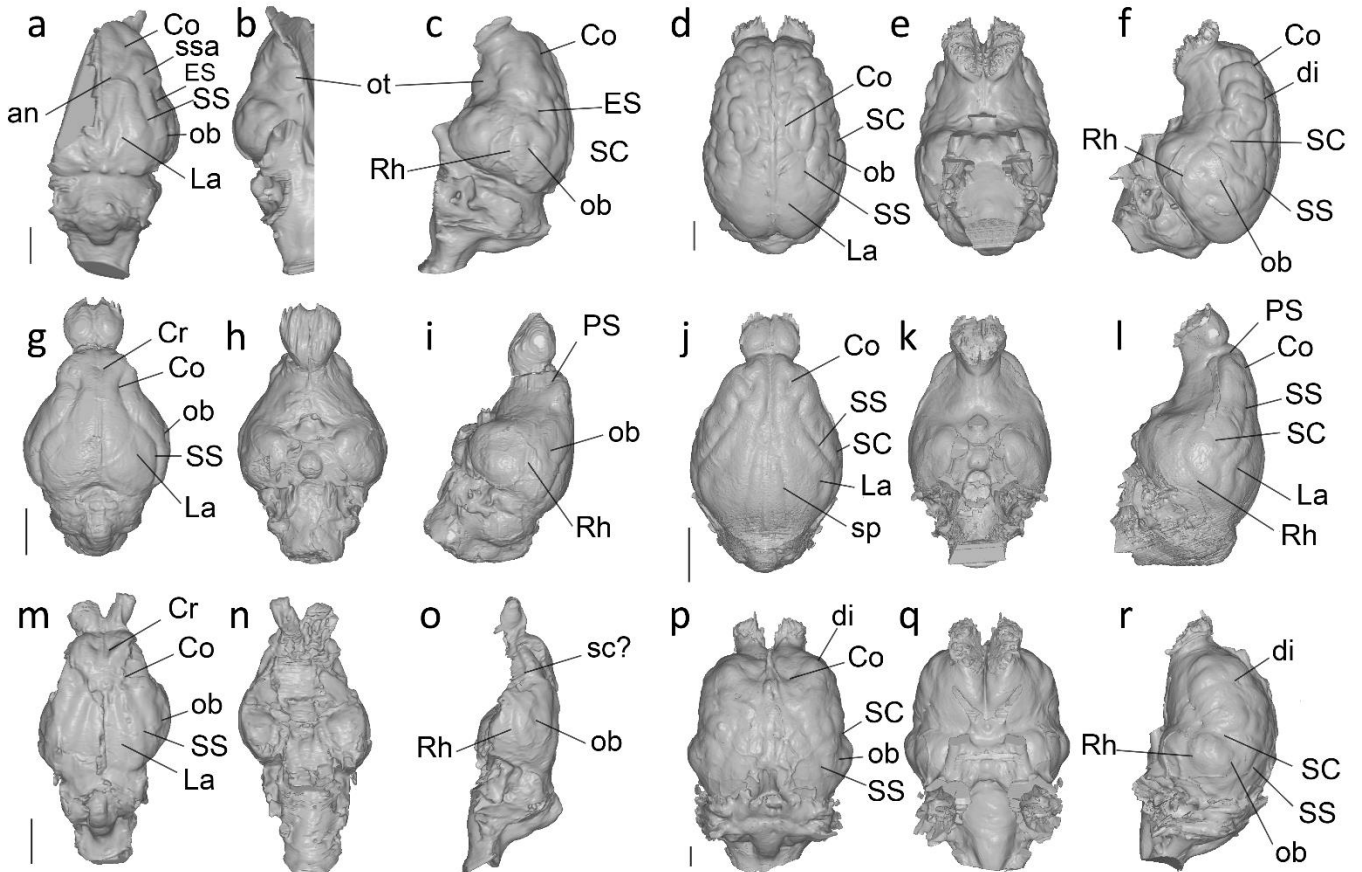
There are wide, salient, olfactory tubercles on the *Palaeochoerus* endocast (Fig. 5B-C), just like in modern representatives of the group (Saraiva 2017:fig.4; Barone and Bortolami, 2004:pl.158)

**Midbrain exposure and cerebellum:** In *Palaeochoerus*, the midbrain is not exposed dorsally and the posterior expansion of the neopallium covers the anteriormost part of the vermis and the paramedian lobes. It is also the case in modern Tayassuidae (*Tayassu pecari*, Saraiva 2017:fig.7) and Suidae (*Sus scrofa domesticus*, Saikali et al. 2010). The vermis of *Palaeochoerus* is wide relative to the paramedian lobes, and its subdivisions are impossible to identify; the shape of the paramedian lobes is masked by the sinuses surrounding the petrosal region. In modern suoids, the vermis appears smaller than the paramedian lobes (Barone and Bortolami 2004:pl.113; Saraiva 2017).



Knowledge of the endocranial morphology of Suoidea remains highly limited, even for modern taxa. The general morphology of the brain of *Palaeochoerus* indicates an advanced stage of neopallial expansion (Fig. 5A, C), as soon as the lower Oligocene, even if it is less convoluted than that of modern suoids. Its pattern is closer to Tayassuidae than to Suidae.

**Ruminantia** – Compared to their great specific diversity, documentation of ruminant endocasts remains limited, especially for Paleogene times. We briefly describe and illustrate here the endocast of *Leptomeryx* sp. (AMNH 53596; Fig. 5G-I) from the Early Oligocene of South Dakota (Brule Formation, Orellan stage). In addition, we report the endocast of the Early Pleistocene cervid *Antifer ensenadensis* (Fontoura et al. 2020).



**Figure 5** – Endocast morphology of crown artiodactyl clades: A-F (top line) , Suoidea; G-L (middle line), Ruminantia; M-R (bottom line), Hippopotamoidea with A-C, *Palaeochoerus* sp. (MHNT\_2014\_0\_3075); D-F, *Tajassu pecari* (UM V79); G-I, *Leptomeryx* sp. (AMNH 53596); J-L, *Moschiola memmina* (UM V68); M-O, *Microbunodon minimum* (UP LM1967MA300); P-R, *Choeropsis liberiensis* (MRAC RG 35715). Illustrations in dorsal (A, D, G, J, M, P), ventral (B, E, H, K, N, Q), and lateral (C, F, I, L, O, R) views. Scale bars = 1cm.

**Olfactory bulbs.** The endocast of *Leptomeryx*, earliest Ruminantia from our sample (early Oligocene) presents large olfactory bulbs (Fig.5G-I) compared to modern representatives of the group (Tab. 1). The olfactory bulb chamber, or ethmoidal fossa, is globular and the two bulbs are closely apposed on their whole length. The endocasts of *Dremotherium* (Sigogneau 1968:fig.16-18) and of *Amphitragulus*? (Sigogneau 1968:fig.28-29) from the late Oligocene-early Miocene of Saint-Gérard-le-Puy show less globular, divergent olfactory bulb chambers. Unfortunately, 3D models of these specimens are not available yet, and the olfactory bulb chamber volume cannot be measured. Regarding olfactory bulb chamber morphology, *Leptomeryx* is closer to modern tragulids (e.g., *Moschiola memmina* Fig.5J-L), than to extant



or extinct bovids or cervids (for illustrations of the latter see Palombo et al. 2008:figs.7-9, 11). The endocast of the cervoid Palaeomerycidae *Aletomeryx* from the late Miocene of Nebraska (Lull 1920) does not preserve the olfactory bulbs portion. As for *Dremotherium* and *Amphitragulus?*, the endocast of the late Miocene giraffid *Samotherium* (Black 1915) also presents set apart, rather slender olfactory bulb chambers. The olfactory lobes of *Antifer ensenadensis* are strongly separated, similar to those of the current cervid species with which they are compared (*Mazama*, *Blastocerus*, *Ozoterus*; Fontoura et al. 2020).

**Cerebral hemispheres:** Modern Ruminantia show a wide panel of neopalleal pattern from rather simple patterns like in Tragulidae (e.g., *Moschiola memmina* Fig.5J-L; *Hyaemoschus aquaticus* Friant 1939:fig.21), to complex, highly convoluted neopallium (e.g., Giraffidae, Bovidae, Cervidae, Friant 1940; Palombo et al. 2008; Graïc et al. 2017). The gyrification pattern has been demonstrated to be relevant at a systematic level, between families (Palombo et al. 2008) and within (Oboussier 1979). Regarding the main neopalleal sulci, the early Oligocene *Leptomeryx* shows the simplest pattern with a small, faint, lateral sulcus, and a long suprasylvia prolonged by an anteriorly extended coronal sulcus. A short cruciate and a short oblique sulci are also present, as well as a short presylvia (Fig.5G-I). On the lateral aspect, the rhinal fissure lies fairly high and shows a marked inflexion between the pre- and postsylvia; however, no pseudosylvia, the hallmark of an incipient operculization, is visible. The simple pattern observed in *Leptomeryx* is close to that of modern tragulids (*Moschiola memmina*, Fig.5J-L) that also show a very faint lateral sulcus and a long suprasylvia anteriorly prolonged by the coronal sulcus. However, tragulids show a long dorsal exposure of the splenial sulcus and a clear operculization of the central area with a marked sylvian complex. The neopalleal pattern of the late Oligocene/early Miocene *Amphitragulus?* (Sigogneau 1968:fig.28-29) is slightly more complex than that of *Leptomeryx* and shows a long anterior suprasylvia and a diagonal sulcus; pathway of the middle cerebral artery indicates that some part of the ventral margin of the neopallium is operculized. The pattern of *Dremotherium* (Sigogneau 1968:fig.16-18), of similar age, is even more complex, with more ramifications and elongation of the diagonal and oblique sulci. Operculization is also more important and the sylvian complex is visible as a deep depression on the surface of the endocast. A complex pattern is also observed in the late Miocene palaeomerycidae *Aletomeryx* (Lull 1920:fig.6) where the ansate also seems to be present. Highly complex, branched, neopalleal pattern are observed in late Miocene and plio-pleistocene Bovidae, Giraffidae and Cervidae.

The neopallium of *Leptomeryx* covers ca. 56% of the cerebral hemisphere; this value is slightly inferior to that of the modern tragulid *Moschiola* (Tab. 1). The olfactory tubercles are not salient on ruminant endocasts.

**Midbrain exposure and cerebellum:** The midbrain is not exposed in ruminant endocasts documented so far. In *Leptomeryx* the posterior extension of the neopallium abuts the cerebellum and most probably covers part of the paramedian lobes. The vermis is slender and posterior divisions are visible on the endocast (Fig.5G-I). The vermis is also slender in *Amphitragulus?* (Sigogneau 1968:fig.28) and *Dremotherium* (Sigogneau 1968:fig.16). In bovids and cervids, the paramedian lobes seem to be smaller in dorsal view, the vermis looking relatively wider in these taxa.

**Hippopotamoidea** - As mentioned above the number of endocasts of fossil hippopotamoids described in the literature remains very limited. Recent data about two phylogenetically distant taxa, the Microbunodontinae *Microbunodon minimum* and the Bothriodontinae *Merycopotamus medioximus* shed some light on important steps in their brain evolution (Thiery and Ducrocq 2015). Again, most of the discussions is focused on the evolution of the neopallium. Regarding modern hippopotamines, some morphological specificities of their endocast are related to modifications of their skull for semiaquatic habits. Indeed, focus has been made on the angle

between the two optic nerves (Fig.5Q), considered as an indicator of laterally projected, dorsally protruding eyes related to amphibiosis (Anthony 1948; Dechaseaux 1961). Documentation of hippopotamoid endocasts remains very fragmentary and nothing is known prior to the late Oligocene.

Olfactory bulbs. Hippopotaminae present among the smallest relative size of the olfactory bulb chamber of our artiodactyl sample (2 to 3 %; Tab. 1). Compared to other Artiodactyla, olfactory bulbs of modern hippopotamines are separated along their entire length (e.g., pygmy hippopotamus, *Choeropsis liberiensis*, Fig.5P-R). Despite deformations of the fossil specimens, the olfactory bulbs of *Microbunodon* are obviously proportionally larger than that of modern and subfossil hippopotamines (Fig.5M-O).

Cerebral hemispheres: The neopallium of modern hippopotamines is extended on a very large portion of the cerebral hemisphere (Tab. 1). It shows a complex folding pattern (Garrod 1880; Anthony 1948; Pilleri 1962; Butti et al. 2014), with a partial operculization of the gyrus I. Identification of the cortical foldings in *Choeropsis liberiensis* differs slightly depending on the authors (see Friant 1940; Pilleri 1962; Butti et al. 2014). Friant (1940) describes a rather linear organisation of the sulci, and characterizes modern hippos by the presence of a “K lobe” corresponding to a special folding induced by a bifid sylvian complex (Friant 1940:fig.2). Instead, Butti et al. (2014) highlight a pattern similar to cetaceans, with a concentric organization of the three main gyri of the lateral aspect (suprasylvian gyrus, ectosylvian gyrus, and perisylvian gyrus) around an almost vertical Sylvian fissure (Butti et al. 2014:675). Organization of the foldings relative of the Sylvian fissure in *Choeropsis* rather seems to be close to that of *H. amphibius* and we follow here the interpretation of Friant (1940) that main foldings have a mostly longitudinal organization. Our observations indicate that the recording of neopallial structure on endocasts is quite blunt in *C. liberiensis* (Fig.5P) and *H. madagascariensis* due to meninges thickness and sulci only leaving faint depressions (see Anthony 1940:pl4,figs.4-5). The rhinal fissure is only distinct in its posterior part and the cleft visible anterior to the rhinal angle corresponds to the pseudosylvia (Fig. 5R). Neopallial structures are almost completely obscured in *H. amphibius*. A complex neopallial pattern is retrieved on the natural endocast of the “advanced bothriodontine” *Merycopotamus medioximus* with the potential presence of a “K lobe” (Thiery and Ducrocq 2015). The partial preservation of the specimen, however, does not allow for precise description. The microbunodontine *Microbunodon minimum*, phylogenetically more distant from modern hippopotamines than is *Merycopotamus*, shows a much simpler pattern with only two main elongated parallel sulci: a long lateral sulcus and a long corono-sylvia (Thiery and Ducrocq 2015:fig.2; Fig.5M-O). Anterior to the coronal sulcus, joining the interhemispheric fissure is a small cruciate sulcus, and, on the lateral aspect, the neopallium shows a shallow oblique sulcus. The specimen is damaged at the level of the rhinal angle making the presence of a Sylvian complex uncertain, the presence of a K lobe seems most unlikely. There is no apparent olfactory tubercles on hippopotamoid endocasts (Fig. 5N-O; Q-R), even though modern hippopotamines do present large tubercles on the ventral aspect of actual brains (Pilleri 1962:figs.2, 4).

Midbrain exposure and cerebellum: The packing of the posterior part of the cranium in modern hippos drastically impacts the braincase; besides, the presence of wide sinuses dorsal to the cerebellum completely hides the dorsal aspect of the latter. In modern hippopotamuses, the anterior part of the cerebellum is covered dorsally by the posterior extension of the cerebrum (e.g., Garrod 1880:fig.2; Butti et al. 2014:fig.1). The late Oligocene *Microbunodon minimum* shows no midbrain exposure (Fig.5M). Its vermis is salient and protrudes dorsally above the level of the cerebrum (Fig. 5O). The cerebellum is not preserved in *Merycopotamus* and cannot be described.

**Cetacea** - Endocranial morphology of cetaceans is only partly documented back to late Eocene. However, correspondence between the brain size and shape and the endocranial cast is not complete due to the presence of extensive adnexa.

Olfactory bulbs: The brain of modern cetaceans is characterized by a great reduction of the olfactory apparatus (e.g., Edinger 1955; Pihlström 2008; Godfrey et al. 2013; Berta et al. 2014; Kishida et al. 2015), and modifications of the olfactory tract occur in the earliest phase of cetaceans' history (e.g., Orliac and Thewissen 2021). An elongation of the olfactory tract has been described in archaeocetes (Pakicetidae, Kishida et al. 2015; Remingtonocetidae, Bajpai et al. 2011; Basilosauridae, Edinger 1955; Uhen 2004; Godfrey et al. 2013) and in raoellids (Orliac and Thewissen 2021). Regarding Neoceti, early mysticetes present massive, elongated, olfactory peduncles (*Llanocetus*, Mitchell 1989); these peduncles and associated ethmoidal chambers are still present, though relatively small in modern representatives of the group (e.g., *Balaena mysticetus*, Duffiel et al. 1992; *Balaenoptera acutorostrata*, Godfrey et al. 20013; *Megaptera novaeangliae*, Hof and Van der Gucht 2007). In early foetal stages of odontocetes, the olfactory bulbs, nerve, and tracts are present, but these structures then degenerate and are completely absent from mature odontocete brains (Ridgway 1988; e.g., *Platanista*, Kamiya and Pirlot 1980). The olfactory apparatus is present in archaic odontocetes and has been described in Oligocene taxa (*Simocetus*, Fordyce 2002; USNM 299482, fig. 5E; platanistoid odontocete, Hoch 2000, figs.6-7), in the early Miocene prosqualodontid *Prosqualodon davidi* (Flynn 1948), and in the Miocene *Squalodon* sp. (Dart 1923).

Cerebral hemispheres: Increased neocortical size and complexity is one of the hallmarks of the modern cetacean brain (Marino et al. 2000, 2004, 2007), however, the presence of endocranial vascular networks and other adnexa makes it impossible to access the neopallial pattern of most fossil cetaceans, as evidenced by basilosaurids in which the pattern could not be described (Pilleri 1991). In protocetids and remingtonocetids, the extension of the retia is limited; three faint oblique sulci have been mentioned on a natural endocranial cast of the protocetid *Indocetus* (Bajpai et al. 1996) and a faint one, close to the cerebral midline, is visible on the 3D reconstruction of the endocast of *Remingtonocetus harudiensis* (Bajpai et al. 2011:fig.7). The raoellid *Indohyus*, sister taxon to the Cetacea clade, shows a very simple neocortical pattern, limited to two major sulci (suprasylvia and lateral sulcus) plus a small coronal sulcus (Orliac and Thewissen 2021). This pattern is similar to the primitive neocortical pattern retrieved in Eocene terrestrial artiodactyls (see Orliac and Gilissen 2012). Endocasts of extant and extinct Neoceti mainly give access to the overall shape of the cerebral hemispheres and to the cranial vasculature. Some major neocortical sulci might be observed too, such as the Sylvian fissure, and sulci in the anterior portion (Pilleri 1991; Racicot and Colbert 2013; Bisconti et al. 2020), however, the groove pattern cannot be described nor compared with accuracy. The brain-stem flexure is highly pronounced in the modern representatives of Cetacea (Kruger 1966), and they show a concentric organization of the three main gyri of the lateral side of the cortex (suprasylvian gyrus, ectosylvian gyrus, and perisylvian gyrus) around an almost vertical Sylvian fissure. As far as we know, this organization, potentially linked to the highly derived conformation of the cranium of crown cetaceans, is not documented in the earliest archaeocetes (e.g., Dart 1923; Bajpai et al. 1996; Bajpai et al. 2011).

Midbrain exposure and cerebellum: In modern cetaceans, the caudal extension of the neopallium covers a large part of the cerebellum, both in mysticetes (e.g., *Balaena*, Raghanti et al. 2019:fig.1B) and in odontocetes (e.g., *Stenella*, Kamiya and Pirlot 1974:pl.1; *Platanista*, Kamiya and Pirlot 1980:fig.10D). Regarding extinct taxa, the midbrain area is impossible to visualize on endocasts of Neoceti and basilosaurids because of the presence of endocranial vascular networks and other adnexa. In archaeocetes, *Indocetus* (Bajpai et al. 1996:fig.1C) and *Remingtonocetus* (Bajpai et al. 2011:fig.7) have a posteriorly expended neopallium that most probably covers the midbrain and abuts the cerebellum. Compared to archaeocetes, *Indohyus*

*indirae* has a much limited extension of the neopallium and a wide midbrain exposure (Orliac and Thewissen 2021:fig.2), greater than in middle and late Eocene endemic European artiodactyls (e.g., *Dichobune*, *Cebochoerus*, Dechaseaux 1961, 1969a; Orliac and Gilissen 2012; Fig. 4J-K), and Eocene North American taxa (e.g., *Agriochoerus*, *Bathysgenys*, Whitmore 1953; Macrini 2009; Orliac and Gilissen 2012; and *Leptauchenia* Fig. 4S-U). The brain of modern Cetacea shows a small and narrow vermis compared to the two voluminous, highly convoluted, cerebellar hemispheres (e.g., Ries and Langworthy 1937; Pilleri 1966a,b; Hanson et al. 2013; Bisconti et al. 2021). Regarding archaeocete endocasts, most of the surface of the cerebellum of basilosaurids is covered with a large rete mirabile (e.g., Breathnach 1955; Pilleri 1991; Geisler and Luo 1998; Uhen 2004), making it impossible to accurately observe the relative size of the vermis. The endocasts of *Indocetus* (Bajpai et al. 1996) and *Remingtonocetus* (Bajpai et al. 2011) show no major shift in the proportions of the different elements of the cerebellum compared to other artiodactyl groups, with a wide vermis relative to the plausible representation of the cerebellar hemispheres. *Indohyus* has a relatively large vermis compared to its cerebellar hemispheres (Orliac and Thewissen 2021:fig.2), as in earliest artiodactyls, *Diacodexis* (Orliac and Gilissen 2012) or *Dichobune* (Fig. 4J).

### 3.2. Space associated with cranial blood vessels

Mentions of cranial blood vessels in fossil artiodactyls are mostly based on descriptions of the external aspect of the basicranium or on petrosal morphology (e.g., Coombs and Coombs 1982; O’Leary 2010). Works describing endocasts of terrestrial artiodactyls based on intracranial investigations and  $\mu$ CT-scan data (Merycoidontidae, Macrini 2009; early artiodactyls, Orliac and Gilissen 2012; Hippopotamoidea, Thiery and Ducrocq 2015) do not include detailed descriptions of cranial blood supply beyond mention of the orbito-temporal canal. Studies on endocasts of crown cetacean and their relatives do focus more on circulatory casts and sinuses (e.g., Racicot and Rowe 2014; Bajpail et al. 2011; Orliac and Thewissen 2021), mainly in relation with the presence and extension of the retia mirabilia (“wonderful net”, Slijper 1936; Ridgway et al. 2016).

Modern artiodactyls indeed present a selective brain cooling system (Baker and Hayward 1967) enabling them to lower their brain temperature below their body temperature. This system is mediated by the carotid rete, a subdural arterial meshwork that anatomically and functionally replaces the internal carotid artery (O’Brien 2018). It lies on the basisphenoid roof, slightly posterior to the hypophyseal fossa (O’Brien 2015:fig.1; O’Brien and Bourke 2015). The arterial meshwork of the carotid rete is housed within the venous cavernous sinus, a large pool of venous blood that drains from the sphenoparietal and frontal regions of the cerebrum and from the nasal area of the face (O’Brien 2017) and that receives blood that has been evaporatively cooled by the nasal turbinates. This contact between cooled venous blood and the high surface area of the arterial rete enables rapid heat exchange and cooling of the arterial blood destined for the brain. Nearly all modern artiodactyls possess a carotid rete and perform selective brain cooling. However, major arteries supplying the rete are derived from different embryonic aortic arches in the different artiodactyl families (for review see O’Brien 2018). The results of O’Brien (2020) based on ancestral character reconstructions support that this pattern of variation results from independent evolutionary processes and suggest that different modern artiodactyls groups developed a carotid rete convergently. Unfortunately, presence of a carotid rete cannot be determined using endocasts for most artiodactyls, and the presence of a carotid rete is mostly correlated with the absence of major correlates for the internal carotid artery (O’Brien and Bourke 2015). Bony correlates therefore mostly imply the petrosal morphology or the region close to the petrosal and are best seen on bony material than on endocasts.

The intracranial retia of modern cetaceans greatly differ from that of other artiodactyl groups by their size and position: i) the rostral arterial rete is more extensive (e.g., McFarland 1979; Vogl and Fisher 1981), ii) there is a caudal endocranial arterial and venous rete mirabile (in mysticetes only; Breathnach 1955; Pilleri 1991; Melnikov 1997), and iii) there are various retia in the basicranium and thus a high vascularization of the pneumatic sinuses around the petrosal and the ectotympanic bulla (Fraser and Purves 1960). The presence of these retia widely masks the external morphology of the brain, and therefore greatly impacts the shape of the endocasts of modern cetaceans and in basilosaurids (i.e., Pelagiceti; see section 3.1.3). The presence and extension of retia is variable in non-basilosaurid archaeocetes: the protocetid *Indocetus* sp. presents a venous rete, dorsal to the cerebellum, and a caudal rete, medial and dorsomedial to the petrosal (Bajpai et al. 1996:fig.1A), whereas in the remingtonocetids *Dalanistes ahmedi* (Gingerich et al. 1995) and *Remingtonocetus harudiensis* (Bajpai et al. 2011), a rete also probably fills the region dorsomedial to the petrosals, but there is little evidence of the presence of caudal or rostral rete. The raoellid *Indohyus indirae* has no extensive rostral or lateral retia mirabilia, but an intraosseous space dorsal to the cerebellum might have housed a network of diploic veins and arteries (Orliac and Thewissen 2021:fig.3-4) that might represent the first steps of an incipient caudal venous rete mirabile.

## 4. Brain evolution and paleobiological inferences based on endocast morphology

Artiodactyls follow the same broad lines of evolution of the brain as other gyrencephalic mammals, with general increase of the relative size of the brain, and of the size and complexity of the neopallium, from the early Eocene to modern times. Yet, despite a decent number of endocasts description in the literature, the picture of brain evolution at the Artiodactyla scale remains limited and major gaps remain to be filled regarding the earliest history of modern groups such as Suoidea, Hippotamoidea and Cetacea. Besides, quantitative data remain very scanty and the trends described in the following paragraphs are built on a very limited sample and only provide a very first step to understand brain evolution at the Artiodactyla scale.

### 4.1. Morphological brain diversity: General picture of brain evolution in Artiodactyla

#### 4.1.1 Olfactory bulbs

Still very few data are available regarding the relative size of the olfactory bulbs in Artiodactyla, or in mammal in general. The data collected for terrestrial artiodactyls (Tab. 1) based on 3D models suggest a general trend toward a reduction of relative olfactory bulb size through time at the Artiodactyla scale (Fig. 6A). Morphologically speaking, the earliest artiodactyls show bulbous olfactory chambers, joined on most of their length (Figs. 4, 7). The shape of the olfactory chamber is quadrangular in modern taxa and they are separated on most of their length in most extant representatives of modern groups (Figs. 5, 7). In the latter, the olfactory chambers appear anteroposteriorly compressed and a large portion of their surface corresponds to the cribriform plate and bears imprints of the foramina for olfactory nerves.

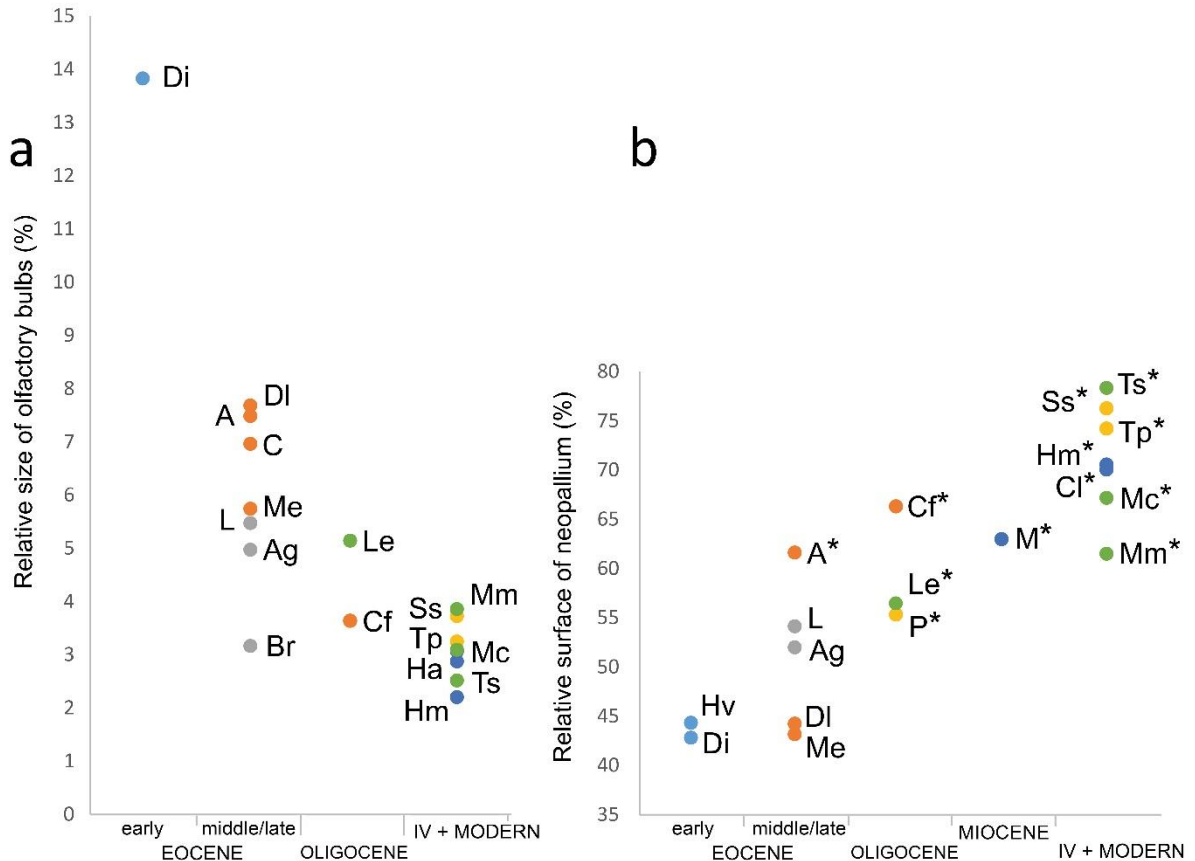
Cetacea show progressive lengthening of the olfactory tract and concurrent reduction of the relative size of the olfactory bulb chamber. Indeed, the nose of cetaceans underwent great modifications as a result of their adaptation to obligate aquatic lifestyle. The raoellid *Indohyus* shows an elongated olfactory tract, with narrow olfactory bulbs and peduncles (Orliac and Thewissen 2021). An elongation of the olfactory tract has also been described in archaeocetes,



Pakicetidae (Kishida et al. 2015), Remingtonocetidae (Bajpai et al. 2011), and Basilosauridae (Edinger 1955). This narrowing and lengthening of the olfactory tract might be directly related to modifications of the intertemporal region in early cetaceans and relatives and has been proposed as a synapomorphy of the clade (Orliac and Thewissen 2021:fig. 5). These authors also suggests that the modification of the postorbital morphology and the concurrent elongation of the olfactory tract would primarily originate from modifications of the masticatory apparatus, related to specialized diet. Neoceti exhibit a reduction of the major olfactory structures (ethmoturbinates, cribriform plate and maxilloturbinates) including olfactory bulbs, with further reductions and subsequent losses within Odontoceti (Berta et al. 2014).

#### 4.1.2 Neopallium size and complexity

The representation of a global picture of artiodactyl brain evolution in a rough phylogenetic and temporal context shows that the size of the neopallium relative to other components of the brain shows an increase with time in Artiodactyla in general and within all artiodactyl clades (Tab. 1; Fig.7). The expansion of the neopallium surface can notably be appreciated through i) its posterior extend, ii) its lateral extent and the location of the rhinal fissure on the lateral aspect of the endocast, iii) the operculization of the central area and the invagination of the external part with increasing neopallial surface.



**Figure 6** – Proportions of olfactory bulbs volume (A) and neopallium area (B) through time, generated on the basis of the data in table 1. Colors: light blue, *Diacodexis*; orange, European Endemic artiodactyls; grey, Oreodontoidea; green, Ruminantia; dark blue, Hippopotamidae; yellow, Suoidea. Asterisks (\*) indicate operculized taxa. Time periods abbreviations: EE, early Eocene; M/LE middle /late Eocene; O, Oligocene; MI, Miocene; IV + M, quaternary plus modern; Taxa abbreviations: A, *Anoplotherium* sp.; Ag, *Agriochœrus* sp.; Br, *Bathygenys reevesi*; C, *Cebochoerus* sp.; Cf, *Caenomeryx filholi*; Cl, *Choeropsis liberiensis*; Di, *Diacodexis ilicis*; Dl, *Dichobune leporina*; Ha, *Hippopotamus amphibius*; Hm, *Hippopotamus madagascariensis*; Hv, *Homacodon vagans*; L, *Leptauchenia* sp.; Le, *Leptomeryx* sp.; Me, *Mouillacitherium elegans*; Mc, *Moschus chrysogaster*; M, *Microbunodon minimum*; Mm, *Moschiola memmina*; P, *Palaeochoerus* sp.; Ss, *Sus scrofa*; Tp, *Tayassu pecari*; Ts, *Tragelaphus scriptus*.

Earliest artiodactyls from the early Eocene show the smallest neopallium surface relative to the surface of the cerebral hemisphere (Tab. 1, Fig. 6B), and a concurrent wide midbrain exposure (Fig. 7). *Indohyus indirae* from the middle Eocene also shows a widely exposed midbrain and concurrent small neocortex expansion (Orliac and Thewissen 2021), and some middle Eocene European endemic taxa also show small midbrain exposure (Figs. 6B, 7). All artiodactyls from the Oligocene and on, have extended neopallium and no midbrain exposure. The area of the neopallium relative to the total surface of the cerebral hemisphere shows a trend to increase with time (Tab. 1, Fig. 6B), with the lowest values retrieved in Early Eocene and middle/Late Eocene taxa, and highest values observed for modern taxa. Yet, relatively high values are also found in endemic European Paleogene taxa (Fig. 6B) such as the large bodied *Anoplotherium* (Anoplotheriidae; body mass estimate = 150 kg, Hooker 2007) and the small *Caenomeryx* (Cainotheriidae, body mass estimate = 1.5 kg) highlighting that the picture will get more complicated as the data available increase and that independent tempos are to be expected in the various artiodactyl clades. Besides, as soon as operculization occurs, the external surface of the neopallium is necessarily an underestimation of the total neopalleal surface, which tempers the relevance of direct comparisons of values.

Earliest artiodactyls exhibit a very simple sulcal pattern of the neopallium with only two sulci, the suprasylvia and the lateral sulcus, converging in their anterior-most part and delimiting an almond-shape gyrus III + presylvia. This simplest pattern, found in early Eocene diacodexoids, homacodontids, and helohyids, is also observed in some middle/late Eocene endemic European taxa (“Dichobunoidea” with *Mouillacitherium* Fig. 4G, Amphimerycidae with *Pseudamphimeryx*, *Amphimeryx*, Dechaseaux 1969a:fig.17). A slightly more complicated pattern with the addition of a coronal sulcus occurs in middle/late Eocene taxa such as early oreodontoids, some endemic European taxa (*Tapirulus*, Orliac and Gilissen 2012; *Cebochoerus*, Dechaseaux 1969:fig.13), and the raoellid *Indohyus*. Small additional sulci such as ectolaterals (*Dichobune* Fig. 4J), diagonal sulcus and/or oblique sulcus (*Leptauchenia* Fig. 4J; *Dacrytherium* Dechaseaux 1969a:fig.2) also occur in middle/late Eocene taxa. Anoplotheriidae, which include the largest of endemic European taxa, *Anoplotherium*, present, as soon as the late Eocene, a rather complex and extended neopallium with: i) a longitudinal organization of the coronolateral sulcus and suprasylvia and additional sulci, ii) the presence of a sylvian complex, hallmark of an operculization. A growing cortical complexity and diversity is observed in the different artiodactyl clades in the Oligocene, with branched patterns resulting from ramification of the main sulci and from the extension of the anterior part of the suprasylvia (suoids, oreodontids, ruminants, camelids), of the ansate sulcus (suoids, oreodontids, camelids), and of the oblique sulcus (cainotheriids, suoids, oreodontids, ruminants, camelids). Dorsal exposure of the cruciate and splenial sulci is variously present in ruminants, suids and hippopotamoids. Camelids, on the contrary, experience gradual introversion of posterior longitudinal sulci into the sagittal plane, and simultaneous eversion of sulci from the frontal region (Repérant 1971a). The presence of a small neopallium and very simple neopalleal pattern in raoellids, sister taxon to Cetacea and therefore lying very high in the Artiodactyla tree, implies that a simple pattern was most probably present at the base of all modern groups and that neopallium complexity arose independently in the different crown clades of artiodactyls. This is consistent with the differences in neopalleal patterns observed today. The overview of neopalleal pattern in Artiodactyla through time highlights their diversity and the relevance of a neocortical pattern blueprint for phylogenetic and taxonomic purpose. The same is true for neopalleal extension and concurrent operculization of part of the central territory. Based on the available sample, operculization seems to be present in all artiodactyl taxa from the Oligocene onward. But the extension of the neopallium in the various artiodactyl clades did not imply the same areas, and operculization occurred independently in all crown clades and in major extinct

clades. This is highlighted by the variety of operculization patterns observed, with the Sylvian complex following the rhinal margin plan only (Cainotheriidae), forming an open triangle on the rhinal (Anoplotheriidae), not connecting the rhinal (Hippopotaminae), or with the anterior ectosylvia pointing anteriorly (e.g., ruminants), or posteriorly (e.g., suines).

## 4.2 Brain-size evolution and Encephalization Quotient

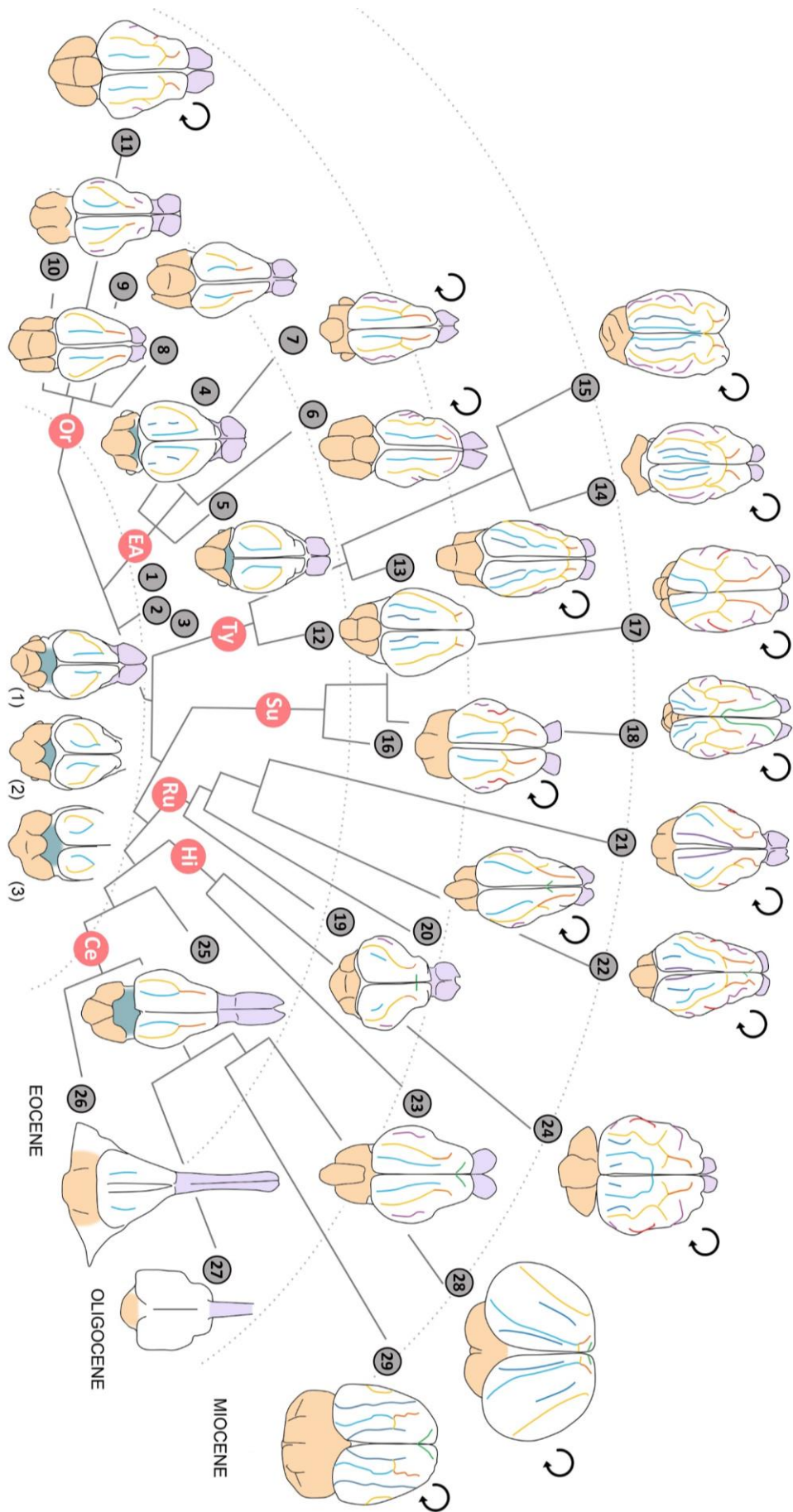
Encephalization corresponds to the increase in brain size beyond that expected from the allometric brain-body relation (see Jerison 1970, 1973 and 1982 for historical reviews). It is often determined by calculating the residual value for a given species relative to the allometric regression line (Jerison 1985). Specifically, the encephalization quotient (EQ, Jerison 1970) has been defined as the ratio of the observed brain mass over the expected brain mass for a given body mass. The EQ is therefore rather straightforward to interpret; if a species/specimen has a greater brain mass than expected, the ratio is above 1, and if not, the ratio is under 1.

Before going further, a point must be raised. In a large brain a high quotient of encephalization might correspond to the addition of many grams of brain tissue (and a correspondingly large number of brain cells), whereas in a small brain the same quotient of encephalization would correspond to the addition of a comparatively small amount of brain tissue. When comparing species, brain size is often considered as proportional to neural information processing capacity, and the evolution of encephalization as the evolution of an increase in information processing capacity. It would therefore appear that large brains require more tissue than small brains to achieve the same increase in information processing capability. This paradox, raised by H.B. Barlow in Jerison (1985) has not yet been answered satisfactorily and must be kept in mind when interpreting trends in brain size evolution.

The main challenge in calculating the EQ is to estimate the expected brain mass, which is commonly calculated by an allometric formula with defined parameters. The general allometry formula  $Y = aX^b$  can be used to calculate an expected brain mass (Y) for a given body mass (X). As a power function, this relationship can be illustrated by plotting the logarithm of the measurement against the logarithm of the size, thus transforming the previous equation into a linear relationship:  $\log(Y) = b \log(X) + \log(a)$ .

Authors have used various values for the parameters a and b, and at various scales: some at the class level (e.g., Mammalia, Jerison 1970; Eisenberg and Wilson 1978), others at the order scale (e.g., rodents, Pilleri et al. 1984; primates, Martin 1990). The parameters used are assumed to represent the group of interest (i.e., that they do not vary much within this group); the relevance of parameters a and b therefore depends of the group of interest, and may not be relevant/suitable to another group or scale.

More precise and complex methods often deal with phylogenetic comparative methods (PCM; Cornwell and Nakagawa 2017) but these require a well-supported phylogenetic context. The phylogenetic relationships within Artiodactyla are still debated and if the relationships between crown groups are rather consensual on molecular grounds (Hassanin et al 2012), the position of extinct taxa are still highly disputed (e.g., Geisler and Theodor 2009). This lack of a clear/robust phylogenetic framework deprives us of the use of phylogenetic comparative methods on residuals at the artiodactylan scale. We therefore use here the EQ to provide (limited) state-of-the-art of the data.



**Figure 7** – Morphology, phylogenetic relationships and temporal distribution of artiodactyl endocasts and brains. Endocasts and brains are figured in dorsal view, anterior tip (olfactory bulbs) pointing upwards. Taxa: 1, *Diacodexis ilicis* (AMNH 16141), 2, *Homacodon vagans* (AMNH 12695); 3, ?*Helohyus* (AMNH 13079), 4, *Dichobune leporina* (MNHN QU16586), 5, *Mouillacitherium elegans* (UM ACQ 6625); 6, *Anoplotherium* sp. (3D surface of plaster cast illustrated by Dechaseaux 1969:fig.6); 7, *Caenomeryx filholi* (UM PDS 2570); 8, *Bathygenys* sp. (after Macrini 2009:fig.1); 9, *Agriochoerus* sp. (AMNH 95330); 10, *Leptauchenia* sp. (AMNH 45508); 11, *Merycoidodon culbertsoni* (after Black, 1920:fig. 18); 12, *Protylopus* (after Edinger 1967:fig.1 and Repérant 1971a:fig.1); 13, *Poebrotherium* (after Repérant 1971a:fig.1); 14, *Procamelus* (after Edinger 1967:fig.3 and Repérant 1971a:fig.1); 15, *Lama glama* (after Repérant 1971b:pl.VIID); 16, *Palaeochoerus* sp. (MHNT\_2014\_0\_3075); 17, *Tajassu pecari* (UM V79); 18, *Sus scrofa* (after Anthony and Grzybowski 1931); 19, *Leptomeryx* sp. (AMNH 53596); 20, *Dremotherium feignouxii* (after Sigogneau 1968); 21, *Moschiola memmina* (UM V68); 22, *Moschus chrysogaster* (UM N401); 23, *Microbunodon minimum* (UP LM1967MA300); 24, *Choeropsis liberiensis* (after Pilleri 1962:fig.1); 25, *Indohyus indirae* (NM RR 207); 26, *Remingtonocetus harudiensis* (after Bajpail et al. 2011:fig.6); 27, *Xenorophus* sp. (after Marino et al. 2003:fig.6C); 28, *Tursiops truncatus* (after Morgan et al. 1990:fig.2); 29, *Balaena mysticetus* (after Duffield et al. 1992:fig.7B, and Ragnanti et al. 2019:fig.1C). Color code: light orange, cerebellum; turquoise, midbrain exposure; violet, olfactory bulbs and peduncles; neopalleal sulci: blue, lateral; orange, coronal; yellow, suprasylvia (+ anterior suprasylvia and ansate for some taxa); green, cruciate; purple, splenial; pink, oblique and diagonal. Turning arrows indicate operculization. Abbreviations: Ce, Cetacea; EA, endemic artiodactyls; Hi, Hippopotamoidea; Or, Oreodontoidea; Ru, Ruminantia; Su, Suoidea; Ty, Tylopoda. Phylogenetic relationships are based on Hassanin et al. (2012) for crown groups branching, fossil taxa relationships rely on Thewissen et al. (2007) for Cetacea, Geisler et al. (2007) for Tylopoda, Métais and Vislobokava (2007) for Ruminantia, Orliac (2012) for Suoidea, Oreodontoidea and endemic European taxa are here considered as monophyletic groups, relationships within endemic European taxa rely on Weppe et al. (2020a). Not to scale.

#### 4.2.1 Brain size in Artiodactyla

To accurately describe the evolution of brain size through time within Artiodactyla, we define and use an empirical EQ formula based on a sample of 113 extant artiodactyl species. Fig. 8A shows a plot of log (brain mass) against log (body mass) with the regression line based on extant species only. The equation for the regression is  $0.6008x - 1.1278$ . The expected brain mass equation is thus  $0.3237(\text{body mass})^{0.6008}$  and the corresponding EQ formula for Artiodactyla (EQartio) is as follows:  $\text{observed brain mass} / 0.3237(\text{body mass})^{0.6008}$ . The previous scaling exponents of Jerison (1970) and of Eisenberg and Wilson (1978) for Mammalia are, respectively, 0.667 and 0.74, which are slightly higher than the scaling exponent of 0.6008 proposed here for artiodactyls. With a lower slope value, a negative allometry between brain and body mass in artiodactyls is thus clear in our study compared to previous works at the Mammalia scale. A striking fact about artiodactylans relative brain size (Fig. 8A) is the duality between Cetacea and non-cetacean artiodactyls. Indeed, convex hulls for both groups of extant species do not overlap, and both extant and fossil cetaceans are generally above the regression line of Artiodactyla, while non-cetaceans are below this line. We therefore calculated two separate EQ formulas, one for non-cetacean artiodactyls with  $\text{EQ}_{\text{noncet}} = \text{observed brain mass} / 0.3405(\text{body mass})^{0.5603}$ , and one for cetacean artiodactyls with  $\text{EQ}_{\text{cet}} = \text{observed brain mass} / 16.0007(\text{body mass})^{0.3490}$ . Linear models of log(brain mass) relative to log(body mass) for extant species of non-Cetacea and Cetacea reveal a correlation between log(brain mass) and log(body mass) ( $p < 2.2 \times 10^{-16}$ ) and a difference between both groups ( $p < 2.2 \times 10^{-16}$  in both tests). Additionally, there is a difference between the slopes of each group over time ( $p = 6.053 \times 10^{-7}$  in a t-test of slope comparisons), highlighting a difference in allometry equations between each group (Fig. 8A). In a comparable analysis (but using phylogenetic generalized least squares - GLS - regressions), Smaers et al. (2021) also found a lower encephalization slope for cetaceans and a higher encephalization intercept for cetaceans (both odontocetes and delphinids compared to ferungulates). Brain/body mass allometry is more negative in Cetacea (scaling exponent of 0.3490) than in other artiodactyls (scaling exponent



of 0.5603, closer to that of the whole order, 0.6008). This does not imply a lower encephalization (their EQ is greater than other artiodactyls, as is their EQ variation; Fig. 8B), but may rather results from a massive increase in body mass for this clade (see Montgomery et al. 2013; Fig. 8A) and/or may simply reflect the greater homogeneity of Cetacea when compared to other artiodactyls.

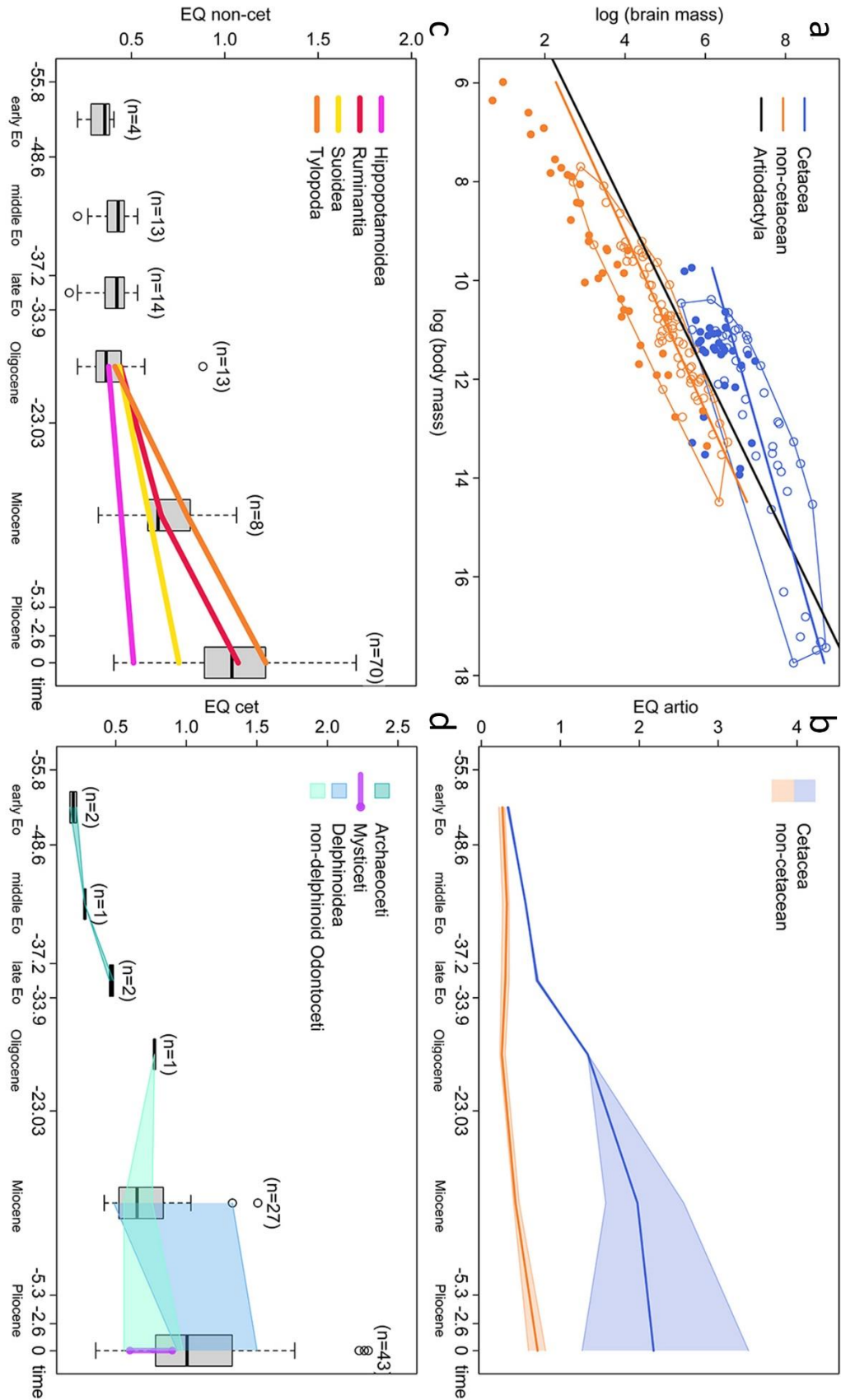
Encephalization differences between cetaceans and non-cetacean artiodactyls is even clearer in a temporal framework (Fig. 8B). In both groups, there is a significant linear increase in EQ through time until the present ( $p=9.401 \times 10^{-4}$  and  $R^2=0.13$  in cetaceans,  $p<2.2 \times 10^{-16}$  and  $R^2=0.58$  in non-cetacean artiodactyls). Cetaceans EQ appears to increase particularly between late Eocene and Oligocene, while the EQ increase in non-cetacean artiodactyls seems to only start in the Oligocene. Moreover, residuals of both regressions are not homoscedastic ( $p=0.00305$  in cetaceans and  $p=0.01022$  in non-cetacean artiodactyls for Breusch-Pagan tests) and their variance increases through time ( $p=2.669 \times 10^{-3}$  in cetaceans and  $p=9.956 \times 10^{-3}$  in non-cetacean artiodactyls for linear models). This highlights two differing and diachronic patterns of EQ increase for cetacean and non-cetacean artiodactyls during the Cenozoic.

#### 4.2.2 Brain size in non-cetacean artiodactyls

Figure 8C illustrates the evolution of EQ in non-cetacean artiodactyls over time, based on the non-cetacean artiodactyl equation. There is a significant difference between EQ values of Paleogene (Eocene-Oligocene), and Neogene (Miocene-Pliocene) and Quaternary non-cetacean artiodactyls ( $p<2.2 \times 10^{-16}$  in a t-test). There are no significant differences between Paleogene modalities in EQ ( $p=0.7104$  in an ANOVA,  $p=0.4122$  in a Kruskal-Wallis test,  $p=0.4212$  in a linear model), translating a stasis in EQ values during Paleogene times, while there is an increase in EQ values from the Oligocene onward supported by differences between each time section ( $p=1.546 \times 10^{-12}$  in an ANOVA,  $p=1.384 \times 10^{-8}$  in a Kruskal-Wallis test,  $1.538 \times 10^{-13}$  in a linear model). There also seems to be an increase in EQ variation during the Neogene and Quaternary, but this is not confirmed by linear models based on squared residuals of each linear model against time ( $p=0.1775$  in ANOVA and  $p=0.5652$  in Kruskal-Wallis test for Paleogene,  $p=0.1258$  and  $p=0.0461$  since Oligocene). The Oligocene Epoch corresponds to the massive appearance of artiodactyl crown groups in the fossil record (except for Cetacea) that progressively replaced stem artiodactyl lineages. Considering EQ variation over time within crown groups, Ruminantia is the only crown group that indubitably shows an increase in EQ ( $p=2.4 \times 10^{-4}$  in an ANOVA,  $p=0.0053$  in a Kruskal-Wallis test,  $p=4 \times 10^{-5}$  in a linear model). EQ increase for Suoidea and Tylopoda, as illustrated in Fig. 8C by the median line, is statistically not as well supported as in Ruminantia. Tylopoda shows significant increase according to ANOVA and linear models ( $p=0.0032$  and  $p=2.7 \times 10^{-4}$ ), while Suoidea do not ( $p=0.0918$ ). By contrast, Kruskal-Wallis test results are in conflict: Suoidea are significant ( $p=0.0455$ ), and Tylopoda are not ( $p=0.0687$ ). Hippopotamoidea EQ seems to remain constant over time ( $p=0.1896$  in ANOVA and linear model,  $p=0.1213$  in a Kruskal-Wallis test). However, EQ increase over time in non-cetacean artiodactyl crown groups (Fig 8C) is based on unbalanced fossil records and has to be interpreted with caution. Further documentation of extinct taxa may change the picture.

#### 4.2.3. Brain size in Cetacea

Studies relative to brain size evolution in cetaceans describe two major encephalization pulses related to two major events: the onset of odontocetes near the Eocene-Oligocene boundary, and within odontocetes, the differentiation of Delphinoidea (15 Ma; e.g., Marino et al. 2004). Regarding the trends accompanying the early steps of their evolutionary history, which comprises the transition to a fully aquatic environment, Marino et al. (2004) concluded that there was no significant increase in brain size during archaeocete evolution, ruling out the



**Figure 8** – Encephalization within Artiodactyla. A, log brain mass vs log body mass plot in Artiodactyla; empty circles indicate extant taxa, full circles indicate fossil taxa; lines indicate regression lines of extant groups; convex hulls group extant taxa. B, evolution of encephalization through time in Artiodactyla using the EQ artio; bold central line is the median, thin lateral lines are the quartiles. C, evolution of encephalization through time in non-cetacean artiodactyls using the corresponding EQ formula; colored lines are the median in each non-cetacean

crown group; values above the boxes indicate the total number of taxa for the corresponding time section. D, evolution of encephalization through time in cetacean artiodactyls using the corresponding EQ formula; interquartile range is represented by a semi-transparent range in non-mysticete cetaceans and by a segment in mysticetes (due to the absence of fossil values in this group); values above the boxes indicate the total number of taxa for the corresponding time section. Brain and body data for extant non-cetaceans artiodactyls are from Perez-Barberia et al. (2007), Shultz and Dunbar (2010), and Weston and Lister (2009), for fossil non-cetaceans artiodactyls from Jerison (1973), Orliac and Gilissen (2012), Lyras (2018), Thiery and Ducrocq (2015), Radinsky (1978), Berthet (2003), Macrini (2009), Janis (1982), Shultz (2009), and Köhler and Moyà-Solà (2004); data for cetaceans mainly come from Marino et al. (2004), and Gingerich (2015). Detailed information about EQ dataset are provided in Supplementary Information.

hypothesis of a correlation between relative brain size increase and aquatic habitats. These conclusions were challenged by Gingerich (2015), based on revised and more robust body mass estimates for archaeocetes but with a smaller sample, who concluded that the relative size of the brain in archaeocetes had doubled between the middle and late Eocene.

Figure 8D illustrates EQ variation over time for Archaeoceti, Mysticeti, non-delphinoid Odontoceti, and Delphinoidea, using the EQcet equation. It shows the general EQ increase during the Cenozoic for Cetacea ( $p=3.604 \times 10^{-4}$  in an ANOVA,  $p=3.489 \times 10^{-6}$  and  $R^2=0.24$  in a linear model) and crown cetaceans (Neoceti;  $p=1.503 \times 10^{-3}$  in an ANOVA,  $p=4.983 \times 10^{-4}$  and  $R^2=0.15$  in a linear model). In the literature, scaling patterns for these groups are based on other (less specific) formulas or other statistical treatment (e.g., Marino et al. 2004; Montgomery et al. 2013; Gingerich 2015; Serio et al. 2019; McCurry et al. 2021; Smaers et al. 2021). Some results are nonetheless congruent in an increase of cetacean relative brain size (see Serio et al. 2019 and McCurry et al. 2021). It also shows an EQ increase over time in Archaeoceti ( $p=0.01939$  in an ANOVA,  $p=7.693 \times 10^{-3}$  and  $R^2=0.91$  in a linear model), as supported by Gingerich (2015), but contra Marino et al. (2004), and indicates a very early pulse of encephalization during cetacean evolutionary history. Regression parameters of archaeocetes and neocetes are not significantly different (t-test;  $p=0.2603$  for slope,  $p=0.6329$  for intercept), indicating no special pulse at the onset of Neoceti. Similarly, the encephalization pulse corresponding to the differentiation of odontocetes near the Eocene-Oligocene boundary is not supported here because the t-tests of the archaeocetes vs. odontocete and neocetes vs. odontocete regression parameters as a whole are not significant ( $p=0.1190$  and  $p=0.3859$ , and  $p=0.7173$  and  $p=0.5672$  for slope and intercept of each comparison). An EQ increase over time is nevertheless observed in odontocetes as a whole ( $p=4.127 \times 10^{-4}$  in an ANOVA,  $p=1.417 \times 10^{-4}$  and  $R^2=0.19$  in a linear model).

The differentiation of Delphinoidea (at ca. 15 Ma) is assumed to coincide with an encephalization pulse at the onset of this superfamily (Marino et al. 2004). In our analyses, Delphinoids and non-delphinoid odontocetes are normally distributed groups regarding their EQ ( $p=0.1561$  and  $p=0.075$  in Shapiro-Wilk tests respectively), which has not increased over time ( $p=0.05785$  and  $p=0.3098$  in linear models respectively). The EQ however differ in their means ( $p=1.334 \times 10^{-6}$  in a bilateral t-test, mean EQs are 1.23 and 0.71 respectively) and variance ( $p=9.775 \times 10^{-5}$  in a bilateral F-test, EQ variances are 0.23 and 0.05 respectively). Even though EQ did not increase over time in each odontocete subgroup, delphinoids have a general higher EQ together with a larger EQ range (as seen in Figure 8D). The hypothesis of the initial encephalization pulse at the onset of delphinoids is thus supported, and the increase of EQ over time described at the Odontoceti scale (since Oligocene) might reflect that EQ pulse (since the Miocene). The more thorough analyses of Serio et al. (2019) found the high relative brain mass of odontocetes to be plesiomorphic, meeting partially our results: they found a high relative brain mass at the onset of odontocetes (as found here), but without increase since (as also found by McCurry et al. 2021). Smaers et al. (2021), using phylogenetic GLS regressions, also found that encephalization increases in mean at the onsets of odontocetes (both body and brain size decreasing, the former faster than the latter), but tightens in variance (variance of brain size

diminishing faster than do that of body size). They also found, concurrently to our results, another encephalization increase at the onset of delphinids, both in mean (with decreasing body size and increasing brain size) and in variance (variance of brain size increasing faster than do that of body size). Finally, within Neoceti, EQ values of extant mysticetes do not differ from those of Oligocene odontocetes ( $p=0.8594$  in a t-test and  $p=0.8438$  in a Mann-Whitney test). Of the two clades, the odontocetes are particularly diverse and more frequently documented in the fossil record than mysticetes. Assuming that Oligocene odontocetes are the closest estimates for ancestral EQ values in Neoceti would imply that EQ did not change during mysticete evolution. As a corollary, non-delphinoid odontocetes and extant mysticetes do not differ in EQ. Based on an EQ formula built solely on cetacean artiodactyls, there would only be two EQ increases/pulses in Cetacean history: a first one during archaeocete evolutionary history (in agreement with Gingerich 2015) and a second one at the onset of delphinoids (in agreement with Marino et al. 2004).

## 5. Future directions: outstanding questions and perspectives

A long tradition of paleoneurological studies in artiodactyls, based both on rich fossil documentation and solid neontological foundations, provides a substantial body of data to discuss the evolutionary history of brain structures in artiodactyls.  $\mu$ CT-scan imagery techniques now allow for a detailed investigation of all endocranial structures as well as for quantitative studies of the evolution of the brain components. Yet, the number of these studies remains small and entire sections of Artiodactyla brain history remain undocumented, particularly concerning modern crown groups, especially Hippopotamoidea and Suoidea. Increasing the documentation of extinct and present-day species endocasts, both for qualitative and quantitative perspectives, is now crucial to complete the picture of artiodactyl brain evolutionary history and fully exploit this promising source of data for phylogenetic and palaeoecological reconstructions.

The nomenclature used to describe the artiodactyl neopallium is largely based on the resemblance between the sulcal pattern of present-day artiodactyls and that of the dog, but it is clear that the first artiodactyls have a very different pattern and that the recognition of the different cortical areas is only partially applicable. This is all the more difficult for large clades without extant representatives because i) following the placement of the sulci during ontogeny is impossible or highly improbable (mainly used to formulate homologies between crown groups), and ii) some patterns have no equivalent in modern artiodactyls, which themselves most probably have convergent complex patterns. Increasing the documentation of endocasts morphology of extinct representatives of crown artiodactyl clades is necessary to refine homology hypotheses. Finally, the study of the brain of artiodactyls has so far been largely synonymous with the study of their neopallium, but the cerebellum also shows great variation in form and structure and its study will allow for comparing cerebrum and cerebellum evolutionary trajectories.

Regarding quantitative prospects, quantitative works focused on the size of the brain as a whole, notably through EQ calculation, to discuss cognitive abilities (Jerison 1973), or habitat predation intensity (Jerison 1973), or to question the impact of socialization (Schultz and Dunbar 2010; Pérez-Barbería et al. 2007), domestication (e.g., Ballarin et al. 2016; Minervini et al. 2016), or differential locomotor faculties (Pilleri et al. 1984) on brain size would be needed. Consideration of other quantitative data such as olfactory bulb size, cerebellum size, or neopallial surface will allow for addressing questions relating to species abilities that could be put into perspective with their ecology. Again, the constitution of a large database on modern taxa endocranial casts is necessary to be able to exploit further the data collected on fossils.

## 6. Concluding remarks

We provide here a very first glance into artiodactyl brain evolutionary history, including Cetacea. The diversity highlighted in this first overview of the external morphology of the brain at the scale of Artiodactyla underlines the potentiality of a “neopalleal blueprint” and its relevance at the systematic and phylogenetic level. The inclusion of endocast characters to taxon-character matrices will certainly bring a promising new phylogenetic signal. Yet, our understanding of the setting up of neopallium folding in the different artiodactyl groups is still very partial and at this point, the poor resolution of the phylogenetic relationships at the base of the artiodactyl tree, and small number of endocast of extinct representatives of moderns clades limit our understanding of brain evolution at the order scale. A better resolution of the phylogenetic relationships of Artiodactyla and a substantial increase of quantitative and qualitative data for extinct members of crown clades are now needed in order to take advantage of the increasing quality of data extracted from endocasts and to further exploit endocasts for paleobiological inferences.

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