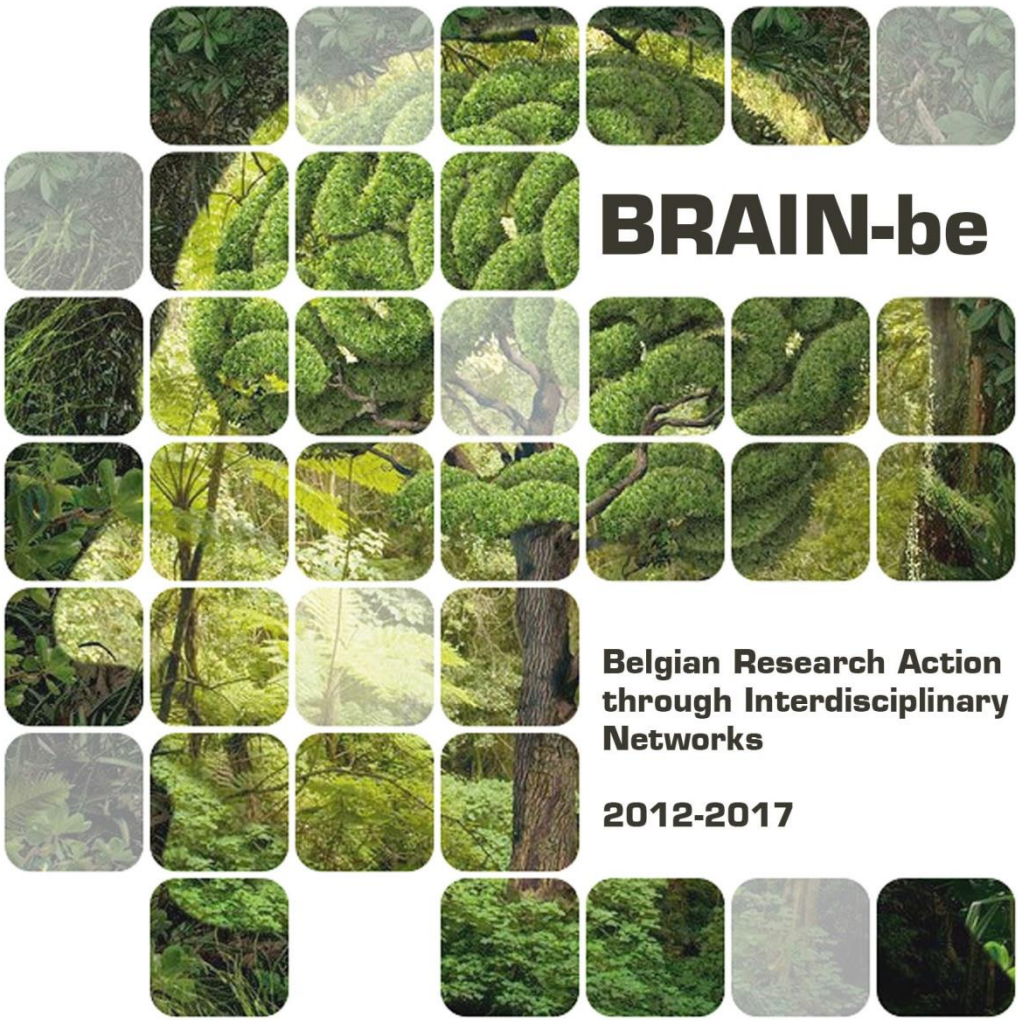

PalEurAfrica

Origin of the European modern faunas through Palaeogene Central Africa collections

BR/121/A3/PalEurAfrica

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Axis 3: Cultural, historical and scientific heritage

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NETWORK PROJECT

PALEURAFRICA

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Contract - BR/121/A3/PalEurAfrica

FINAL REPORT

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ABSTRACT

Recent advances in the study of vertebrate evolution suggest that the earliest modern mammals such as primates, perissodactyls (odd-toed ungulates) and artiodactyls (even-toed ungulates), which appeared suddenly with other vertebrate groups in all three Northern hemisphere continents at the Paleocene-Eocene Thermal Maximum, 56 myr ago, likely originated during the late Paleocene in tropical habitats farther south. Interestingly, there is a unique collection of Paleocene vertebrates from Central Africa in the federal heritage resulting from Belgian expeditions by Edmond Dartevelle in the Democratic Republic of Congo and Angola. The aim of this project was to identify the Paleogene vertebrate faunas of Central Africa and to look for ancestors of modern vertebrates from Europe and elsewhere. This required the study of historic archives and digitization/cataloguing of specimens, the relocation and excavations of fossil sites in Central Africa, India and Europe and analysis of vertebrate specimens, with a focus on their relevance for reconstructing climate and faunal evolution in the Paleogene. The six partners and collaborators of the PalEurAfrica research project have created a network of 146 researchers during the six years of the project. Sixty seven full articles and 72 abstracts have been published or presented at congresses, all related to Paleogene vertebrate faunas and their environments. Numerous new species, genera and even families have been made new to science. An important discovery is that some faunal exchanges between Europe and Africa involved the Indian subcontinent as it drifted towards Asia.

Keywords

Paleogene, Vertebrates, Africa, India, Europe

1. INTRODUCTION

Knowledge about the evolution of the earliest modern vertebrates has made giant leaps during the last two decades thanks to important studies and discoveries by researchers in North America, Europe, North Africa and Asia. In this context, Belgian scientists have contributed to the study of modern vertebrates from western Europe, analyzing the historical Paleogene key collections of the Royal Belgian Institute of Natural Sciences in two previous projects (Belspo MO/36/011 and 020). Collaboration of Belgian scientists with leading experts from eight different countries has resulted in joint projects in North America, China (Belspo BL/36/C54) and most recently Vastan in India (five fieldwork grants from the National Geographic Society). These Belgian initiatives led to the publication of more than 50 scientific A1 papers in the last 10 years concerning, what the great paleontologist George Gaylord Simpson termed “The Beginning of the Age of Mammals” (Figure 1).

Recent advances in the study of vertebrate evolution suggest that the earliest modern mammals such as primates, perissodactyls (odd-toed ungulates) and artiodactyls (even-toed ungulates), which appeared suddenly in all three Northern hemisphere continents at the Paleocene-Eocene Thermal Maximum (PETM, 56 myr ago), likely originated during the late Paleocene in tropical habitats farther south.

The PETM is a first and most prominent of a series of Cenozoic hyperthermals, short-lived events of extreme global warming, and is considered among the most important analogues for current global warming. Using isotopic data, PETM studies have demonstrated its effect on past mammal dispersal, evolution and ecology and highlighted potential biotic effects of future climate change.

Numerous international expeditions have been conducted on northern continents and high quality collections exist from the PETM, among which is the Belgian Dormaal collection at the RBINS, recognized as the international reference level for Europe (Figure 2).

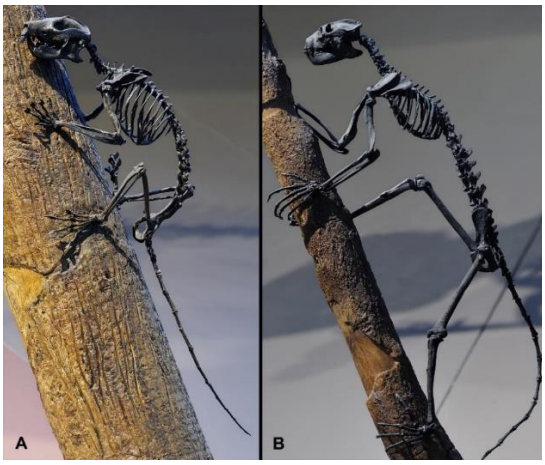

Figure 1. A. Primitive arboreal mammal (Plesiadapiforme) from the late Paleocene. B. Modern mammal (Primate) from the early Eocene (Photos: Eric De Bast, RBINS).

Figure 2. *Dormaalocyon*, one of the most primitive carnivoraforms, from the Belgian site of Dormaal during the PETM 56 myr ago (Credit: Charlène Letenneur, MNHN and Pascale Golinvaux, RBINS).

Nevertheless, only two fossil localities in the tropics have yielded vertebrates from around this time interval, the Cerrejon coal mine in Colombia and the Vastan lignite mine in India. Extraordinary discoveries have been made including early primates, bats, artiodactyls and other modern vertebrates. It has been suggested that Africa was an important source area for the origin of many modern mammal groups but its Paleogene record is poorly sampled, especially from sub-Saharan Africa.

Interestingly, a unique collection of Paleocene vertebrates from Central Africa resides in the federal heritage resulting from Belgian expeditions of the Royal Museum for Central Africa by Edmond Dartevelle in the Democratic Republic of Congo and Angola. The aim of this project is to study the Paleogene vertebrate faunas of Central Africa and to explore relationships across faunas from Europe, Africa and elsewhere.

The goal of our international and multidisciplinary team was to study and digitize the Belgian Paleogene collections from earlier expeditions in Belgium (RBINS) and in Congo and Angola (RMCA). The history of earlier African expeditions was traced, and the excavation sites were relocated through the use of archives. New excavations were conducted to complement existing collections, using modern screen-washing techniques to enable the team to find small vertebrates. A partnership was developed with international specialists in Central African fieldwork and faunas (a consortium including Duke University and Ohio University in the USA). Targeted sampling of these sites also enabled the team to date and characterize them in detail, based on microfossils (Ghent Univ.) and isotopic data (Namur Univ.).

Faunal turnovers and the influence of dispersals during the Paleogene, especially the early Paleogene, were analyzed by comparison with European faunas, North American faunas, and Chinese and Indian faunas in order to develop evidence of modern vertebrate groups that may have originated in Africa.

2. STATE OF THE ART AND OBJECTIVES

2.1. Scientific background and context at international level

The **early Paleogene** (65-45 Ma) is the time period during which **modern vertebrates begin to diversify** and the current mammal orders appear. The most obvious example for this is the Paleocene-Eocene Boundary (PEB, 55,84 Ma) when the iconic APP taxa appear: **A**rtiodactyls (even-toed ungulates), **P**erissodactyls (odd-toed ungulates) and **P**rimates (Gingerich, 2006). Not only are the APP taxa highly popular with and easily recognizable by the general public, these groups, appear simultaneously in Europe, North America and Asia, and do so exactly at the PEB. Other vertebrate groups, such as rodents, carnivorans or bufonids (toads) make their first appearance slightly earlier in the late Paleocene, or somewhat later during the early Eocene, as do chiropterans (bats) and cetaceans (whales) (Rage, 2003; Smith et al., 2012; Gingerich, 2012). By the end of the Eocene, the direct ancestors of virtually all modern vertebrates are present (Rose, 2006). The early Paleogene therefore really holds the key to understanding the current global vertebrate biodiversity patterns.

This period is also climatically very interesting, and the potential link between climate and evolution of vertebrates is a matter of debate. The Early Eocene Climatic Optimum (EECO, 53-51 Ma) represents one of the warmest sustained periods of the last 65 million years. Superimposed on a warm **greenhouse period,** a series of four **sudden and extreme global warming events (hyperthermals)** disturbed the biological and geological environments between about 55.5 and 52 million years ago. The first of these events, the Palaeocene–Eocene Thermal Maximum (PETM), represents an increase in global temperature of about 5°C within a few thousand years (DeConto et al., 2012). The PETM is characterized by a massive input of carbon, ocean acidification and has been explicitly accepted as the best deep time analogue for the current anthropogenic global change (Zachos et al., 2008).

The **changes in terrestrial and oceanic ecosystems** during the PEB coincide with the start of the PETM and were most probably directly or indirectly caused by it. Some of these climatic effects such as northward range extensions of existing taxa and opening of high latitude land bridges (Wing et al., 2005, Smith et al., 2006) seem **obvious and straightforward**. Others however, such as the transient dwarfing of up to 76% in some mammals are **much more surprising** (Gingerich, 2006) and require additional research to understand their causal mechanisms in the past and their implications for the future.

Similarly, even if the appearance of the modern APP taxa at the PEB throughout the Northern Hemisphere has been recognized since the end of the 19th century, the precise evolutionary and geographic origins of these and most other modern vertebrates remain a mystery. The synchronicity of the PETM warming with the appearances of modern forms may seem highly suggestive of dispersal across northern land bridges (Hooker & Dashzeveg, 2003; Smith et al., 2006). But alternative migrations across more southern routes and at earlier or later intervals have also been documented (Smith et al., 2007, 2010; Missiaen, 2011) necessitating additional studies of the **directionality, selectivity and duration of these migrations**.

For reasons of availability of sediments and convenience, historical research on the terrestrial early Paleogene has mostly focused on North America and Europe. The fossil record in **North America** is long known to be extraordinarily rich, still yielding exceptionally preserved specimens (e.g. Simmons et al., 2008) and temporal resolutions of sometimes only a few thousand years (e.g. Gingerich & Smith, 2006). The terrestrial fossil record in **Europe** for the Paleogene is much spottier, although Europe too has some exceptional sites, including most notably the Messel site (Koenigswald et al., 2005; Franzen et al., 2009). Recent studies therefore apply modern techniques to compare and correlate the rich historic collections such as those from the Paris Basin, Dormaal and Messel, and complement them with new targeted fieldwork. In the framework of Belspo MO/36/011 and 020, Belgian scientists demonstrated that the very first primates passed through Belgium before reaching North America and already had a skeleton and ecology similar to their modern relatives (Smith et al., 2006; Gebo et al., 2012).

After some early fieldwork in the 1920's and 1970's, studies of the early Paleogene of **Asia** were only taken up recently, including several bilateral projects initiated by the RBINS and funded by Belspo (BL/36/C12 and BL/36/C54). This research has yielded important specimens and seemingly has answered some long-standing questions, such as the origin of rodents, Asian

carpolestids and arctostylopids (Meng et al., 2003, Smith et al., 2004; Missiaen et al, 2006) and on the age correlations of these sites (Missiaen, 2011). But despite the fact that our knowledge of the Asian Paleogene is **somewhat rudimentary** and a lot more needs to be done, the chances of finding the origin of modern orders in Asia seem to be decreasing. The modern APP taxa appear in Asia only in the earliest Eocene, as they do elsewhere, and none of the newly studied Asian Paleocene sites have yielded new potential ancestors of modern forms. Results in the field clearly show that after their first arrival the APP taxa and other modern vertebrates rapidly migrated throughout the Northern Hemisphere, but still offer **no support for an origin in the Northern Hemisphere**.

The situation in the Southern Hemisphere is highly different, where the continents and their faunas are mostly characterized by isolation and endemism after the breakup of Gondwana. Australia has a relatively poor fossil record for the Cenozoic, but except for bats, modern placental mammals only appear during the Quaternary. South America has a relatively good fossil record despite some major hiatuses in its tropical regions and in the earliest Cenozoic (Gelfo et al., 2009) - Primates invade South America in the Oligocene but caviomorph rodents appear in middle Eocene supporting a trans-Atlantic dispersal from Africa (Antoine et al., 2012), and all other **modern forms only appear much later** in the late Neogene.

The **Indian subcontinent** long seemed to hold **great promise**, because this poorly known region drifted northward from its Gondwanan position to collide with Asia at about the same time that modern vertebrates appeared. Explorations of the early Paleogene of Indo-Pakistan only started to yield their first results in the 21st century. Funded by National Geographic, RBINS researchers participated in some of these discoveries, including a highly diverse bat and primate fauna (Smith et al., 2007; Rose et al., 2009) or the suggestion of unexpected faunal exchanges between India and Europe that bypassed Asia, via the Tethys seaway and/or North Africa (Smith et al., 2010). Bombinatorid and rhacophorid frogs too may have their origin in India (Folie et al., in press), whereas at least some types of perissodactyls arrived from elsewhere (Missiaen & Gingerich, 2012). Currently all evidence favouring or dismissing an Indian origin for the APP taxa is **still inconclusive**.

Africa has so far largely been ignored in the quest for the origin of modern terrestrial vertebrates, even if Africa represents a major landmass with interesting past migration opportunities and a high current biodiversity. Some information is available about the early Paleogene of Northern Africa, suggesting an African origin for strepsirhine primates, proboscideans, hyaenodontids, and anomalurid squirrels (Tabuce et al., 2009; Gheerbrant et al., 1996; Solé et al., 2009; Marivaux et al., 2011). Recently, similar groups of vespertilionoid bats known from the early Oligocene of Fayum in Egypt (Gunnell et al., 2008) have been reported from the early Eocene of Tunisia, indicating a possible origin of modern bats on the African continent (Ravel et al., 2012). **Sub-Saharan Africa however is a real paleontological blind spot**. Only one continental early Paleogene mammal fauna is known from Namibia (Pickford et al., 2008) and a partial skeleton of an enigmatic bat from Tanzania (Gunnell et al., 2003). While a few problematically dated fossil sites from Senegal and Mali might turn out to be Middle Eocene in age (Seiffert, 2010), no Paleocene or early Eocene mammals have been found.

This lack of data on the early Paleogene of Africa is increasingly problematic because of the debate on the geographic origin of modern mammals going on between paleontologists and molecular biologists. On one hand, paleontologists often favour an origin somewhere in the northern hemisphere based on available paleobiogeographical data. **Molecular phylogeneticists** on the other hand, using molecular phylogenies of recent species, **favour an African origin for mammals**, pointing to the basal position of typical African taxa in their phylogenetic hypotheses (Murphy et al., 2001; Hunter & Janis, 2006). Both hypotheses are almost diametrically opposed but remain untested due to the lack of early Paleogene fossil data from Africa.

A second reason for the heightened international interest in vertebrate fossils from the **early Paleogene of tropical Africa** is linked with the extremely warm temperatures during this period. Vertebrates and vertebrate communities not only respond to their environments, they can also be used as a proxy for paleotemperature estimate. Recent climate models along with study of late Paleocene vertebrates from Colombia both point to a tropical Mean Annual Temperature (MAT) of 31-32°C for this period, with **temperatures possibly reaching 38-40°C** during hyperthermal events such as the PETM. If correct, these extremely warm temperatures undoubtedly had severe impacts on vertebrate communities, including the possibility of massive widespread equatorial heat-death for mammals if MATs rose above the lethal threshold of about 35°C (Head et al., 2009). Additional data from early Paleogene African fossil vertebrates could therefore **contribute to climate models** for the tropics during this period, and could give insights into how vertebrates **responded ecologically** to extremely warm temperatures in the past and possibly the future.

2.2. Objectives of the project

1. Relocate, re-identify and catalogue all Paleogene vertebrate specimens from the Dartevelle collections housed in the Royal Museum for Central Africa, as well as any other archived information pertaining to them.

2. Study the historic archives of Dartevelle's paleontological expeditions and determine the geographic and geologic origin of the specimens he collected.

3. Collect, analyze and interpret any associated geological samples. Update the geological context of the Dartevelle collection based on these new data and available international literature, with a focus on stratigraphic position, age and environmental factors, including paleoclimatic information.

4. Revisit key areas visited by Dartevelle in Congo and Angola yielding information about the early Paleogene of Equatorial Africa. Search for additional vertebrate specimens. Perform high-resolution stratigraphic sampling of vertebrate-bearing of sections. Collect samples for microfossil, sedimentological and isotopic studies.

5. Analyze and interpret the vertebrate specimens, with a focus on their relevance for early Paleogene faunal and climatic evolution.

2.3 Relevance to society

Besides its paleontological core focus, this project generates ample opportunities for **multidisciplinary scientific interactions** and **public outreach**. Scientifically, this basic research into the early Paleogene vertebrates of tropical Africa is expected to have relevance even for molecular biologists and for modelers of current and future climate and ecology. Not only this project therefore valorizes underappreciated historical collections, but its visibility and interesting narrative helps **emphasize the importance of collection management** towards both policy makers and the general public.

Especially during the first phases of the project, substantial effort went to collection management tasks: locating the relevant vertebrate specimens from the Dartevelle collection, cataloguing and digitizing them, verify if they are being preserved in optimal conditions and whether or not they need restoration, check if samples of sediments were taken with the fossils (for isotopic studies). Similar care has been taken of any new material collected during new fieldwork. Although these tasks are useful within the scope of the research project, they also serve dual purposes, **making valuable heritage specimens more accessible and visible** for all stakeholders, leading to optimizations in their curation, and **ensuring their preservation for future generations**.

The **primary scientific goal** of this project is to improve our understanding of the **origin and evolution of modern vertebrates during the early Paleogene**, filling in the glaring lack of data on equatorial Africa. Given the very poor knowledge of the African tropics during this key period, the chances of a sweepstake discovery revolutionizing the field are certainly not to be excluded. At the very least, these much needed data significantly reduce the uncertainties concerning the historical local faunal diversity.

Set up in a modern multidisciplinary fashion, this study collects potentially relevant **geological, climatic and environmental markers**. These data obviously offer a rich background in which to situate the mammal evolution. However, already by itself this dataset may form an important contribution to the understanding of the **climatic conditions and ecological interactions** of the African tropics during a period of extreme climate perturbations. Climate conditions during this period are the closest available deep time analog to the **projected effects of the global change now being experienced**. Our new data on terrestrial environments from the African tropics provide some missing pieces of information to **climate modelers**, whereas data on the vertebrate communities may be highly valuable for **ecological modeling.**

This project leads to a better documentation of the expeditions and work of Edmond Dartevelle, an inspiring example of the African explorers of the first part of the 20th century, their broad interests and their collaboration with local people. The **powerful narrative of Dartevelle's** life provides ample means for **public outreach** through various outlets including exhibitions or workshops, contacts with the popular press and online multimedia. Combining the attractive story behind a heritage collection with its new, enhanced potential and applications, this project promotes the value of heritage collections and their potential for the future.

During new fieldwork in DRC, the project members searched to **collaborate fully with local experts and stakeholders**. Not only is this a standard good practice for all of the obvious

pragmatic and ethical reasons, but it also contributes to an **increased paleontological awareness and expertise** at the local level. Here too, the respect of Edmond Dartevelle for local people may stimulate their interest and collaboration.

For this project, previously disparate Belgian and international experts with complementary expertise on Paleogene research topics **closely collaborate**. This ensures richer, more multidisciplinary results to the project itself, but also lead to the formation of **new national and international research networks** and the creation of new opportunities for future joint projects.

3. METHODOLOGY

3.1. Digitization and contextualization of heritage collections

At the onset of the PalEurAfrica project, relevant early Paleogene specimens from the RMCA Dartevelle collection, and archival data related to them were located, evaluated and catalogued by RMCA collection staff, assisted by the RBINS collection staff. Joining their independently acquired expertise, RMCA collection managers have determined and implemented the applicable best practices for optimal cataloguing and preservation. Based on the collections and all associated archives, we retraced the history and origin of the vertebrate specimens as accurately as possible. The Dartevelle archives were already partly digitized, but the project aimed to maximally extract relevant information. This allowed the team to refine and update historic entries and to enrich them with additional metadata (Figure 3).

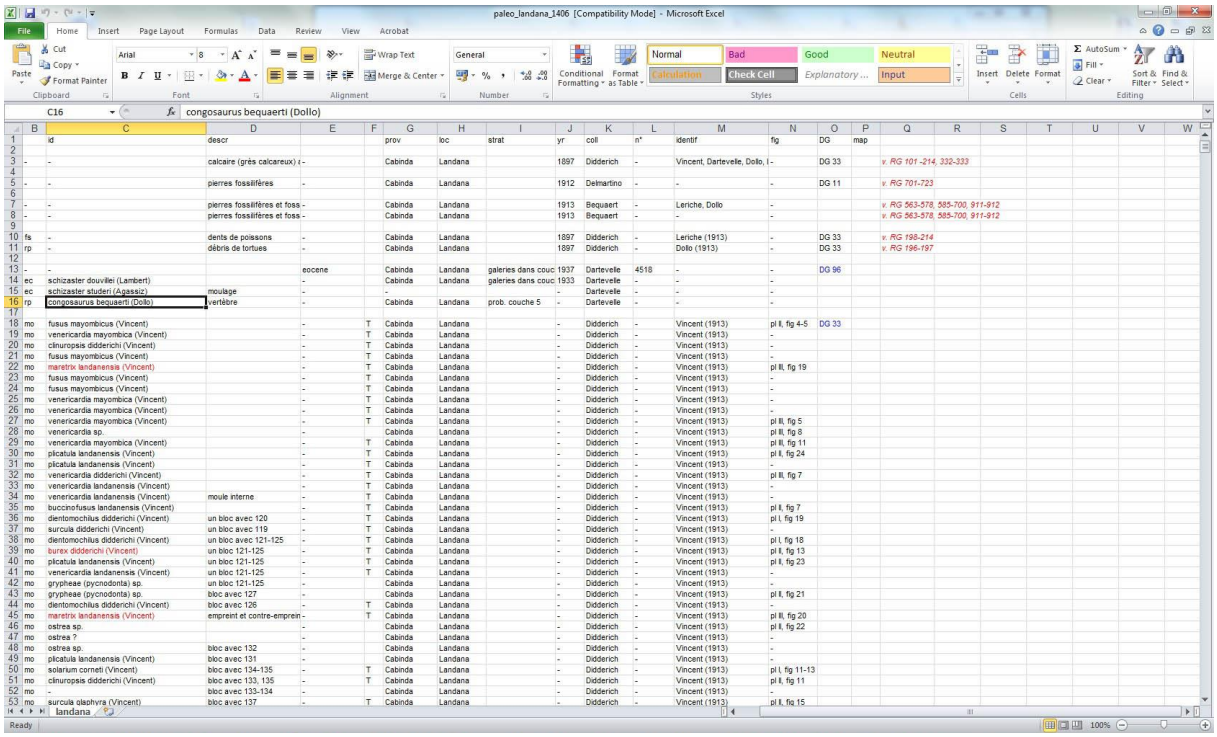

Figure 3. Overview of the digital cataloguing of the specimens from Landana collections at RMCA.

During the 1st PalEurAfrica meeting organized on December 17th 2013 all participants from the six partner institutions had the opportunity to visit the RMCA and RBINS collections. At this

occasion rock samples from the RMCA collected during Dartevelle's expeditions in the Paleogene Landana section, Angola were selected. This was made possible thanks to the cataloging of the paleontological specimens from DRC and Angola in an Excel database with more than two thousand entries.

3.2. Field excavations

Based on the upgraded information from the archives as well as on more recently published studies, new fieldwork expeditions were organized. These explorations provided new, complementary data both by finding new vertebrate specimens and by gathering high resolution field observations and samples for sedimentological, isotope geochemistry and microfossil analyses. To find new vertebrate fossils, expedition members not only used the classic surface prospection technique, but also 1) the advanced screen-washing techniques by the Paleogene vertebrate specialists of the RBINS, and 2) a very high-resolution "level by level" sampling. These techniques not only guaranteed an optimal and unbiased sampling of the full fossil faunal diversity, but also allowed a fine control of stratigraphy and age of the resulting specimens. The organization of new fieldwork received support of local experts such as Prof. Dr. Valentin Kanda Nkula (Centre de Recherches Géologiques et Minières and University of Kinshasa), and built on the expertise of our international network partners, Drs. Gregg Gunnell and Nancy Stevens. All members were not only experts in the field of Paleogene vertebrates and geology, but also seasoned organizers and field members of paleontological expeditions in tropical areas including central Africa and India, target areas of this project.

The following eight field excavations were conducted during the PalEurAfrica project, two of them in DRC and six in India:

2014.09.11-2014.09.24 First exploration in **Bas Congo**, **DRC** to relocate the fossil localities of Manzadi and Bololo discovered by the Belgian expeditions of 1937 with the CRGM (Kinshasa: Nicole Kitambaya Yaya) and Ohio university (Athens: Nancy Stevens). 5 participants.

2015.03.08-2015.03.24 Excavation of early Eocene vertebrates of Tadkeshwar Lignite Mine, **Gujarat, India** with UGent (T. Steeman), UNamur (C. Noiret), Johns Hopkins Univ. (Baltimore: K. D. Rose), Garwhal Univ. Garwhal Univ. (Srinigar: R. S. Rana) and Institute of Himalayan Geology (Dehradun: K. Kumar). 9 participants.

2016.01.11-2016.01.26 Excavation of early Eocene vertebrates of Tadkeshwar Lignite Mine, **Gujarat, India** in collaboration with Johns Hopkins Univ. (Baltimore: K. D. Rose), Garwhal Univ. (Srinigar: R. S. Rana) and Institute of Himalayan Geology (Dehradun: K. Kumar). 6 participants.

2016.09.07-2016.09.22 Exploration for paleontological and geological Paleogene outcrops in **Bandundu**, **DRC** in collaboration with the Centre de Recherches Géologiques et Minières (Kinshasa: Nicole Kitambaya Yaya) and the Royal Museum of Central Africa (Tervuren: T. De Putter). 6 participants.

2017.02.08-2017.02.20 Excavation of early Eocene vertebrates of Tadkeshwar Lignite Mine, **Gujarat, India** in collaboration with Johns Hopkins Univ. (Baltimore: K. D. Rose), Garwhal Univ. (Srinigar: R. S. Rana) and Institute of Himalayan Geology (Dehradun: K. Kumar). 8 participants.

2018.03.04-2018.03.19 Excavation of early Eocene vertebrates of Tadkeshwar Lignite Mine, **Gujarat, India** with Johns Hopkins Univ. (Baltimore: K. D. Rose), Garwhal Univ. (Srinigar: R. S. Rana) and Institute of Himalayan Geology (Dehradun: K. Kumar). 8 participants.

2019.03.09-2019.03.24 Excavation of early Eocene vertebrates of Tadkeshwar Lignite Mine, **Gujarat, India** with Johns Hopkins Univ. (Baltimore: K. D. Rose) and the Garwhal Univ. (Srinagar: R. S. Rana). 7 participants.

2020.03.05-2020-03-18 Excavation of early Eocene vertebrates of Tadkeshwar Lignite Mine, **Gujarat, India** with Des Moines Univ. (R. Dunn), Garwhal Univ. (Srinigar: R. S. Rana) and Institute of Himalayan Geology (Dehradun: K. Kumar). 7 participants.

The first DRC trip in September 2014 (see http://www.paleurafrica.be/?page_id=289), based on Dartevelle's 1937 expeditions. Our aim was to relocate the old fossil localities of **Bas-Congo** based on the combination of archived material and geodetic parameters. Several fossiliferous localities yielding vertebrates in the area of **Manzadi** (today Tzadi-Congo) and **Bololo** were re-visited by a small team of geologists and palaeontologists from RBINS, Ohio University, and the Centre de Recherches Géologiques et Minières, Kinshasa (CRGM) to collect sediments for sedimentological, microfossil and isotopic analyses (Figure 4). Only a few fossils of marine vertebrates were found. Nevertheless, the results allowed us to connect the projects through time and publish one of the most important multidisciplinary papers on the subject (Solé et al., 2019).

Figure 4. Geologist Nicole Kitambala Yaya from the CRGM (in blue) tries to re-localize old fossil localities discovered during the 1937 Dartevelle's expedition with inhabitants of Manzadi village (Photo: Thierry Smith, RBINS).

The second DRC field trip, two years later, took place in Kikwit (Bandundu; see PalEurAfrica website http://www.paleurafrica.be/?page_id=1187). This destination was selected in order to

look for Eocene localities inside the Congo Basin. Because E. Dartevelle died at the age of 49, he did not have the opportunity to prospect more the hinterland and mainly focused on the Bas-Congo. However, RMCA archives attracted our attention on the J. Lepersonne's long missions in Bandundu. In 1948, he explored the South of Bandundu in more detailed and took notes of his observations in four notebooks. We used them for a second expedition of the PalEurAfrica team in September 2016. By this way and thanks to the cartographic archives of the RMCA, GPS geolocation technologies (GIS) and with the precious help of local authorities, we were able to find, prospect, and sample the magnificent Lukwila Canyon and several localities considered to be of Paleogene age (Figure 5). Samples were taken for sedimentological, micropaleontological and geochemical analyses in **Gungu, Lukwila, Maïdombé**, and along the N1 road between Kikwit and Kinshasa.

Figure 5. Sampling of the Lukwila sections: Florias Mees (RMCA) cleans the outcrop; Thierry De Putter (RMCA) describes the sediments; Nicole Kitambala Yaya (CRGM, from back) collects samples (Photo: Thierry Smith, RBINS).

This was done by a small team of geologists and palaeontologists from RMCA, RBINS, and CRGM. Because this part of DRC is far from large cities, more problems occurred such as resources in water or electricity to charge laptops and other electronic equipment. Nevertheless, the trip was successful thanks to the assistance of sisters from the St Joseph de Turin mission at Gungu. The results of this second field campaign are still being processed.

After the two DRC fieldtrips, we planned a fieldtrip in the famous Landana locality in the **Cabinda exclave of Angola**. Unfortunately, no real scientific agreement exists between Belgium and Angola and we were not able to obtain the mandatory field permits and visas, even after a long process of discussion with the university of Luanda and with American and Portuguese colleagues who worked in Angola. However, we did not give up and decided to study the specimens housed at the RMCA. In this framework, we studied a fossil fish (Taverne et al., 2019), some fossil turtles (Perez-Garcia et al., 2020), a fossil snake (Folie et al., 2021)

and a hyracoid mammal (Tabuce et al., 2021). We also revised the biostratigraphy of the Landana section (Solé et al., 2019) and published the dinoflagellates cysts (Steeman et al., 2019). The last two papers are due to the wise advice of Philip Muchez during the first follow-up committee meeting on March 6th, 2015 who proposed to enhance the geological aspects.

In addition, 12 publications by team members were completed based on previous field campaigns done in other parts of Africa, in the **Rukwa Basin of Tanzania** (Blackburn et al. 2014; McCartney et al 2014; Borth & Stevens 2017; Epa et al 2018; Muller et al., 2018, Claeson et al., 2021, McCartney et al., 2021), in the **Fayum of Egypt** (Sallam et al., 2016; Miller et al., 2017), in the localities of **Khouribga and Dakhla in Morocco** (Kocsis et al 2014; Benammi et al., 2017), and in **Chambi & Bir el Ater, Tunisia** (Solé et al., 2016).

Six other field excavations, made in the framework of PalEurAfrica, took place all at **Tadkeshwar mine, Gujarat, India** (see PalEurAfrica website http://www.paleurafrica.be/?page_id=291, http://www.paleurafrica.be/?page_id=1051, http://www.paleurafrica.be/?page_id=1712, http://www.paleurafrica.be/?page_id=1732). Since 2004, a join Indian-American-Belgian team excavated the Vastan Lignite Mine in the Gujarat Province thanks to the support of the National Geographic Society. This locality yielded a rich early Eocene vertebrate fauna from the Cambay Shale Formation that showed the first mammals of European affinities. In March 2014, our field crew composed by members from RBINS, UGent, UNamur, Johns Hopkins University, Garhwal University, and Wadia Institute of Himalayan Geology has discovered new vertebrate layers (Figure 6).

Figure 6. Discovery of a new fossiliferous layer with vertebrates two days before the end of the expedition. The outcrops are getting smaller (Photo: Thierry Smith, RBINS).

Among the fascinating vertebrates are taxa with Gondwanian affinities mixed with taxa of European affinities. Moreover, Tadkeshwar mine yielded the first large vertebrates of the early Eocene of India. After these excellent results of the 2015 field campaign, a new join Indian-American-Belgian team excavated for fossil vertebrates in Tadkeshwar Lignite Mine. Several important primate specimens were discovered and this time the expedition was supported by the Leakey Foundation. Some layers exploited in 2015 were unfortunately no more accessible later due to the fast progression of lignite digging by the mining company. However, more

specimens were collected from a channel deposit discovered previously. Rock samples were also collected for microfossil and isotopic analyses. In February 2017, layers between the two main lignite seams were well exposed but relatively poor in terrestrial vertebrates. This was due to the rarity of continental lenses in that part of the exploited mine. Nevertheless, numerous remains of aquatic animals and some terrestrial mammals were discovered. In March 2018, the mining activities operated in different locations of the mine at the same time. This allowed us to better correlate the stratigraphic layers between the different fossil spots. In March 2019 and March 2020, the layers were unfortunately less rich in fossil remains.

The scientific results are numerous (see 4.1) with 11 articles already published (Rose et al., 2014; Rana et al., 2015; Smith et al., 2015, 2016; Dunn et al., 2016; Bemis et al., 2017; Rose et al., 2018; Koenigwald et al., 2018; Zack et al., 2019; Solé et al., 2020, Zaher et al., 2021), nine of them in journals with Impact factors about fossil mammals, birds, fishes.

It is thanks to our Indian colleagues who helped us with the local logistic and the support of local mine authorities that we discovered the Tadkeshwar mine after years of excavations in the Vastan lignite mine, finished and dumped in 2012-2013. Now, after several expeditions in Tadkeshwar mine, the latter is reaching the end of the exploiting process by the mining company. Nevertheless, we have a new opportunity with some artiodactyl specimens recently discovered in middle Eocene layers in Kashmir (Rana et al., 2021).

Next to these important field campaigns, specimens from **European collections** (mainly French and Belgian ones) have been studied in order to find the origin of the first modern mammals in the Northern Hemisphere. This led to the publication of nine papers on the Belgian faunas (Gebo et al., 2015; De Bast and Smith, 2016; Perez-Garcia and Smith, 2016, 2017, Gunnell et al., 2017; Mayr and Smith, 2018, 2019a,b; Morse et al., 2019, Perez-Garcia and Smith, 2021), 10 publications on French faunas (Martin et al., 2014; Solé et al., 2015, 2019, 2021b; Smith et al., 2014, 2015a,b, 2016; Delfino et al., 2017; Mayr and Smith, 2017; De Bast et al., 2018), and two publications about birds from Wyoming, USA (Mayr et al., 2019, 2020). Other studies were not focused on a particular locality but summarized the knowledge on specific taxa (Orliac et al., 2014; Solé and Ladevèze, 2016; Bastl et al., 2017; Dagosto et al., 2017; Solé et al., 2018, 2021) or geological data (Storme et al., 2014; Yans et al., 2014; Noiret et al., 2016). Finally, one paper is on the Quercy (France) specimens housed in historic Belgian collections (Solé et al., 2021a).

3.2 Research strategy activities

In order to meet all the goals of the project, the following meetings or actions were done:

2013.12.17 First PalEurAfrica Coordination Meeting at RBINS and RMCA.

2014.02.06 Sampling of Paleogene sediments at RMCA.

2014.03.11 Return to RMCA of 13 drawers containing shark specimens from DRC that were on loan at RBINS from Edgar Casier's period.

2014.06.18 Work meeting at the RMCA, preparation of the first field campaign in DRC.

2014.10.22 Second PalEurAfrica Coordination Meeting at UNamur.

2014.11.03 Discussion on the Landana locality, Angola with Prof. Louis Jacobs (Southern Methodist Univ., USA) at the RMCA.

2014.11.14 Work meeting at UNamur with Johan Yans and Corentin Noiret.

2015.03.06 First follow-up committee meeting organised at Belspo.

2015.12.14 Third PalEurAfrica Coordination Meeting at UGent.

2016.10.18 Second follow-up committee meeting organised at RBINS.

2016.12.01 First extension of the PalEurAfrica project until 2018.12. 31.

2018.12.14 Second extension of the PalEurAfrica project until 2019.12. 31.

2019.12.18 Third extension of the PalEurAfrica project until 2020.06. 30.

Our first step was a team meeting at the RBINS in December 2013, soon after the approval of the project with all the partners. The first field localities to prospect and recruitments of PhD students and postdoctoral researchers have easily been accepted by all the partners.

In February 2014, we decided to analyse some rock samples from the RMCA collections collected during the Dartevelle's expeditions in the Paleogene Landana section, Angola for Carbon and Oxygen isotope analysis and for palynologic analysis. Each selected sample was divided in two: one for analysis in UNamur (isotope analysis) and one for analysis in UGent (palynologic analysis).

In March 2014, during the inventory and moving of some RBINS collections, 13 original drawers containing shark specimens from Central Africa belonging to the RMCA collections have been discovered (Figure 7). These drawers were likely at the RBINS since Edgar Casier's period when he studied African specimens in 1950th. We therefore decided to return these collections to the RMCA.

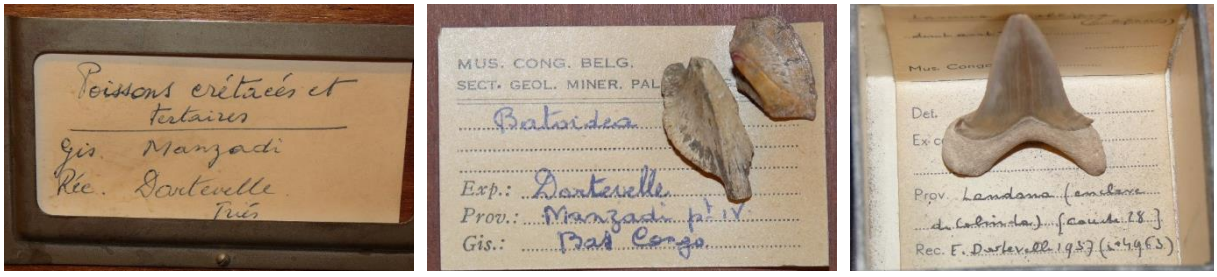

Figure 7. Top left: label of the drawer 165 from RMCA collections found at the RBINS in March 2014. Top right: Fish remains from Manzadi, Bas-Congo, DRC. Bottom left: shark tooth from Landana, Cabinda, Angola (Photos: Annelise Folie, RBINS).

In June 2014, a meeting at the RMCA allowed us to discuss more precisely about the localities that could be prospected during the first field campaign in DRC in September (see 3.1). Afterward, in October 2014, a new meeting occurred in UNamur to debrief this first campaign and present the main results. Again, the US partners where present to actively take part to the discussion. We also planned the written of the first annual report of the project, the publication

strategy concerning new results on Landana, Manzadi, and Bololo sections). We also prepared the first follow-up committee meeting, the positions still available for PhD students and postdoctoral researchers, fieldwork in 2015, development of the PalEurAfrica website (www.paleurafrica.be).

In November 2014, two additional small meetings occurred. The first one at the RMCA was an important discussion with Prof. Louis Jacobs (Southern Methodist Univ., USA), leader of the field campaign and research study in Angola. The aim was to find a agreement to prospect the Paleocene-Eocene deposits of the Landana section in the Cabinda exclave. Prof. Jacobs was open to a collaboration because he was mainly working and studying the Cretaceous faunas and not the Paleogene ones. The second meeting was at the UNamur to discuss on the PhD thesis of Corentin Noiret.

In March 2015, the first follow-up committee meeting took place at Belspo (Figure 8).

Figure 8. First follow-up committee meeting, March 6, 2015 at Belspo. From left to right: Rodolphe Tabuce (Université de Montpellier, France), Eric De Bast, Thierry Smith (RBINS), Thierry De Putter (RMCA), Philippe Muchez (KU Leuven), Julie De Weirdt, Thomas Steeman, Stephen Louwye (UGent), Maaike Vancauwenberghe (Belspo), Patrick Semal (RBINS) (Photo: Annelise Folie, RBINS).

The meeting included nearly all the follow-up committee, the partners of the PalEurAfrica project and the Belspo program manager, Maaike Vancauwenberghe. All the present promoters and several members of the project presented the results of the first two years of the project. At this step, the specimens from the Dartevelle's collection at the RMCA were already digitised and relocated in the drawers; relevant historic notes, drawings, and publications related to Dartevelle's expeditions at the RMCA were scanned; a first field campaign was done in the Bas-Congo, DRC; and the first papers were published (9 published papers, 4 manuscripts submitted; 17 congress communications). We also presented the future prospects. During the meeting, the discussions with the members of the follow-up committee were active. The importance of the digitization of the specimens and their metadata and their dissemination to the public was strongly underlined. Moreover, Philippe Muchez proposed to work on the global stratigraphy of the Paleogene sections known from Africa. Later, the Landana biostratigraphy was revised and a publication went out (Solé et al., 2019). Our fear was that reviewers of the manuscript we wrote on the Landana integrative study would request new sampling in order to complete the RMCA sampling done in the 1930th. However, this did

not happen because the RMCA rock collections were of better quality than expected. For this reason, the rest of the specific field budget was used for fieldwork in India in order to complete the budget obtained from a grant of the Leakey Foundation.

On December 14, 2015 we organised a new coordination meeting at UGent. We discussed the 2015 results, the redaction of the second annual report of the PalEurafrica project and discussed the second field campaign in DRC as the trip in Angola was not possible to organise (see 3.1). We thus discussed during the meeting about new localities to prospect in DRC and a second field campaign was organised in September 2016 in the Bandundu region (see 3.1).

After this, in October 2016 was organised the second follow-up meeting at the RBINS. The PalEurAfrica team members explained their results and the new updates made on the PaEurAfrica website. A visit in the RBINS collections was organised and it was the opportunity to show the new discovered boxes containing samples and microfossils from DRC. The analysis of these boxes revealed the presence of fossil invertebrates sampled from different localities in DRC (Bololo, Manzadi, …) and Angola (Landana, San Antonio, …). Among them, one box contained the type specimens published by Vincent 1913 from Cabinda, Angola (Figure 9). The expertise of Florias Mees (curator of Paleontological Collection at RMCA, Tervuren), indicated that these samples actually belong to the RMCA collections. Therefore, all the 34 boxes were transferred to Tervuren on October 28th in order to be housed in their original institution as it was the case for the drawers in 2014. The partners of the projects took benefit of this meeting to discuss future researches and publications for 2017.

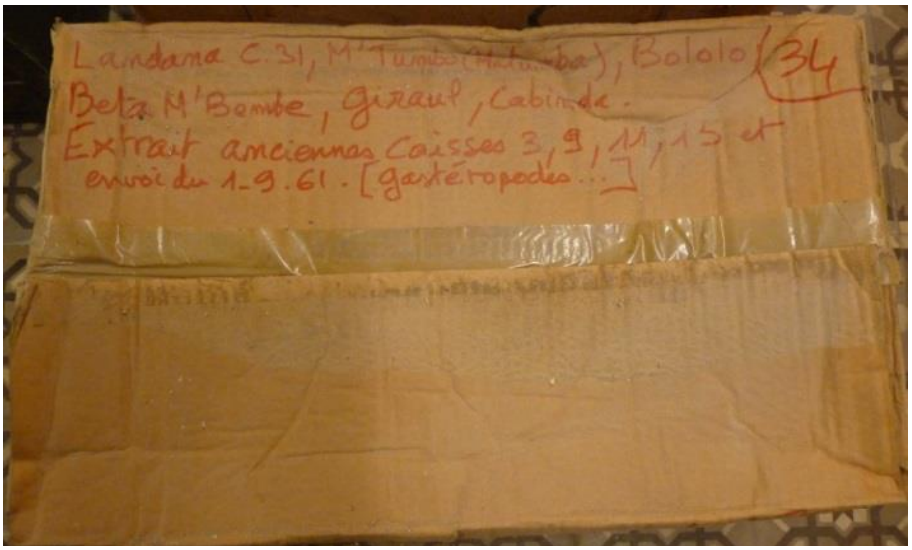

Figure 9. Picture of box n°34 containing samples from Landana and Bololo, Cabinda, Angola.

At the end of 2016, we asked a first extension of the project for one year (extension to December 31, 2018) because Thomas Steeman was hired as PhD student for four years at UGent (contract from December 2014 to November 2018).

On September 20, 2017, one of the promotors, Gregg Gunnell unexpectedly died while undergoing treatment for lymphoma, a diagnosis he received only a few weeks before his death. This was a choc for the team. However, the collaboration with Dr. Gunnel's colleagues continued. Because the project situation was relatively stable and the focus was on the written

of the last papers, we did not organise new coordination meetings. Some small meetings in Belgium occurred and international congresses were the occasion to meet and discuss with the second partner from United States, Nancy Stevens.

At the end of 2018, a second extension was required until December 2019 in order to meet all the good conditions and time necessary for the organization of the PalEurAfrica international symposium (see 3.5).

A third extension for six months was requested end of 2019 in order to finalize the project and to allow one of the PhD student to defend his PhD thesis in the timeframe of the project.

3.3 Publications

The results of the studies were regularly published, all in peer reviewed journals. In total, our team produced 67 full articles during the six years of the project (see 6.1.). Among them, 65 articles were published in impact factor journals and one as a chapter of a book. We also edited a special volume of the journal *Geobios* that followed the international PalEurAfrica congress of September 2019 (double issue 66-67 available online; printed version in press).

The journals have been selected following the subjects of the manuscripts and the possibility to publish in good impact journals (e.g. *Journal of Vertebrate Paleontology; Nature Communications*; *Newsletters on Stratigraphy*; *Palaeogeography, Palaeoclimatology, Palaeoecology*; Minerals; *PLoS ONE*; *Proceedings of the Royal Society B*; Journal of Mammalian Evolution; *Zoological Journal of the Linnean Society*). The fact that the journal is in open access or not was not frequently considered because many of them are still expensive and we can easily share pdf of papers via emails. Moreover, this last dissemination system often offers opportunity to create new contacts and start new collaborations.

3.4 Congresses and international conferences

The results of the studies were regularly presented during diverse international congresses. In total, 72 abstracts (29 published and 43 unpublished abstracts) were submitted in the scope of the participation to international conferences, meetings and congresses (see 6.2. and 6.3.).

The diversity of meetings concerning paleontology is not so huge and in order to reach a large audience, all 24 published abstracts have been presented at the *Annual meetings of the Society of Vertebrate Paleontology* which gather each year more than 1,000 vertebrate paleontologists. Beside this, smaller European meetings were attended such as the annual meeting of the *European Association of Vertebrate Paleontologists* (EAVP; 2 communications); or the annual meeting of the *Association Paléontologique Française* (APF; 7 communications). These meetings are smaller but can strategically create contacts with European colleagues working on the early Paleogene faunas. Our team also presented 11 communications at the *International Symposium PalEurAfrica - Evolution and Paleoenvironment of Early Modern Vertebrates during the Paleogene* (see 3.5 for further details).

3.5 PalEurAfrica international conference

In the framework of the ending of the PalEurAfrica research project (see http://www.paleurafrica.be), we received from September 10th to 13th 2019, 62 experts from 14 countries of four different continents at the RBINS for an international symposium related to the *Evolution and paleoenvironment of early modern vertebrates during the Paleogene* (http://www.paleurafrica.be/?page_id=2547) (see 6.4.). This symposium gathered specialists who worked on macro- and micropaleontology, bio- and isotope stratigraphy, paleoenvironment, paleogeography, and geology of Paleogene vertebrate bearing sites. This international meeting also celebrated the memory of one of our PalEurAfrica partners, Gregg Gunnell (1954 – 2017), who died tragically and unexpectedly in the middle of his career, having made significant contributions to our understanding of Paleogene vertebrate evolutionary history (Figure 10).

Figure 10. Group picture of the *International Symposium PalEurAfrica* attendees (Photo: Thierry Hubin, RBINS).

The organisation composed of a host committee of 6 persons (the promotors of the project) and a scientific committee of 14 international researchers were united by a common scientific interest: Paleogene vertebrates and their environments. Talks have been presented unopposed in a single venue, the main auditorium of the RBINS. We followed a theme linked to the continents (Europe, Africa and Asia) (Figure 11).

Time	Tuesday 10 Sept 10th	Wednesday 11 Sept 11th	Thursday 12 Sept 12th	Friday 13 Sept 13th
8h30	Registration			
8h45				
9h00	Welcome	Keynote 02: Mayr G.	Keynote 03: Stevens et al.	Field work Maret, Dormaal, and Boutersem
9h15	Keynote 01: Sallam H.			
9h30		Rabenstein et al.	Mayr G.	
9h45	Miller et al.	Černanský & Smith	Jouve et al.	
10h00	Borths et al.	Rabi et al.	Lambert et al.	
10h15	Gingerich et al.	Solé F.	Zouhri et al. (02)	
10h30	Coffee Break & Posters (VIP room)	Coffee Break & Posters (VIP room)	Coffee Break & Posters (VIP room)	
10h45				
11h00	Speijer & Pälike	Zouhri et al. (01)	Tabuce et al.	
11h15	Rose et al.	Gheerbrant E.	Lihoreau et al.	
11h30	Zaher et al.	Elboudali et al.	Godinot et al.	
11h45	Rana et al.	Steeman et al.	Quesnel et al.	
12h00	Group Photo	Lunch Break (12:00-13:30)	Lunch Break (12:00-14:00)	
12h30	Lunch Break (12:00-14:00)			
13h00				
13h30				
14h00				
14h00	Li Q.	Visit RMCA (Paleogene collections and new African exhibitions)	Codrea et al.	
14h15	Wang et al.		Beard et al.	
14h30	Bai et al.		Tissier et al.	
14h45	Paepen et al.		Métais et al.	
15H00	Coffee Break & Posters (VIP room)		Coffee Break & Posters (VIP room)	
15h15				
15h30	MacLaren J.		Kynigopoulou et al.	
15h45	Bronnert C.		Jehle et al.	
16h00	Vallée Gillette et al.		Bertrand et al.	
16h15	Yans et al.			
16h30	Guided tour RBINS (Exhibitions and collections)		Workshop: cast exchange (Dollo Room)	
16h45				
17h00				
17h15				
17h30				
17h45				
18h00	Icebreaker Party (VIP room)			
19h00			Conference Dinner (*L'Horloge du Sud*)	
22h00				
Sessions:	Europe	Africa	Asia	

Figure 11. International Symposium PalEurAfrica meeting program.

In total, 51 abstracts have been presented (38 talks in technical sessions, 10 posters, and 3 keynote lectures). They are available in an Abstract book.

Three famous vertebrate localities have been reopened for the meeting: Maret (middle Paleocene, MP1-5, Figure 12), Dormaal (earliest Eocene, MP7, Figure 13), and Hoogbutsel-Boutersem (early Oligocene, MP21, Figure 14) in eastern Belgium. More information about these localities can be found in a field guide.

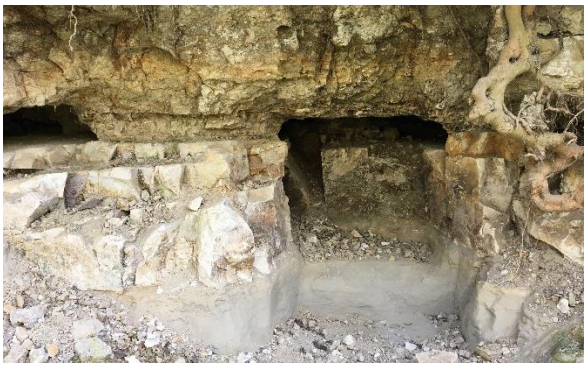

Figure 12. Outcrop section at Maret with the marls of Gelinden sandwiched between the middle Paleocene Heers Formation (MP1-5) and the late Paleocene Hannut Formation (Photo: Thierry Smith, RBINS).

Figure 13. The sunken path of Dormaal along which the fluvial deposits of the earliest Eocene Tienen Formation are exposed (MP7) (Photo: Thierry Smith, RBINS).

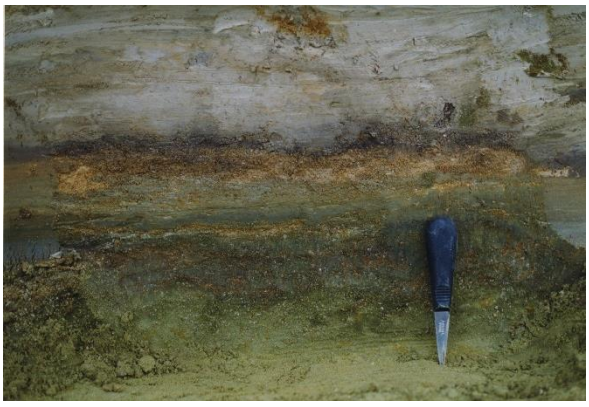

Figure 14. Outcrop section at Boutersem-TGV in the early Oligocene Boutersem Sand Member of the Borgloon Formation (MP-21) (Photo: Thierry Smith, RBINS).

At the end of the conference, the Chief Editor of the international journal *Geobios*, Dr. Gilles Escarguel, offered us the opportunity to publish papers dedicated to the general theme of the PalEurAfrica congress in a thematic volume (i.e., part of the regular series of the journal). Eight to twelve papers are needed to edit the volume and we succeeded to have 14. The submission deadline was originally set on December 31, 2019 in order to publish the volume in Autumn 2020, after a complete review process. However, due to the Covid crisis, the editing procedure was delayed and the printed volume is planned for July 2021. Nevertheless, all papers are already accepted and available online.

4. SCIENTIFIC RESULTS AND RECOMMENDATIONS

4.1 Scientific Results

4.1.1. Refined dating of the early placental mammals in Morocco, using carbon isotopes on various materials

Fossil biogenic apatites were studied for their geochemical composition across the late Cretaceous–early Eocene Moroccan phosphate series in the Ouled Abdoun and Ganntour basins in Morocco in order to characterize paleoenvironmental conditions and to improve stratigraphy. The vertebrate remains show particularly good structural, mineralogical and chemical preservations, which relate to the favorable depositional environment of the phosphorite. The main studied fossils show large range in $^{13}C_{carborg}$ values from−14 to +6‰, which can be coupled to different carbon sources. Enameloid yielded mostly positive ^{13}C isotopic compositions that are comparable with values reported from modern teeth. Coprolites have the lowest ^{13}C values that reflect burial conditions with intensive organic matter recycling. The large variation in $^{18}OPO4$ values of the shark teeth can be related to ecological differences. However, the mean $^{18}O_{PO4}$ data reflect important temporal variation along the series, together with the corresponding average ^{13}C values.

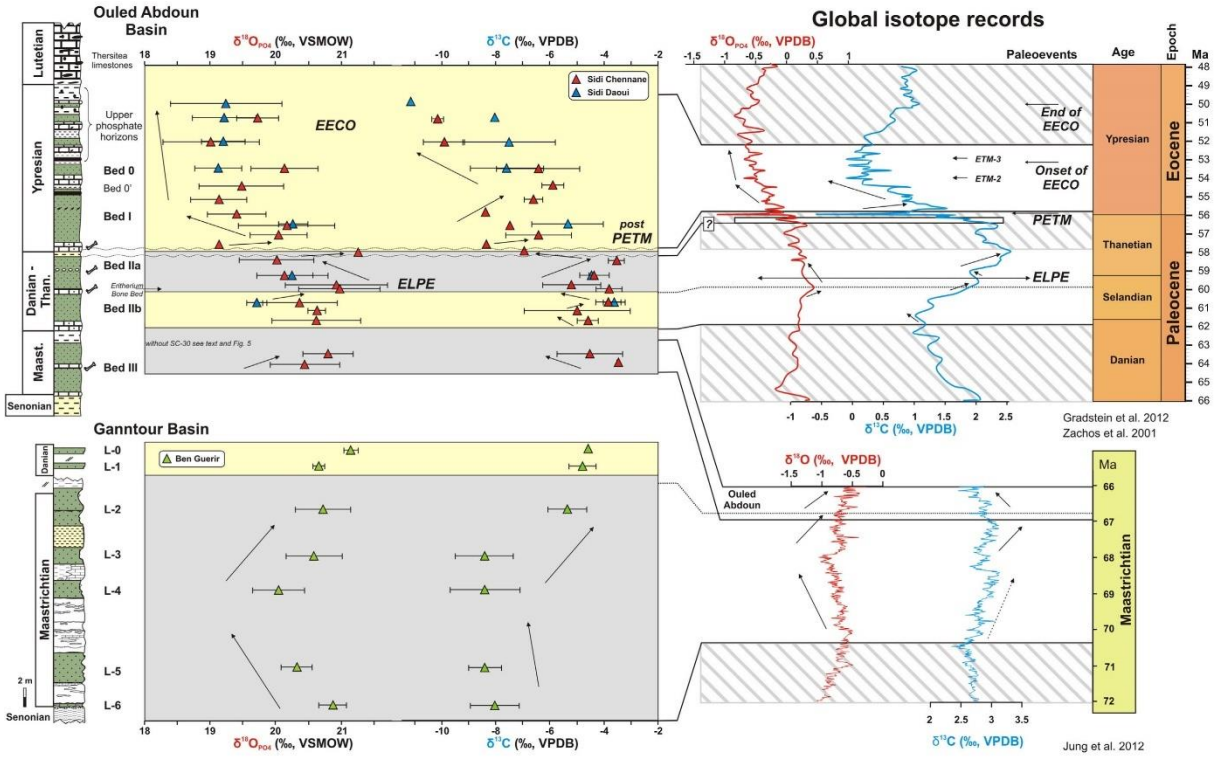

Figure 15. Integrated phosphate oxygen ($\delta^{18}O_{PO4}$) and carbon $\delta^{13}C$ (dentine) isotope data from the Ouled Abdoun and Ganntour basins and their comparison to the global record.

Comparisons with the global isotope records (Figure 15) allow identifying the Early Eocene Climatic Optimum in the top of the Ouled Abdoun series (above Bed 0). The isotope data further suggest a sedimentary gap during the latest Thanetian and the Paleocene Eocene Thermal Maximum. The top of the Paleocene series (Bed IIa) can be dated to late Selandian–early Thanetian, with the recognition of the Early Late Paleocene Event (ELPE). The Eritherium Bone Bed, that yielded the earliest known placental mammals from Africa, would be located below the ELPE and therefore, cannot be younger than late Selandian. The isotope data from the older Paleocene (Bed IIb) and Cretaceous (upper Bed III) beds in the Ouled Abdoun Basin can be correlated with the latest Danian – early Selandian and the latest Maastrichtian global isotope record, respectively. Based on the 18OPO4 data, the Cretaceous layers of the Ganntour Basin cover most of the Maastrichtian period except the very early part.

A paper describing these results is published in Palaeogeography, Palaeoclimatology, Palaeoecology (Kocsis et al., 2014).

4.1.2. First Clarkforkian Equivalent Land Mammal Age in the Latest Paleocene Basal Sparnacian Facies of Europe: Fauna, Flora, Paleoenvironment and (Bio)stratigraphy

The Paleocene-Eocene Thermal Maximum (PETM) is correlated with the first occurrences of earliest modern mammals in the Northern Hemisphere. The latest Paleocene Clarkforkian North American Land Mammal Age, that has yielded rodents and carnivorans, is the only exception to this rule. However, until now no pre-PETM localities have yielded modern mammals in Europe or Asia. The new terrestrial vertebrate and macroflora assemblages found at Rivecourt, in the north-central part of the Paris Basin, were analyzed through a

multidisciplinary study including sedimentologic, stratigraphic, isotopic, and palynological aspects in order to reconstruct the paleoenvironment and to evaluate biochronologic and paleogeographic implications. The mammals are moderately diverse (Figure 16) and not abundant, contrary to turtles and champsosaurs. The macroflora is exceptional in preservation and diversity with numerous angiosperms represented by flowers, fruits, seeds and wood preserved as lignite material, revealing an abundance of *Arecaceae, Betulaceae, Icacinaceae, Menispermaceae, Vitaceae* and probably *Cornaceae*. Results indicate a Late Paleocene age based on Carbon isotope data, palynology and vertebrate occurrences such as the choristoderan *Champsosaurus*, the arctocyonid *Arctocyon*, and the plesiadapid *Plesiadapis tricuspidens*. However, several mammal species compare better with the earliest Eocene. Among these, the particular louisinid *Teilhardimys musculus* suggests a younger age than the typical MP6 reference level.

Nevertheless, the most important aspect of the Rivecourt fauna is the presence of dental remains of a rodent and a “miacid” carnivoran, attesting to the presence of two modern mammalian orders in the latest Paleocene of Europe. Therefore, Rivecourt represent the first Clarkforkian equivalent Land Mammal Age in Europe.

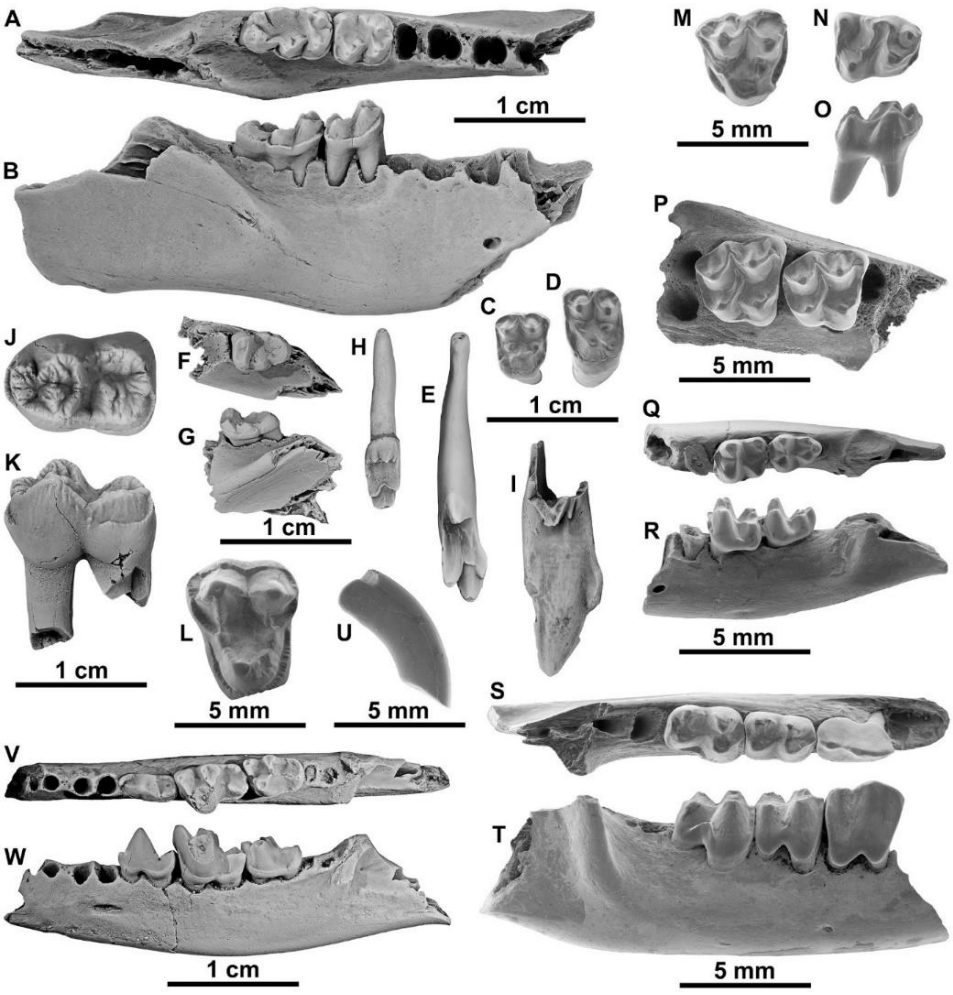

Figure 16. Illustration of several mammals from the late Paleocene locality of Rivecourt.

A long paper describing this new locality is published in *PLOS ONE* (Smith et al., 2014).

4.1.3. Endocranial morphology of Paleocene *Plesiadapis tricuspidens* and evolution of the early primate brain

Expansion of the brain is a key feature of primate evolution. The fossil record, although incomplete, allows a partial reconstruction of changes in primate brain size and morphology through time. Paleogene plesiadapoids, closest relatives of Euprimates (or crown-group primates), are crucial for understanding early evolution of the primate brain. However, brain morphology of this group remains poorly documented, and major questions remain regarding the initial phase of euprimate brain evolution. Micro-CT investigation of the endocranial morphology of *Plesiadapis tricuspidens* from the Late Paleocene of Europe, the most complete plesiadapoid cranium known, shows that plesiadapoids retained a very small and simple brain (Figure 17).

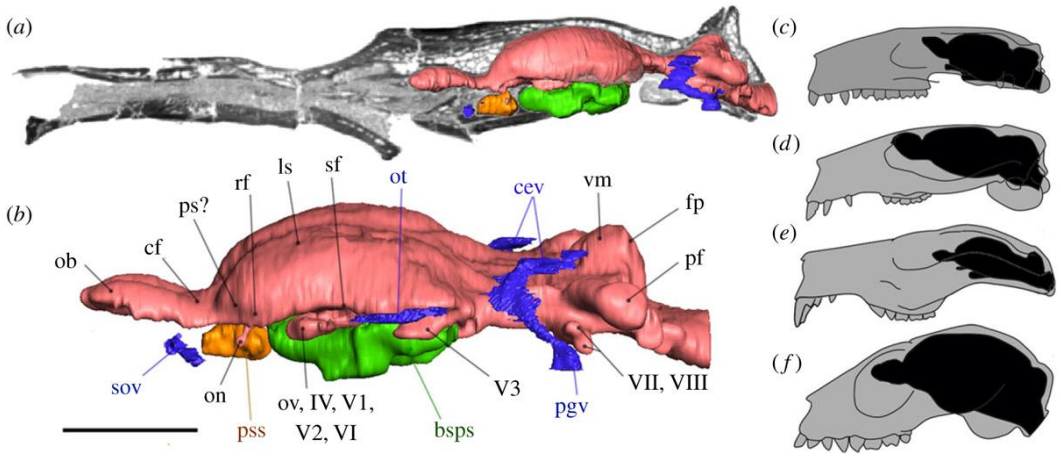

Figure 17. Endocast of *Plesiadapis tricuspidens* (a, b) and comparison with the location and extent of the braincase in plesiadapiformes *Microsyops annectens* (c), *Ignacius graybullianus* (d), *P. tricuspidens* (e), and euprimate *Tetonius homunculus* (f).

Plesiadapis has midbrain exposure, and minimal encephalization and neocorticalization, making it comparable with that of stem rodents and lagomorphs. However, *Plesiadapis* shares a domed neocortex and downwardly shifted olfactory-bulb axis with Euprimates. If accepted phylogenetic relationships are correct, then this implies that the euprimate brain underwent drastic reorganization during the Palaeocene, and some changes in brain structure preceded brain size increase and neocortex expansion during evolution of the primate brain.

These important results are published in *Proceedings of the Royal Society B, London* (Orliac et al., 2015).

4.1.4. Earliest colubroid-dominated snake fauna from Africa

The extant snake fauna has its roots in faunal upheaval occurring across the Paleogene – Neogene transition. On northern continents, this turnover is well established by the late early Miocene. However, this transition is poorly documented on southern landmasses, particularly on continental Africa, where no late Paleogene terrestrial snake assemblages are documented south of the equator. Here we describe a newly discovered snake fauna from the Late Oligocene Nsungwe Formation in the Rukwa Rift Basin of Tanzania. The fauna is small but diverse with eight identifiable morphotypes, comprised of three booids and five colubroids. This

fauna includes *Rukwanyoka holmani* gen. et sp. nov., the oldest boid known from mainland Africa. It also provides the oldest fossil evidence for the African colubroid clade Elapidae (Figure 18). Colubroids dominate the fauna, comprising more than 75% of the recovered material. This is likely tied to local aridification and/or seasonality and mirrors the pattern of overturn in later snake faunas inhabiting the emerging grassland environments of Europe and North America.

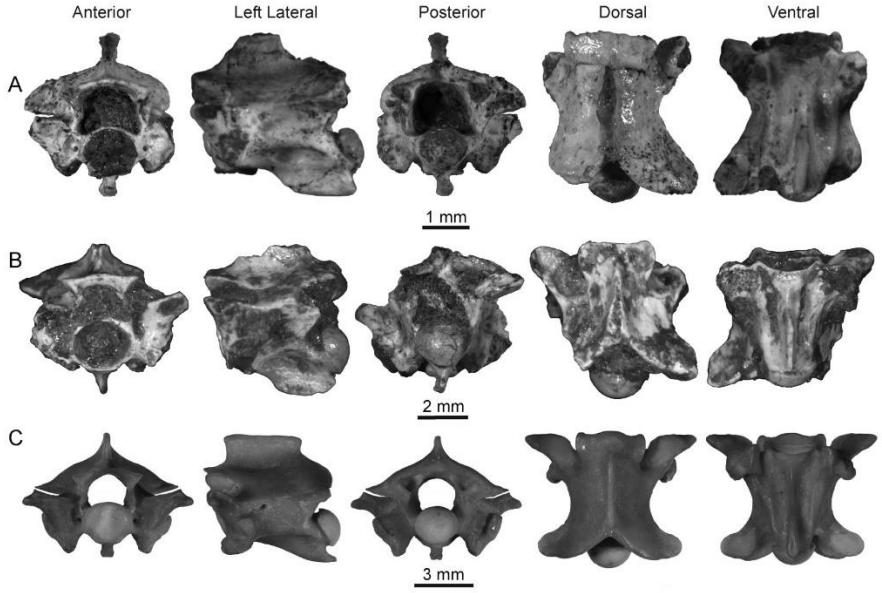

Figure 18. Elapid snakes from late Oligocene of Tanzania (A, B) with comparison to extant *Naja nigricollis* (c).

The early emergence of colubroid dominance in the Rukwa Rift Basin relative to northern continents suggests that the pattern of overturn that resulted in extant faunas happened in a more complex fashion on continental Africa than was previously realized, with African colubroids becoming at least locally important in the late Paleogene, either ahead of or as a consequence of the invasion of colubrids. The early occurrence of elapid snakes in the latest Oligocene of Africa suggests the clade rapidly spread from Asia to Africa, or arose in Africa, before invading Europe.

A paper describing these snakes is published in *PLOS ONE* (McCartney et al., 2014).

4.1.5. Refined dating of the European early placental mammals in the Corbières area, located between reference localities of Northern Europe and Africa.

Utilizing bio- and chemostratigraphy, we published an integrated dating of the upper part of the continental “Sparnacien des Corbières” and the overlying marine “lower-middle Ilerdian” succession of Albas-Le Clot (Corbières, France), in order to refine the position and age of the Le Clot mammalian locality. Our data show that this locality, which has yielded a mammal fauna early Ypresian in age (close to MP7, Mammal Paleogene level), is located above the end of the carbon isotope excursion (CIE) the base of which defines the Paleocene-Eocene boundary (Figure 19). The Le Clot mammalian locality is therefore younger than the Paleocene-Eocene Thermal Maximum (PETM), and also younger than the Dormaal MP7 reference fauna in Belgium, which is correlated with the onset of the CIE (nannoplankton Zone

NP9b). Moreover, we demonstrate that the Le Clot mammalian locality is older than the Eocene Thermal Maximum 2 (ETM2) event, located in the lower part of NP11 Zone. Associated with the ages of benthic foraminifera and dinocysts observed in the succession, our $^{13}C_{org}$ chemostratigraphy suggests that the Le Clot locality is correlated to the upper NP10–lower NP11 Zones. The refined location of the CIE in the Albas-Le Clot section is discussed because two carbon isotope excursions are potentially recorded in the upper "Sparnacien des Corbières", here recognized as mainly Thanetian in age.

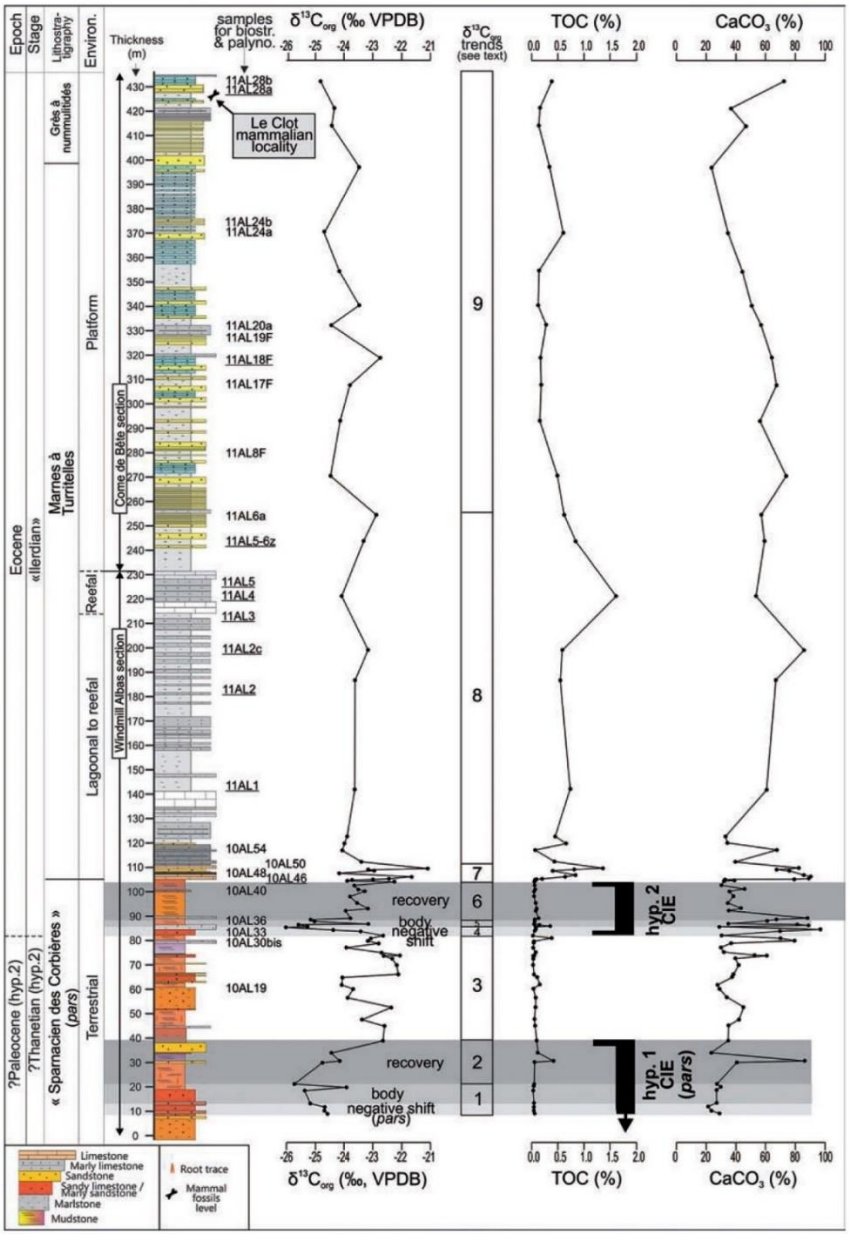

Figure 19. δ13Corg (‰ VPDB). TOC and CaCO3 contents of the Albas-Le Clot section (Corbières). Environ.= environment; biostr.= biostratigraphy; palyno.= palynofacies. Underlined samples= samples for benthic foraminifera study. Note that the two hypotheses related to the CIE are mentioned and further discussed in the text.

A paper describing these results is published in *Newsletters on Stratigraphy* (Yans et al., 2014).

4.1.6. Reference carbon isotopes on organics of the late Danian / early Selandian, to provide isotopic framework for chemostratigraphic correlations.

The Global Boundary Stratotype Section and Point for the base of the Selandian Stage is defined in the Zumaia section (Spain) at an abrupt change in lithology (base of Itzurun Formation), which coincides with the onset of a negative carbonate carbon isotope shift. However, this lithological change is not always very well expressed in other sections. In order to document the stratigraphic position of the Danian/Selandian boundary (DSB) on a more global scale, we have investigated three sections across the DSB, the Zumaia reference section (GSSP), the Loubieng section (auxiliary DSB reference section, France, Figure 20) and the Sidi Nasseur section (Tunisia). The Danian/Selandian boundary interval is subdivided and correlated throughout low latitudes, from the Altlantic Bay of Biscay to the Southern Tethys, on the basis of seven calcareous nannofossil and planktonic foraminiferal events (E-events).

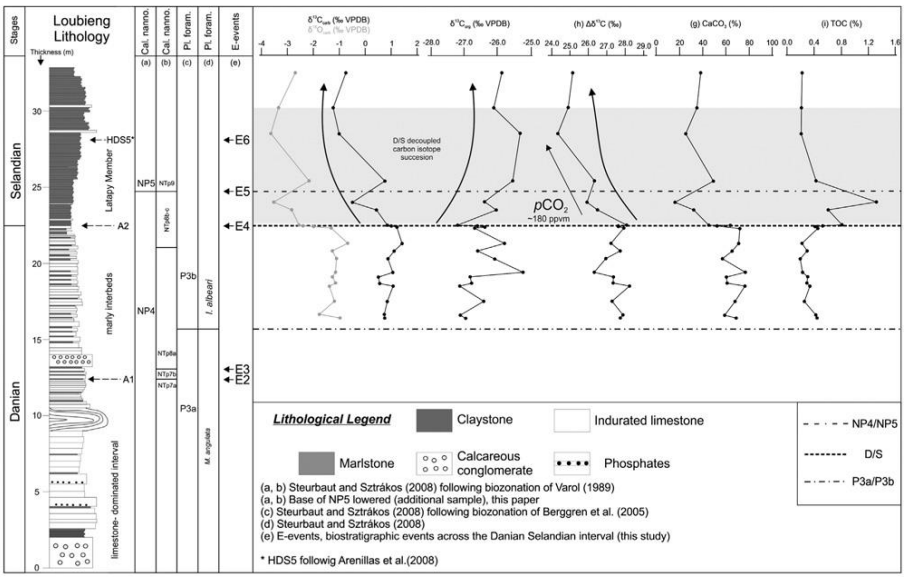

Figure 20. High-resolution geochemistry, carbon isotope, oxygen isotope, $\delta^{13}C$ and biostratigraphy across the Danian–Selandian boundary in the Loubieng section.

The base of the Selandian is proved to coincide with the end of the Braarudosphaera acme, which correlates with the lowest consistent occurrence (LCsO) of *Lithoptychius* aff*. bitectus* (=*Fasciculithus janii* sensu Steurbaut and Sztrákos, 2008) (event E4), but which is slightly posterior to the second radiation of the fasciculiths, up to now considered to represent the primary correlation tool of the DSB. A short-term $^{13}C_{org}$ negative excursion, associated with an increase in pCO_2 is recorded at the very base of the Selandian. It is interpreted as a short period of global warming (hyperthermal), the duration of which is estimated at ~30 kyr. It is followed in all the three studied sections by a long-term decoupled carbon isotope event, marked by increasing $^{13}C_{org}$ and decreasing $^{13}C_{carb}$ values. It may reflect a period of climatic cooling of a few 100 kyr, interpreted as a possible precursor of the global cooling event, marking the late Paleocene in the North Atlantic realm.

This study is published in *Palaeogeography, Palaeoclimatology, Palaeoecology* (Storme et al., 2014).

4.1.7. New fossils suggest the mammalian order Perissodactyla originated in India

Perissodactyla is an order of ungulate mammals that includes the extant hippomorphs (equoids) and ceratomorphs (tapiroids and rhinocerotoids) and their extinct relatives, and other extinct groups (chalicotherioids, “isectolophids,” and brontotherioids). It was during the PETM, that perissodactyls first appeared across the Laurasian continents. Since perissodactyls appeared almost simultaneously in Europe, Asia and North America, the place of their origin has long been disputed and numerous authors have tentatively reconstructed the biogeographic history of the earliest perissodactyls from North America, Central America, Africa, India, or Asia. Cambaytheres are recently discovered early Eocene placental mammals from the Indo–Pakistan region. They have been assigned to either Perissodactyla (the clade including horses, tapirs and rhinos, which is a member of the superorder Laurasiatheria) or Anthracobunidae, an obscure family that has been variously considered artiodactyls or perissodactyls, but most recently placed at the base of Proboscidea or of Tethytheria (superorder Afrotheria). We reported new dental, cranial and postcranial fossils of Cambaytherium, from the Cambay Shale Formation, Gujarat, India (c. 54.5 Myr ago). These fossils demonstrate that cambaytheres occupy a pivotal position as the sister taxon of Perissodactyla, thereby providing insight on the phylogenetic and biogeographic origin of Perissodactyla (Figure 21).

The presence of the sister group of perissodactyls in western India near or before the time of collision suggests that Perissodactyla may have originated on the Indian Plate during its final drift toward Asia.

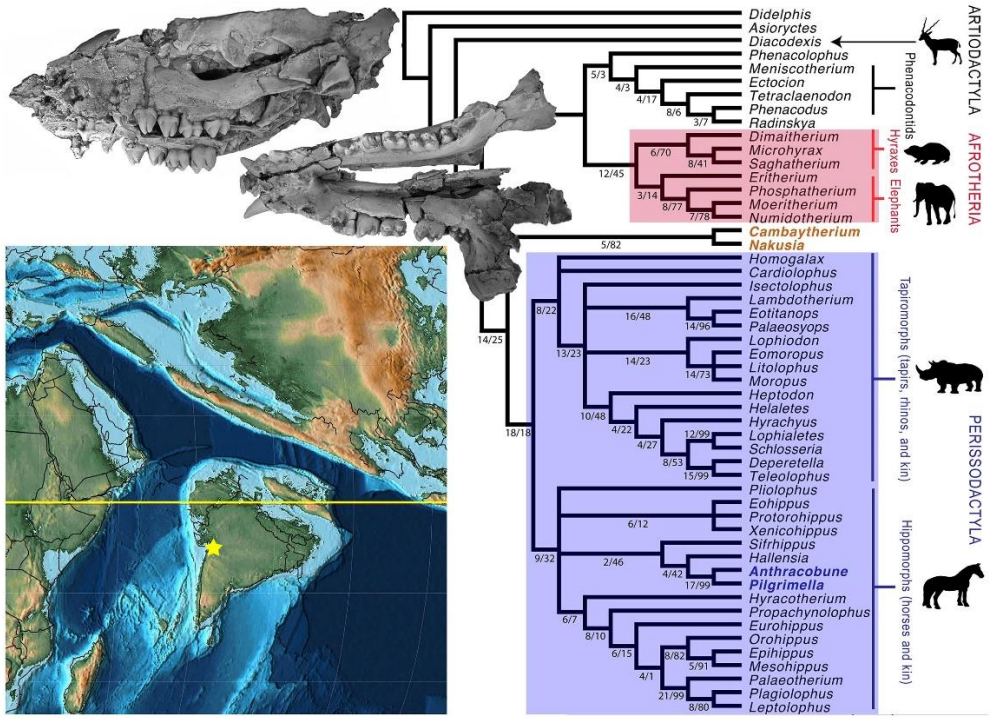

Figure 21. *Cambaytherium thewissi* and the phylogenetic and biogeographic origin of Perissodactyla

This discovery is published in *Nature Communications* (Rose et al., 2014) and well covered by the international press.

4.1.8. New late Paleocene crocodiliform remains from Berru, France, and the origin of the alligatoroid *Diplocynodon*

The fossil record of the extinct alligatoroid crocodilian *Diplocynodon*, is very abundant but limited to Europe. However, when and how *Diplocynodon* dispersed to Europe is still unresolved. Crocodilian remains from the late Palaeocene continental locality of Mont de Berru (Marne, France) offer the opportunity to reassess the taxonomic identity of the oldest diplocynodontid from Europe. Owing to significant morphological differences from previously described species of *Diplocynodon*, a new species, *Diplocynodon remensis*, has been erected in this article (Figure 22).

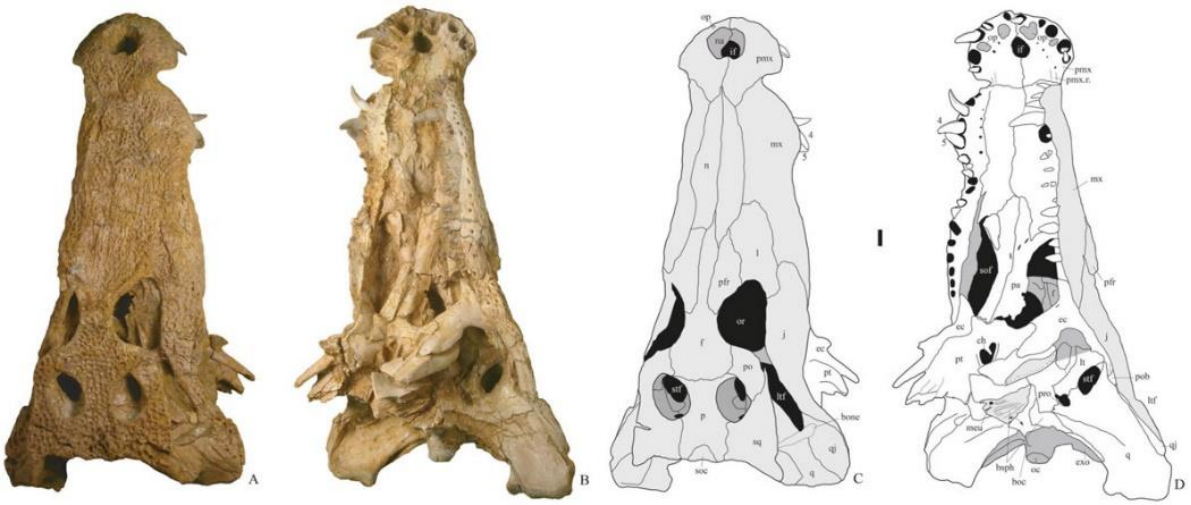

Figure 22. Photographs and line drawings of the skull of *Diplocynodon remensis* from the late Paleocene of Mont de Berru; A, C, dorsal view; B, D, ventral view.

Its inclusion in a phylogenetic framework for Eusuchia leads to its positioning as a derived member of diplocynodontids. Diplocynodontidae are viewed as a basal alligatoroid taxon, and, because morphological affinities with the Late Cretaceous−early Eocene North American genus Borealosuchus were mentioned in earlier studies, a comparison amongst *D. remensis, Leidyosuchus,* and *Borealosuchus* is presented. Although *D. remensis* is the geologically oldest diplocynodontid, according to our results, it is not the phylogenetically most primitive. Other morphological discrepancies are highlighted, indicating that the topology recovered here is only tentative. From a biogeographical point of view, the appearance of *Diplocynodon* in Europe prior to the Palaeocene/Eocene boundary indicates that it did not disperse with North American taxa that reached Europe around the time of the PETM. Therefore, a pre-PETM dispersal from North America at the same times as other vertebrates with clear North American affinities also occurring in the Paleocene of Europe cannot be excluded.

A manuscript detailing this study is published in *Zoological Journal of the Linnean Society* (Martin et al., 2014).

4.1.9. New postcranial bones of the earliest Eocene primate *Teilhardina belgica*

Teilhardina belgica is the oldest primate from Europe – it dispersed probably from Asia during the Mammal Dispersal Event. This earliest fossil primate has often been hypothesized as a

basal tarsiiform on the basis of its primitive dental formula with four premolars and a simplified molar cusp pattern. Until recently, little was known concerning its postcranial anatomy with the exception of its well-known tarsals. In this paper we describe additional postcranial elements for *Teilhardina belgica* and compare these to other tarsiiforms and to primitive adapiforms (Figure 23). The forelimb of *T. belgica* indicates an arboreal primate with prominent forearm musculature, good elbow rotational mobility and a horizontal, rather than a vertical body posture. The lateral hand positions imply grasps adaptive for relatively large diameter supports given its small body size. The hand is long with very long fingers, especially the middle phalanges. The hindlimb indicates foot inversion capabilities, frequent leaping, arboreal quadrupedalism, climbing, and grasping. The long and well-muscled hallux can be coupled with long lateral phalanges to reconstruct a foot with long grasping digits.

Our phyletic analysis indicates that we can identify several postcranial characteristics shared in common for stem primates as well as note several derived postcranial characters for Tarsiiformes.

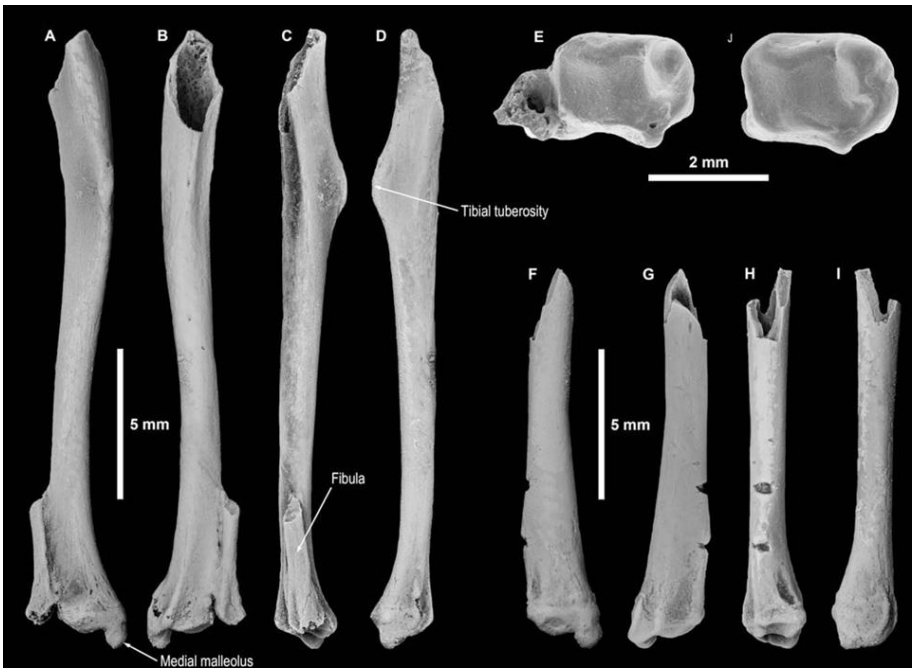

Figure 23. Tibiae. A–E, right tibia; A, anterior view; B, posterior view, C, lateral view; D, medial view; E, distal view. F–J, right tibia; F, anterior view; G, posterior view; lateral view; I, medial view; J, distal view.

This research is published in *American Journal of Physical Anthropology* (Gebo et al., 2015).

4.1.10. The earliest record of the endemic African frog family Ptychadenidae from the Oligocene Nsungwe Formation of Tanzania

The Ranoidea is a cosmopolitan radiation of frogs comprising 19 families and more than 2400 extant species (nearly 40% of all anurans). Studies using time-calibrated molecular phylogenies suggest a Cretaceous origin for the Ranoidea, but the Mesozoic and early Cenozoic fossil record of this diverse clade remains poor. Although many fossils have been attributed to the Ranoidea, typically few diagnostic characteristics are provided to assign fossils to specific taxa within the clade. The Ranoidea is thought to have initially diversified in

Africa, but the African fossil record of anurans in the Mesozoic and Paleogene is generally poor, with the Afro-Arabian record limited primarily to pipoid frogs or taxonomically enigmatic fossils.

These fossils constitute the earliest record of the endemic African ranoid frog family *Ptychadenidae* from the late Oligocene Nsungwe Formation in the Rukwa Rift Basin of southwestern Tanzania. Paleogene anuran fossils are typically rare, but they constitute approximately 13% of materials collected from localities in the Nsungwe Formation. Radiometrically dated at ≈ 25 Ma, Nsungwe Formation localities preserve a diverse vertebrate fauna and a number of novel invertebrate taxa. Nsungwe Formation anuran fossils include vertebrae preserving a unique sacral morphology that provides the earliest record of the Ptychadenidae (Figure 24), the earliest definitive record of any family within the diverse ranoid clade Natatanura, and the first late Oligocene record of anurans from Africa below the equator.

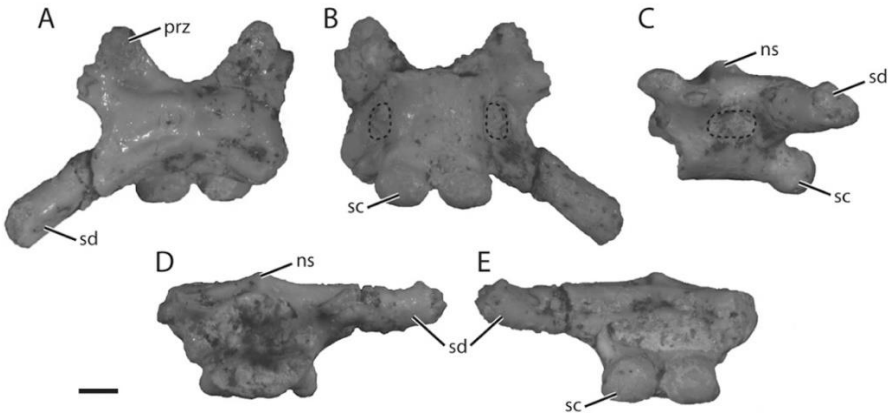

Figure 24. A block-like partial anuran (Ptychadenidae indet.) composite sacral element; A, dorsal view; B, ventral view; C, left lateral view; D, anterior view; E, posterior view.

A paper describing this endemic African frog is published in *Journal of Vertebrate Paleontology* (Blackburn et al., 2015).

4.1.11. New dental elements of the oldest proviverrine mammal from the early Eocene of Southern France support possible African origin of the subfamily

The Paleocene-Eocene Thermal Maximum (PETM), c. 56 Myr ago, is correlated with the first occurrences of modern mammals in Europe (primates, artiodactyls, perissodactyls, carnivoraforms). The carnivorous hyaenodonts are also involved in this faunal event (usually termed Mammal Dispersal Event, MDE). In order to reconstruct the appearance of this group in Europe we studied specimens of hyaenodont mammals from two early Eocene localities of Southern France: Fournes (Minervois) and Fordones (Corbières). Some of these specimens were previously described as cf. *Hyracolestes* sp. (Cimolesta, Sarcodontidae), a taxon only known from Asia, but new arguments allow their referring to the small proviverrine hyaenodont *Parvagula palulae* which was previously only recorded in Palette (Provence).

This new material shows that, by the beginning of the early Eocene, proviverrines already displayed their typical combination of dental features. The comparison between the earliest European proviverrines and sinopines (a mostly North American radiation) supports the divergence of the two subfamilies by this time – a separation that could have taken place in Europe. Moreover, the early proviverrines are morphologically similar to the African hyaenodont *Tinerhodon* (late Paleocene). Consequently, we hypothesized that the history of the European proviverrines is likely rooted in Africa (Figure 25).

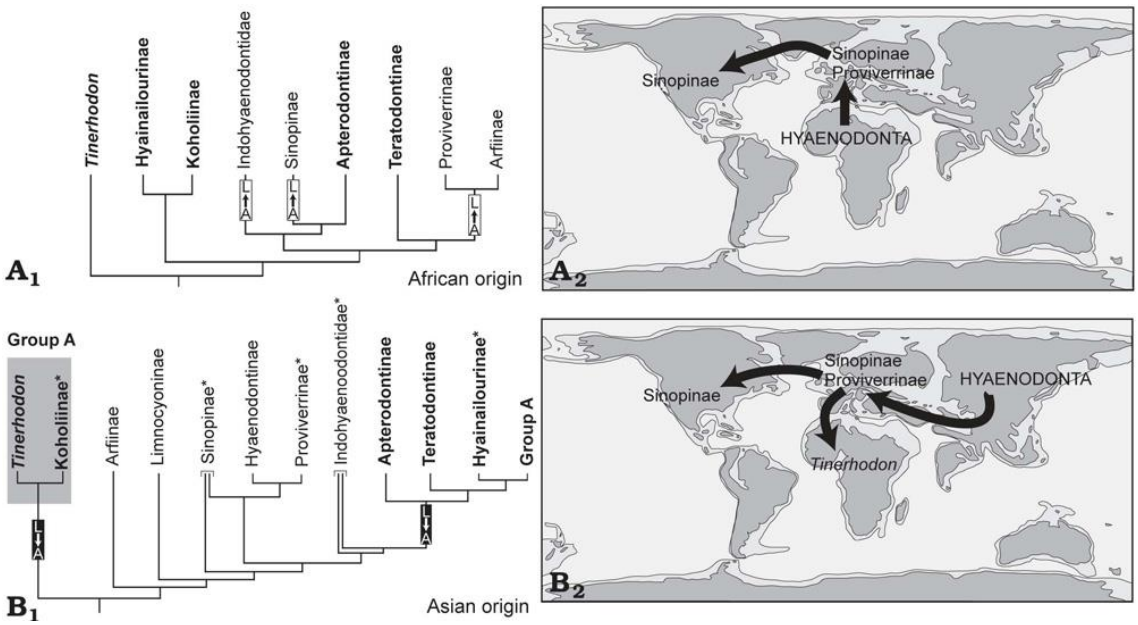

Figure 25. Comparison of phylogenetic trees and of the three hypotheses of hyaenodont origin and dispersals with focus on the Sinopinae and Proviverrinae. A. African origin with subsequent dispersals of the Sinopinae and Proviverrinae into Europe, and of the Sinopinae from Europe to North America. B. Asian origin with subsequent dispersals of Sinopinae and Proviverrinae into Europe, and of *Tinerhodon* from Europe to Africa.

A paper describing the new specimens and presenting these paleogeographic scenarios is recently published in *Acta Palaeontologica Polonica* (Solé et al., 2015).

4.1.12. First cranial and postcranial elements of *Indohyaenodon*, the oldest hyaenodont from India and their implications for ecology, phylogeny, and biogeography of hyaenodont mammals

The reconstruction of the biogeographic history of the earliest hyaenodonts have been importantly affected by the discovery of fossils in the early Eocene of India. We recently reported new remains of the hyaenodont *Indohyaenodon raoi* from the Vastan Lignite Mine in Gujarat, western India, including the first known rostrum, upper dentition, and postcrania, substantially expanding our knowledge of the species and providing insights into its functional morphology and relationships (Figure 26). Craniodental morphology indeed suggests that *I. raoi* had a broad diet, including non-vertebrate material as well as flesh of a diversity of prey species. Postcranial morphology is broadly similar to that of other early hyaenodonts and suggests a scansorial locomotor repertoire.

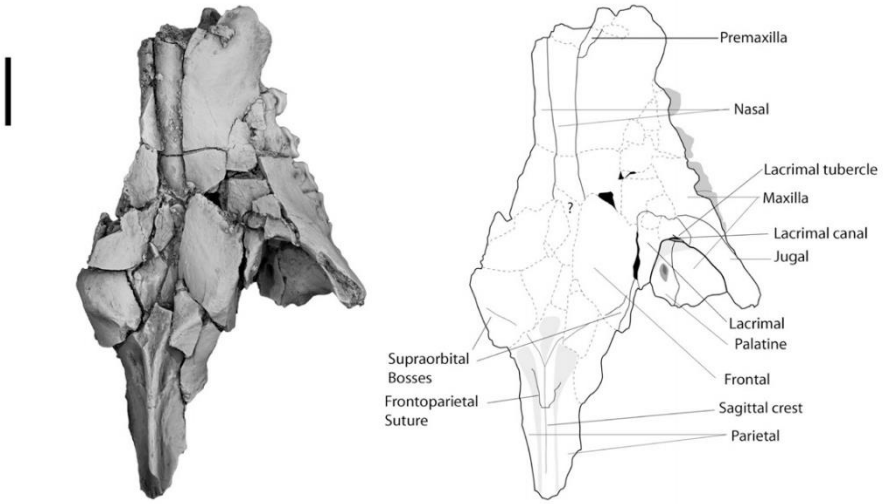

Figure 26. Skull of *Indohyaenodon raoi*. Photographs (left) and interpretive drawings (right) of the partial skull with complete right P2–M3, C and P1 alveoli, and left P1; dorsal view.

Dental morphology indicates that *I. raoi* is closely related to other South Asian hyaenodonts. We also presented the most comprehensive phylogenetic analysis of Hyaenodonta to date, which corroborates this relationship but finds South Asian hyaenodonts to be the stem of a group that includes most African hyaenodonts. This and other higher-level relationships within Hyaenodonta are, however, weakly supported, and substantially different alternative hypotheses of relationships are not significantly less parsimonious, reflecting strong character conflict. Factors contributing to this conflict include the isolation of hyaenodont faunas on different continents during much of the Eocene, canalization and simplification of carnivorous dentitions, and a lack of non-dental material for critical hyaenodont groups. The new phylogeny is finally consistent with either an African or an Asian origin for the group.

This study is published in *Journal of Vertebrate Paleontology* (Rana et al., 2015).

4.1.13. A new large hyainailourine from the Bartonian of Europe the evolution and ecology of massive hyaenodonts

The hyainailourines are very large and hypercarnivorous hyaenodonts that originated in Africa. The appearance of this subfamily in Europe is poorly understood but is interesting because it traduces a profound modification of the European ecosystems. In this paper, we presented described a new large-sized species – *Kerberos langebadreae* – from the Bartonian locality of Montespieu (Tarn, France). The specimens consist of a skull, two hemimandibles and several hind limb elements (fibula, astragalus, calcaneum, metatarsals, and phalanges). Size estimates suggest *K. langebadreae* may have weighed up to 140 kg, revealing this species as the largest carnivorous mammal in Europe at that time (Figure 27). Moreover, the distinctive skull morphology of the new species reflects a powerful bite force; this hyaenodont was indeed possibly a scavenger. The postcranial elements, which are rarely associated with hyainailourine specimens, indicate an animal capable of a plantigrade stance and adapted for terrestrial locomotion. Based on the first phylogenetic analysis of hyainailourines, we demonstrated that *Hemipsalodon*, a North American taxon, is a hyainailourine and is closely related to European *Paroxyaena*.

We reconstructed the biogeographic history of the Hyainailourinae: the first migration to Laurasia occurred during the Bartonian that likely included the ancestors of *Kerberos*, *Paroxyaena* and *Hemipsalodon*, which further dispersed into North America at this time. These migrants have no ecological equivalent in Europe and North America during these intervals and likely did not conflict with the endemic hyaenodonts.

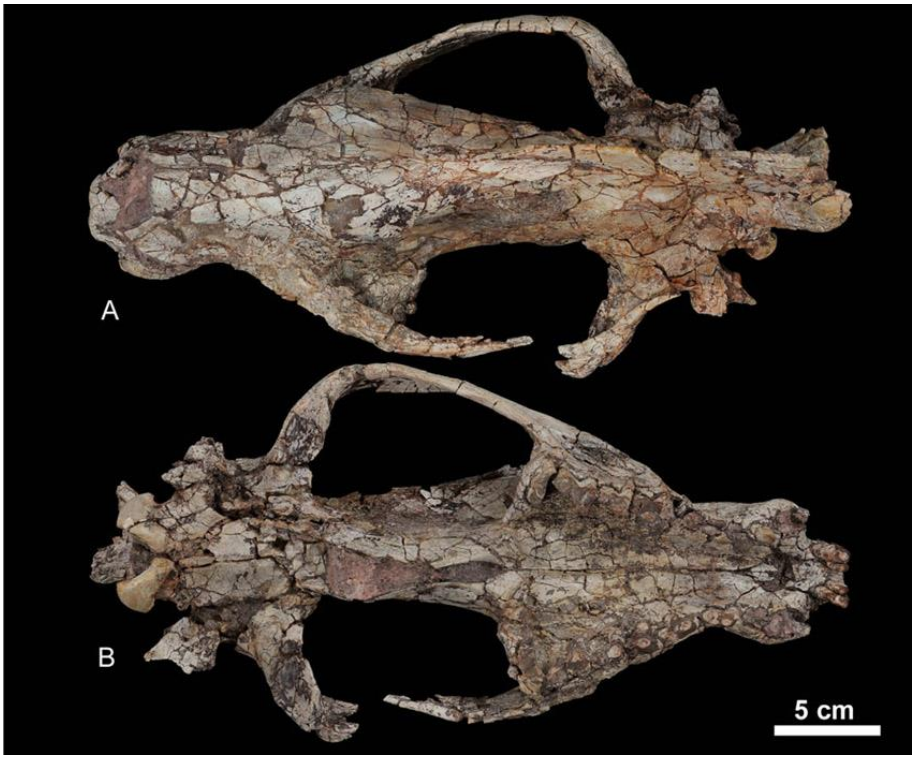

Figure 27. Skull of *Kerberos langebadreae* gen. et sp. nov. A, dorsal view; B, ventral view.

The discovery of *K. langebadreae* shows that large body size appears early in the evolution of hyainailourine but the ancestors of these large hyaenodonts are still unknown in Africa, where this subfamily originated.

A long paper describing this impressive mammal is published in *PLOS ONE* (Solé et al., 2015).

4.1.14. The oldest tapiroid from India and its implication for the paleobiogeographic origin of perissodactyls

The presence of cambaytheres, the sister group of perissodactyls, in western India near or before the time of collision with Asia suggests that Perissodactyla may have originated on the Indian Plate during its final drift towards Asia. With this study, we reinforced this hypothesis by reporting two teeth of the first early Eocene tapiromorph Perissodactyla from the Cambay Shale Formation of Vastan Lignite Mine, which we allocate to a new genus and species, *Vastanolophus holbrooki*. The latter presents plesiomorphic characters typical of the paraphyletic “Isectolophidae,” such as small size and weak lophodonty. However, the weaker hypoconulid and low paralophid, higher cusps, lower cristid obliqua, and the lingual opening of the talonid are found in Helaletidae, the most primitive tapiroid family.

Consequently, *V. holbrooki* may be the oldest and the most primitive tapiroid, suggesting that at least tapiroid perissodactyls originated on India. Its discovery is moreover interesting for reconstructing the early history (i.e. dispersals) of the perissodactyls (Figure 28).

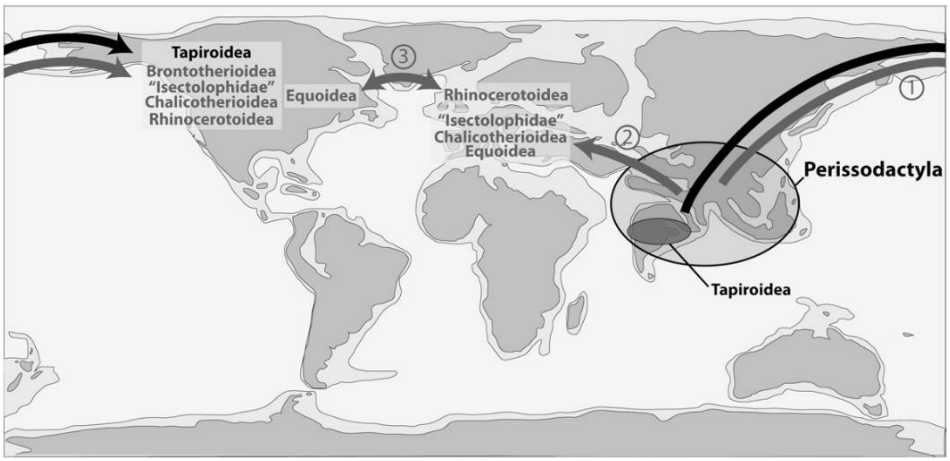

Figure 28. Schematic map showing the geographic dispersal of the early perissodactyls. 1: dispersal via the Bering land bridge; 2: dispersal via land connections across the Turgai Strait and/or along the Tethysian shore; 3: dispersal via the Greenland land bridge.

This study is published in the specialized journal *Palaeovertebrata* (Smith et al., 2015).

4.1.15. New fossil of hyaenodonts from the Ypresian and Lutetian of France and the evolution of the Proviverrinae in Europe

The Proviverrinae are the most numerous and diversified carnivorous mammals from the Eocene of Europe. This hyaenodont subfamily, which is endemic to Europe, is recorded from the Ypresian of France to the Priabonian of Switzerland. The proviverrines from the Ypresian (MP7–MP10) and Lutetian (MP11–MP14) are represented mainly by species recorded in the northern and central parts of Europe (Paris Basin, Belgian Basin, Germany, Switzerland). In this article, we described fossils from southern France: Saint-Papoul (MP8+9; Aude) and Aigues-Vives 2 (?MP13; Aude). One dentary with secant molars from Saint-Papoul represents a new genus and species, *Preregidens langebadrae.*

One of the three dentaries discovered in Aigues-Vives 2 belongs to the hypercarnivorous *Oxyaenoides schlosseri*, previously represented by only two isolated lower molars. This dentary appears to be the most derived of the proviverrines. The two other dentaries from Aigues-Vives 2 support the presence of *Eurotherium theriodis* and provide the first possible evidence of sexual dimorphism in a proviverrine species. A phylogenetic analysis of the proviverrines has been performed to resolve the phylogenetic position of the three taxa. This identifies a close relationship between the new genus (*Preregidens*) and *Oxyaenoides*. The new fossils allow the age of Saint-Papoul and Aigues-Vives 2 to be refined: the first locality is considered to be close in age to Avenay (Ypresian; France), while the second one seems to be close to Egerkingen γ (Lutetian; Switzerland), which is considered to be possibly close in age to the MP13 reference level. Finally, the presence of *O. schlosseri* and *E. theriodis* in the southern part of France supports the hypothesis that the mammals involved in the first intra-Eocene turnover migrated northwards (Figure 29).

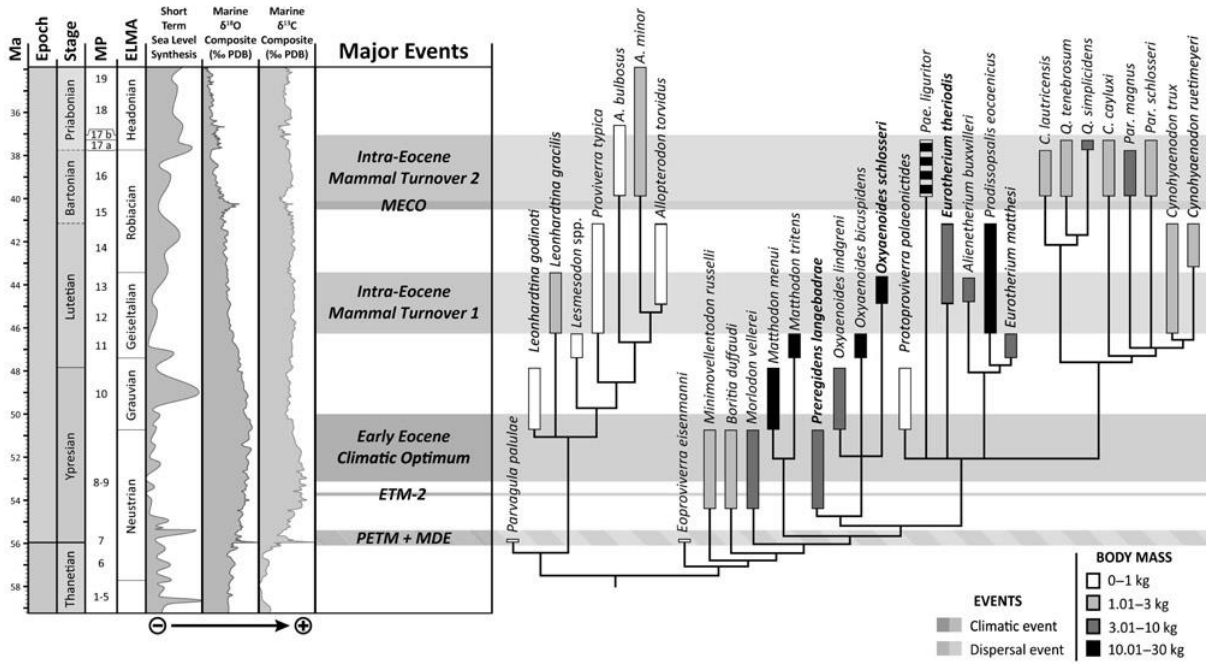

Figure 29. Phylogeny of the Proviverrinae calibrated with stratigraphy and with eustatic and climatic variations.

This study is published in *Palaeontology* (Solé et al., 2015).

4.1.16. The age of supergene manganese deposits in Katanga and its implications for the Neogene evolution of the African Great Lakes Region

Supergene manganese ores record weathering episodes affecting exposed paleosurfaces; hence, they help identifying and characterizing plateau areas, along the margins of major river basins. Supergene Mn ore deposits commonly contain K-rich Mn oxides with tunnel structure, such as cryptomelane, which are suitable for radiometric dating using the 39Ar–40Ar method. In Africa, Mn deposits have been dated by this method for localities in western and southern parts of the continent, whereas only some preliminary data are available for Central Africa. Extending these initial results, we obtained new 39Ar–40Ar ages for Mn oxide samples of the Kisenge deposit, in southwestern Katanga, Democratic Republic of the Congo.

The samples represent supergene Mn oxide deposits that formed at the expense of primary Paleoproterozoic rhodochrosite-dominated carbonate ores (Figure 30).

Main phases of Mn oxide formation are dated at c. 10.5 Ma, 3.6 Myr and 2.6 Myr for a core that crosses a mineralized interval. The latter shows a decrease in age with increasing depth, recording downward penetration of a weathering front. Surface samples of the Kisenge deposits also record a ≥c.19.2 Myr phase, as well as c. 15.7 Ma, 14.2 Myr and 13.6 Myr phases. The obtained ages correspond to distinct periods of paleosurface development and stability during the Mio-Pliocene in Katanga. Because Katanga is a key area bordered to the North by the Congo Basin and to the East by the East African Rift System, these ages also provide constraints for the geodynamic evolution of the entire region. For the Mio-Pliocene, the Kisenge deposits record ages that are not systematically found elsewhere in Africa, although

the 10.5–11 Myr event corresponds to a roughly simultaneous event in the Kalahari Manganese Field, South Africa.

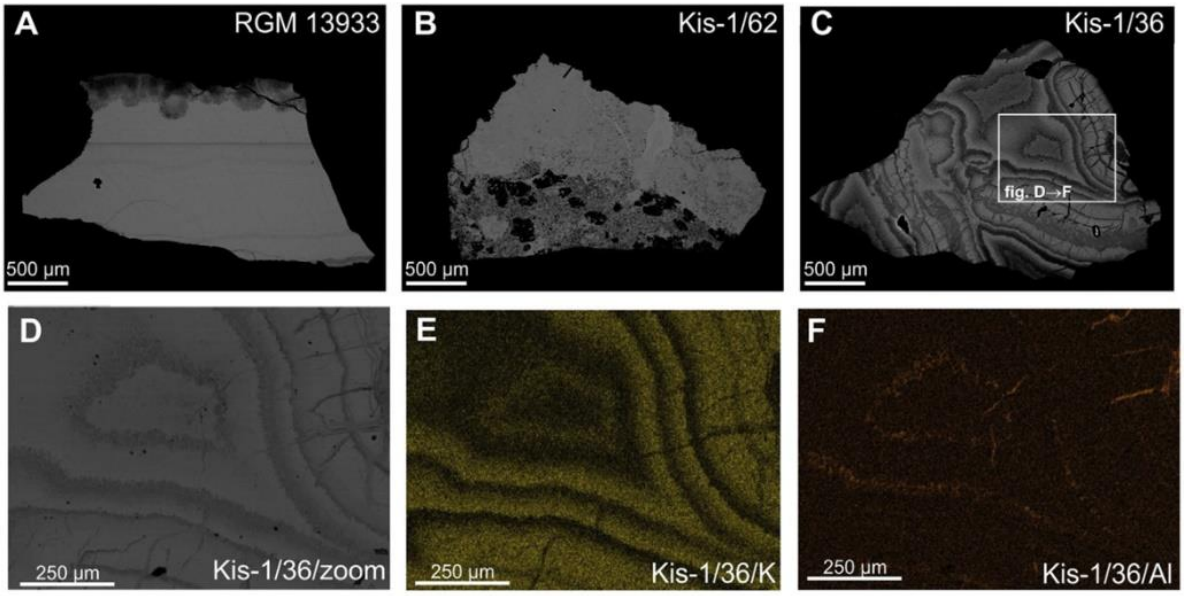

Figure 30. Backscattered electron images and SEM-EDS maps for selected samples.

A paper describing these results is published in *Ore Geology Reviews* (De Putter et al., 2015).

4.1.17. New carnivoraforms from the latest Paleocene of Europe and their bearing on the origin and radiation of Carnivoraformes (Carnivoramorpha, Mammalia)

We recently reported the discovery of the earliest European carnivoraforms, based on two new taxa from the latest Paleocene of France and Romania. A new species of *Vassacyon*, *V. prieuri*, from the locality of Rivecourt (MP6b; Oise, France) is described based on a dentary fragment and isolated teeth. This species displays several primitive features compared with species of *Vassacyon* known from the early Eocene of North America and Europe. A second Paleocene carnivoraform, cf. *Gracilocyon* sp., is described based on fragmentary specimens from the locality of Jibou (MP6b; Transylvania, Romania). Carnivoraformes were previously unknown in Europe before the Eocene, and *Vassacyon prieuri* and cf. *Gracilocyon* sp. are their oldest records in Europe. These discoveries favor the hypothesis of a dispersal of these two genera from Europe to North America during the Paleocene-Eocene Thermal Maximum. *Vassacyon prieuri* and cf. *Gracilocyon* sp. strengthen support for the level MP6b and its correlation with the Clarkforkian (Figure 31). The geographic origin of the Carnivoraformes remains unknown. However, based on the observed biochronological and geographic distributions of the carnivoraforms, we infer a possible Asian origin for this group. In this scenario, *Gracilocyon* and *Vassacyon* dispersed to Europe during the Clarkforkian MP6b time, probably together with rodent taxa, whereas *Uintacyon* dispersed from Asia to North America shortly after rodents and tillodonts.

A paper describing the new specimens and presenting this paleogeographic scenario is published in the worldwide distributed *Journal of Vertebrate Paleontology* (Solé et al., 2016).

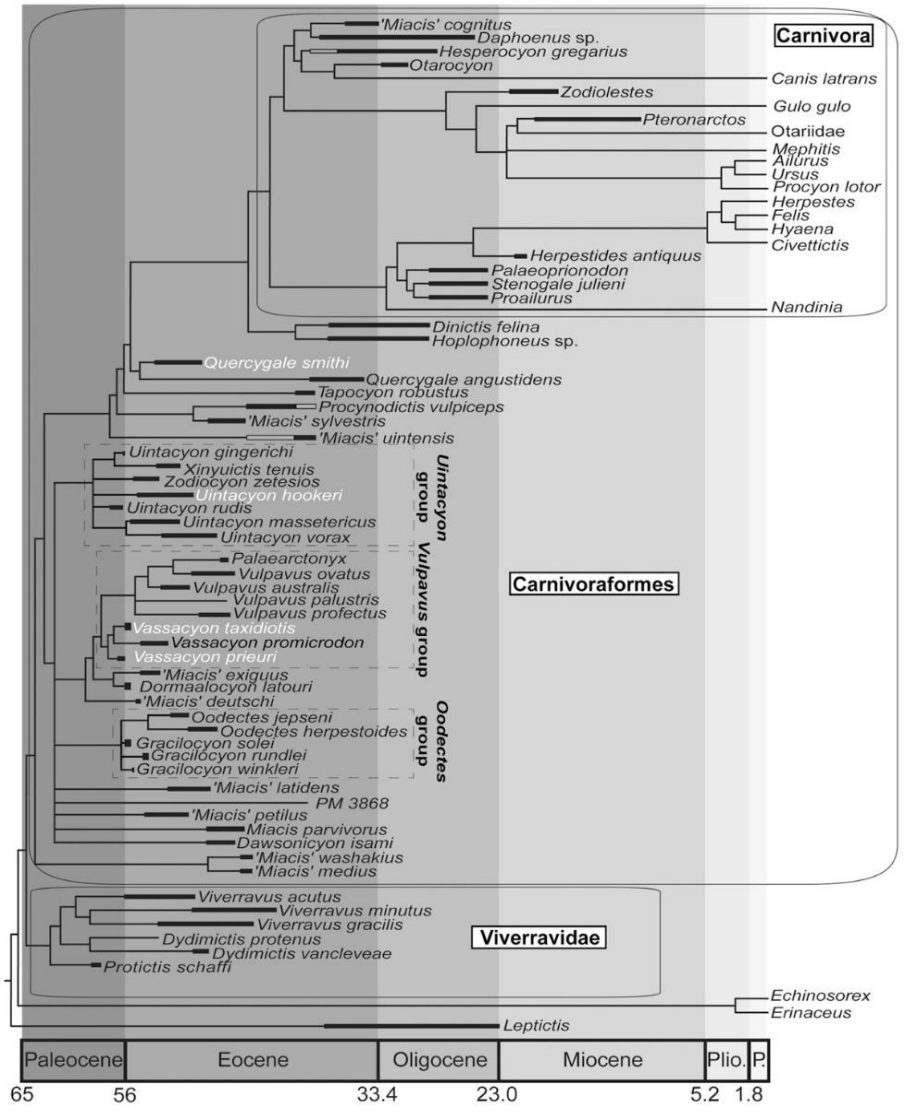

Figure 32. Phylogeny of the earliest carnivoraforms showing temporal distributions. Time ranges indicated by thicker lines. Unfilled lines indicate uncertainty as to occurrence. Plio. = Pliocene, P. = Pleistocene.

4.1.18. New early Eocene vertebrate assemblage from western India reveals a mixed fauna of European and Gondwana affinities

The Ypresian Cambay Shale Formation at Vastan and Mangrol lignite mines in Gujarat, western India, has yielded a rich vertebrate fauna with numerous taxa of European affinities. Here we report a new, approximately contemporary vertebrate assemblage from two fossiliferous layers in the nearby mine of Tadkeshwar. These layers have yielded a similar mammal fauna (perissodactyl-like cambaytheriid *Cambaytherium thewissi*, the adapoid primates Marcgodinotius indicus, and the hyaenodontid *Indohyaenodon raoi*). The presence of these species in both Vastan and Tadkeshwar mines and at different levels suggests that the deposits between the two major lignite seams represent a single land mammal age. There is also a new, smaller species of *Cambaytherium*, and a new genus and species of esthonychid tillodont. This fauna also contains the first large early Eocene vertebrates from India, including an unidentified *Coryphodon*-like pantodont, a dyrosaurid crocodyliform and a new giant madtsoiid snake. Among the Tadkeshwar vertebrates several taxa are of Gondwana affinities,

such as *Pelomedusoides* turtles, dyrosaurids, and large madtsoiids, attesting that the early Eocene was a crucial period in India during which Laurasian taxa of European affinities co-existed with taxa from Gondwana before the India-Asia collision.

Our results suggest that terrestrial faunas could have dispersed to or from Europe during episodes of contact between the Indian subcontinent and different island blocks along the northern margin of the Neotethys, such as the Kohistane-Ladakh island-arc system. Gondwana taxa might represent remnants of ghost lineages shared with Madagascar, which reached the Indian subcontinent during the late Cretaceous; alternatively they might have come from North Africa and passed along the southern margin of the Neotethys to reach the Indian subcontinent (Figure 33).

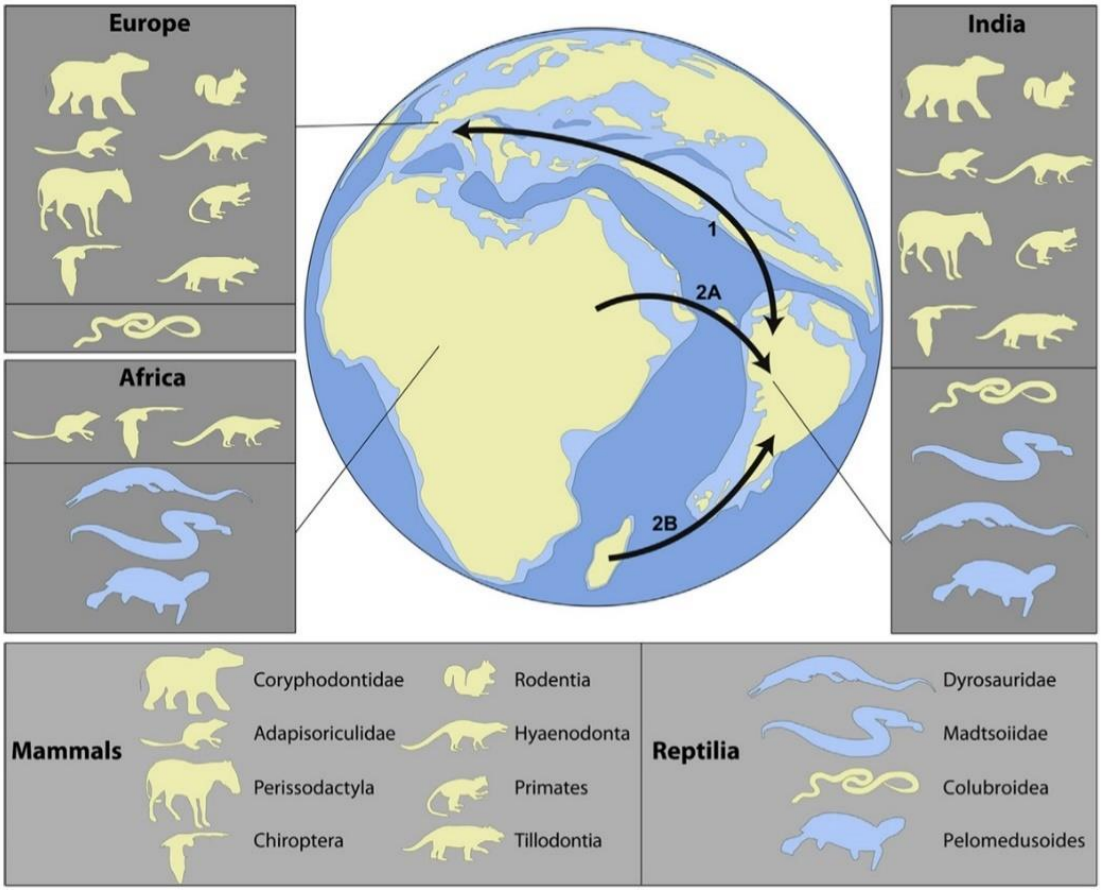

Figure 33. Schematic paleogeographic map showing the hypothetical dispersal routes of vertebrates around 54 My ago. 1, Dispersal of taxa with European affinities between the Indian subcontinent and Europe across the Neotethys via the Kohistane-Ladakh island-arc system. 2A-B, Dispersal of taxa with Gondwanan affinities to the Indian subcontinent (2A) from Africa along the southern margins of the Neotethys or (2B) from Madagascar.

This research iss published in *Geoscience Frontiers* (Smith et al., 2016).

4.1.19. New bio-chemostratigraphic dating of a unique early Eocene sequence from southern Europe results in precise mammalian biochronological tie-points

European early Eocene (Ypresian) mammalian biochronology, covering a timespan of about 8 myr, includes three distinct MP (Mammal Paleogene) reference levels MP7, MP8+9 and MP10.

These are represented in the unique succession of the Minervois (Southern France) by the localities of Fournes (close to MP7), Sainte-Eulalie (close to MP8+9) and Azillanet (close to MP10). Considering homogenous terrestrial organic matter contribution as suggested by palynofacies and Rock-Eval pyrolysis, we here demonstrate that the organic carbon isotope curve of the predominantly continental Ypresian of the Minervois closely matches the marine standard carbonate carbon isotope curve (Figure 34).

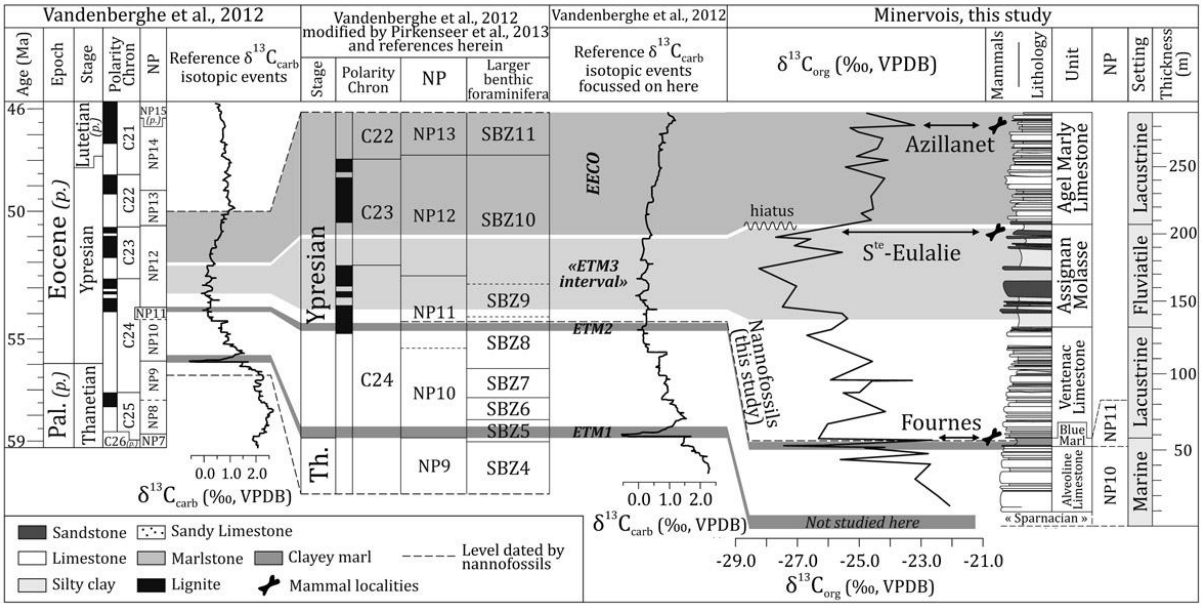

Figure 34. Correlation of the organic carbon (δ^{13}Corg) isotope curve of the Minervois with the standard marine composite bulk carbonate (δ^{13}Ccarb) isotope curve of the Ypresian and with the calcareous nannofossil and larger benthic foraminiferal zones. Black bone indicates mammalian localities; Nannofossils: biostratigraphic control (calcareous nannofossil dating); Pal. = Paleocene; p. = pars.

The here studied mammalian faunas and their supposed corresponding MP levels can thus be accurately dated and correlated on a global scale. The endemic Fournes mammal fauna, located just above the ETM 2, is assigned to mid-Biochron NP11 Calcareous Nannoplankton Zone. Accordingly, the Fournes mammal site is about 2.5 myr younger than the MP7 reference level of Dormaal (Belgium, latest Biochron NP9), about 1 myr younger than the MP7 mammalian locality of Le Clot in the Corbières (Southern France, late Biochron NP10 or early Biochron NP11) and very close to the Wasatchian Wa-5 mammalian biozone of Wyoming. A mid-Biochron NP12 age is inferred for the endemic Sainte-Eulalie fauna because of its position at the very top of (or just above) the isotopically negative “ETM3 interval”, whereas the Azillanet fauna, recorded at the top of a $\delta^{13}C_{carborg}$org positive trend above the “ETM3 interval”, ranges from late Biochron NP12 to early Biochron NP13. Our results indicate that the shortterm hyperthermals ETM2 and ETM3 did not affect the endemic character of the mammalian faunas in Southern and Northern Europe during the MP7 to MP8+9 interval. The end of this mammalian endemism likely occurred during the early phases of the EECO (Early Eocene Climatic Optimum) in early late Biochron NP12.

This analysis is published in *Newsletters on Stratigraphy* (Noiret et al., 2016).

4.1.20. Anatomy and variability of *Cuvierichelys parisiensis*, a geoemydid turtle that crosses the Eocene-Oligocene boundary in Belgium

Abundant material of turtles from the early Oligocene site of Boutersem-TGV (Boutersem, Belgium) is presented here (Figure 35). No information on the turtles found there was previously available. All the turtle specimens presented here are attributable to a single freshwater taxon that is identified as a member of Geoemydidae, Cuvierichelys. It is the first representative of the '*Palaeochelys* s. l.–*Mauremys*' group recognized in the Belgian Paleogene record. This material, which documents all the elements of both the carapace and the plastron of the taxon, cannot be attributed to the only species of the genus *Cuvierichelys* so far identified in the Oligocene, the Spanish form *Cuvierichelys iberica*. Rather, the taxon from Boutersem is recognized as *Cuvierichelys parisiensis*. Thus, both the paleobiogeographic and the biostratigraphic distributions of *Cuvierichelys parisiensis* are extended, its presence being confirmed for the first time outside the French Eocene record. The validity of some European forms is refuted, and several characters previously proposed as different between *Cuvierichelys iberica* and *Cuvierichelys parisiensis* are recognized as subjected to intraspecific variability.

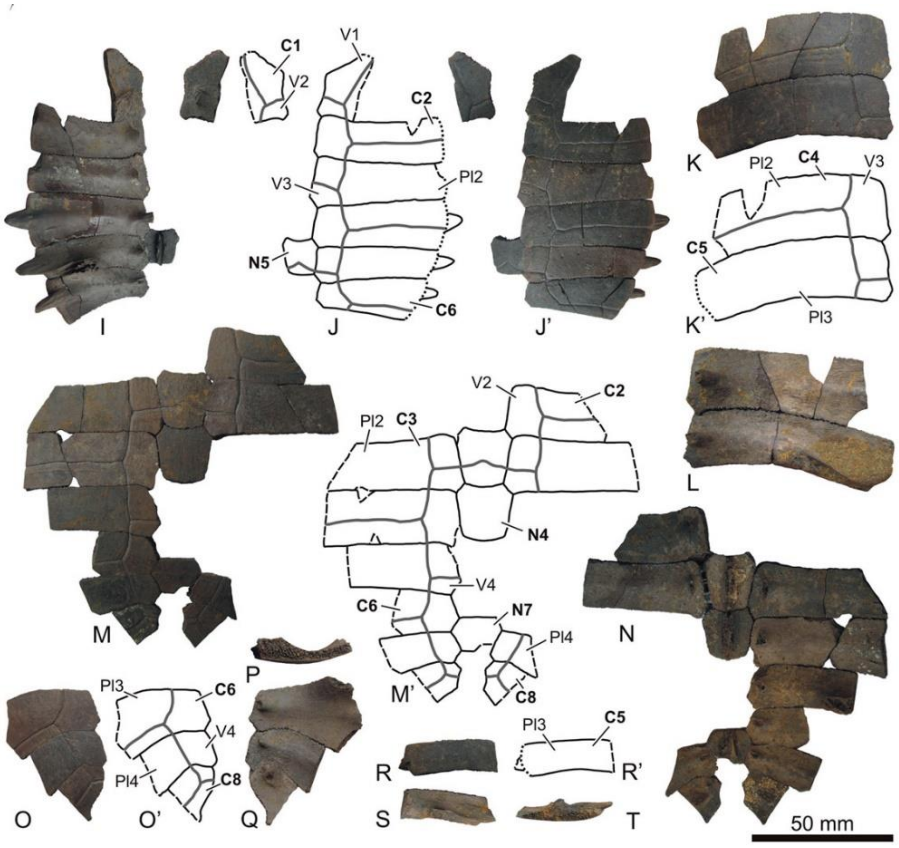

Figure 35. Specimens of *Cuvierichelys parisiensis*, from the early Oligocene of Boutersem (Belgium), corresponding to the carapace. Abbreviations for the plates (in bold): C, costal; N, neural. Abbreviations for the scutes (in normal font): Pl, pleural; V, vertebral. The solid lines represent the edges of the plates. The dashed lines indicate the broken margins. Those composed of a succession of points correspond to unsutured contacts. The scute margins are represented by thicker gray lines.

This study is published in *Journal of Iberian Geology* (Perez-Garcia et al., 2016).

4.1.21. New euprimate postcrania from the early Eocene of Gujarat, India, and the strepsirrhine-haplorhine divergence

The oldest primates of modern aspect (euprimates) appear abruptly on the Holarctic continents during a brief episode of global warming known as the Paleocene-Eocene Thermal Maximum, at the beginning of the Eocene (~56 Ma). When they first appear in the fossil record, they are already divided into two distinct clades, Adapoidea (basal members of Strepsirrhini, which includes extant lemurs, lorises, and bushbabies) and Omomyidae (basal Haplorhini, which comprises living tarsiers, monkeys, and apes). Both groups have recently been discovered in the early Eocene Cambay Shale Formation of Vastan lignite mine, Gujarat, India, where they are known mainly from teeth and jaws

Here, we describe new, exquisitely preserved limb bones of these Indian primates that reveal more primitive postcranial characteristics than have been previously documented for either clade, and differences between them are so minor that in many cases we cannot be certain to which group they belong. Nevertheless, the small distinctions observed in some elements foreshadow postcranial traits that distinguish the groups by the middle Eocene, suggesting that the Vastan primates though slightly younger than the oldest known euprimates may represent the most primitive known remnants of the divergence between the two great primate clades (Figure 36).

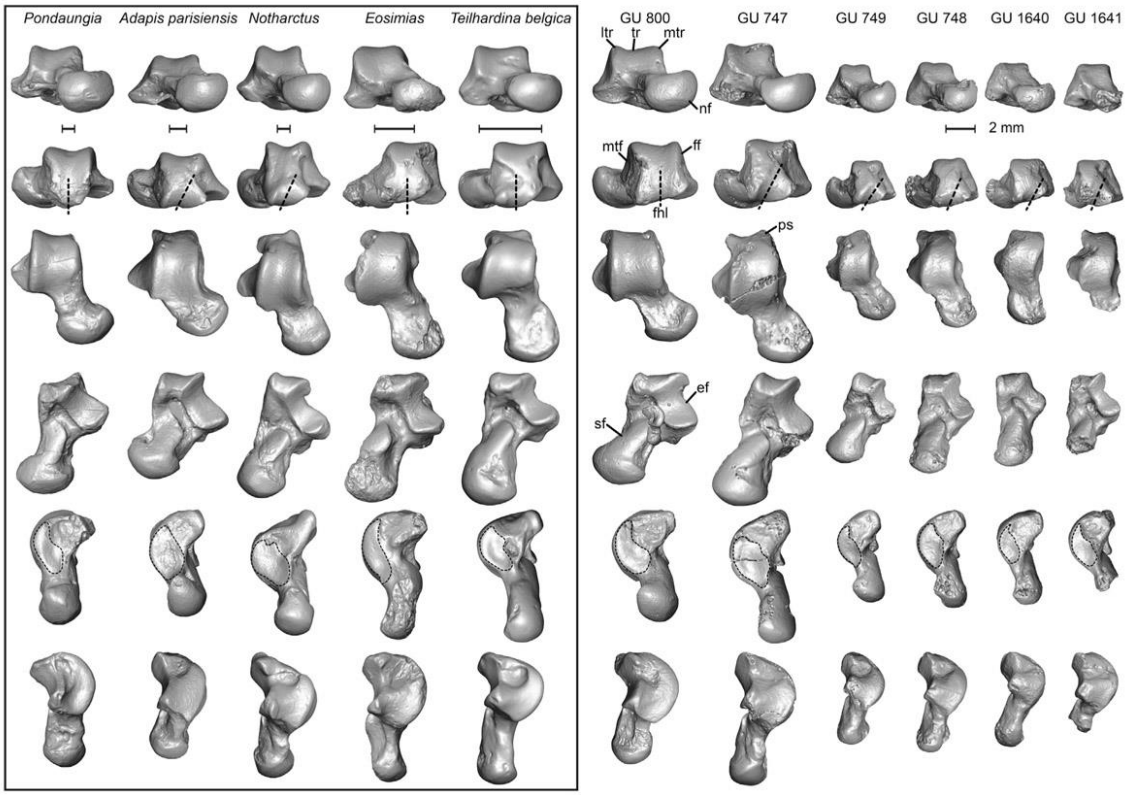

Figure 36. Euprimate astragali from Vastan Mine and comparative specimens. Box contains astragali of *Pondaungia* sp., *Adapis parisiensis*, *Notharctus* sp., *Eosimias sinensis*, and *Teilhardina belgica*.

A paper describing these postcranial bones is published in *Journal of Human Evolution* (Dunn et al., 2016).

4.1.22. New fossils of Hyaenodonta (Mammalia) from the Eocene localities of Chambi (Tunisia) and Bir el Ater (Algeria), and the evolution of the earliest African hyaenodonts

This study presents the description of new fossils from the Eocene North African localities of Chambi (Tunisia; late Ypresian or early Lutetian) and Bir el Ater (Algeria; latest Bartonian or earliest Priabonian). The specimens from Chambi allow recognizing two recently described hyainailourines: *Furodon crocheti* and *Parvavorodon gheerbranti*; these taxa were previously known from the Gour Lazib area (Algeria; late Ypresian or early Lutetian).

The new material from Tunisia includes a fragmentary dentary of *Parvavorodon* that substantially supports the hyainailourine status of this genus and represents the oldest dentary fragment presently known for a juvenile of *Hyaenodonta* in Africa. The presence of *Furodon* and *Parvavorodon* in Chambi strengthens support for the hypothesis of contemporaneity of the Eocene Gour Lazib and Chambi mammal-bearing localities. In addition, the find of a typical teratodontine fourth premolar in Chambi testifies to the presence of a small representative of this group. The fossil record in Bir el Ater is scarcer than in Chambi. However, we recognize specimens attributable to a hyainailourine and a teratodontine. The latter is referred as *Masrasector* cf. *ligabuei*, and is the oldest record for this genus. Based on faunal assemblages, we tentatively identify a modification of the hyaenodont fauna in the Maghreb after the “Early Eocene Climatic Optimum” (EECO). This faunal change might be related to the decrease of the global temperature after the EECO event. It appears contemporaneous of a drastic replacement in the composition of the mammal faunas in Africa. Finally, the end of the Eocene (Priabonian) shows an increase in the subfamilial richness amongst hyaenodonts (Figure 37).

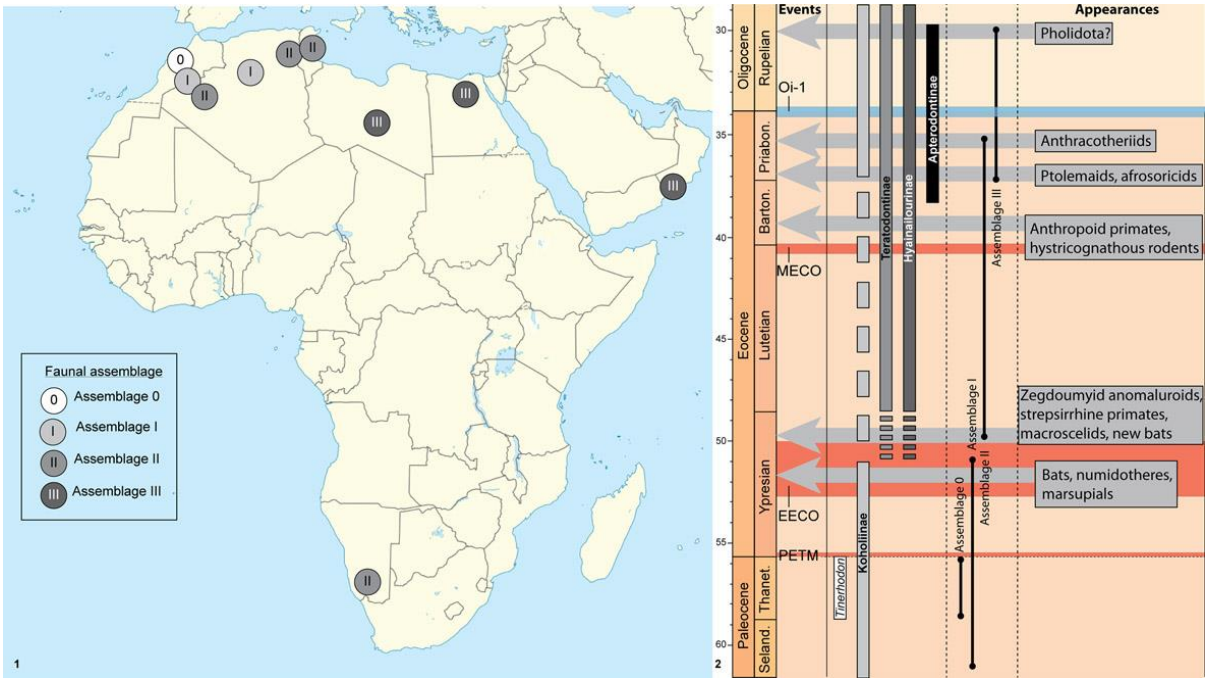

Figure 37. (1) Geographic distribution of the faunal assemblages. (2) Stratigraphic distribution of Tinerhodon and hyaenodont subfamilies in Africa during Paleocene and Eocene, and of the faunal assemblages regarding the main climatic events and mammal appearances.

This study iss published in *Palaeontologia Electronica* (Solé et al., 2016).

4.1.23. The oldest Cenozoic mammal fauna of Europe: implication of the Hainin reference fauna for mammalian evolution and dispersals during the Palaeocene

The mammal fauna of Hainin is particularly interesting in that it is the oldest of the Cenozoic of Europe. For this reason, it has been chosen as the earliest reference-level (MP1-5) of the mammalian biochronological scale for the European Palaeogene. This paper summarizes the mammal taxa discovered in the fauna, describes four new placental genera and species (*Belgoryctes thaleri, Eurolestes dupuisi, Quadratodon sigei,* and *Cingulodon magioncaldai*), and presents an analysis of the fauna as a whole (relative abundance and species richness). The assemblage is relatively small (about 400 dental specimens), characterized by a high diversity and abundance of small insectivorous species and very low abundance of 'plesiadapiforms' and 'condylarths'. By comparison with younger European Palaeocene faunas, 'condylarths' and 'plesiadapiforms' get more and more abundant and diverse through the Palaeocene but collapse at the Palaeocene-Eocene Boundary. 'Proteutherians' decline steadily, while multituberculates remain diverse, although the early Palaeocene is populated mainly by *Kogaionidae* whereas the late Palaeocene is dominated by *Neoplagiaulacidae*. The palaeoecology of Hainin is deduced from the mammal assemblage: the local environment was likely a forested area. Stratigraphically, the Hainin deposits are most likely late Danian, and biochronologically its fauna represents a partial equivalent of the North American Torrejonian Land Mammal Age. Finally, when compared to younger Palaeocene faunas of Europe, the composition of the fauna of Hainin reveals that a relatively important intercontinental dispersal of mammals occurred around the Danian-Selandian boundary, roughly corresponding to the Torrejonian-Tiffanian boundary. This dispersal is marked by the arrival in Europe of typically North American taxa such as arctocyonids, plesiadapids and neoplagiaulacid multituberculates (Figure 38). Additional exchanges of lesser magnitude probably also occurred around the Selandian-Thanetian boundary (i.e. during the Tiffanian), although the evidence is less compelling and mainly concern the plesiadapids Chiromyoides and Plesiadapis, and possibly also the mesonychid *Dissacus*.

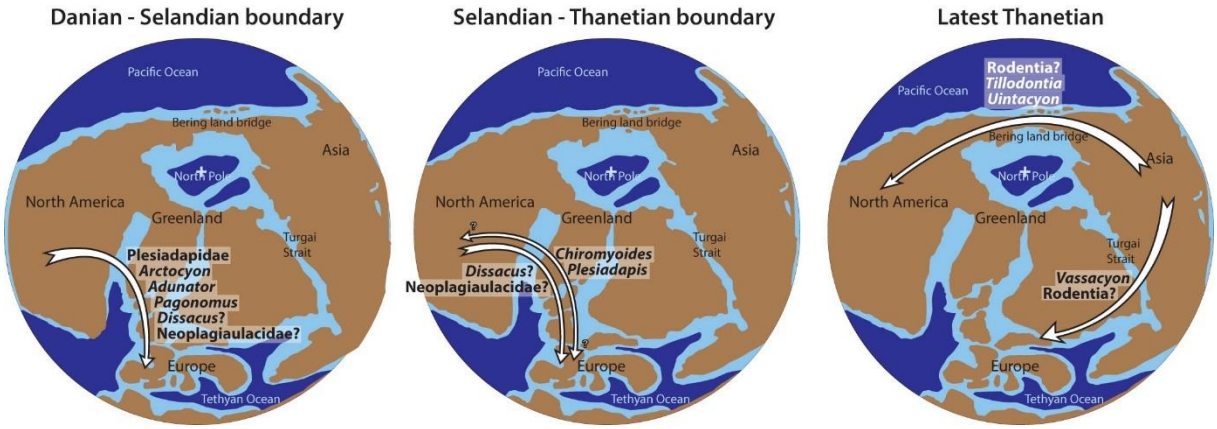

Figure 38. Hypothetical mammal dispersal involving Europe during the Palaeocene. The main dispersal episode likely happened at or around the Danian-Selandian boundary, more or less corresponding to the Torrejonian-Tiffanian boundary. Possible dispersals, involving mainly Plesiadapidae, could have occurred around the Selandian-Thanetian boundary.

This research is published in *Journal of Systematic Paleontology* (De Bast & Smith, 2017).

4.1.24. Deciduous dentition and dental eruption sequence of *Bothriogenys fraasi* (Anthracotheriidae, Artiodactyla) from the Fayum Depression, Egypt

Paleogene anthracotheres are poorly documented from Afro-Arabian localities. This is due, in large part, to the fragmentary nature of the specimens that have been described. However, sediments in the Jebel Qatrani Formation, Fayum Depression, Egypt, preserve the richest anthracothere assemblage in all of Afro-Arabia. Unlike other samples, the Fayum collection includes many complete dentitions, skulls, and partial skeletons. Based on these extensive collections, this study provides the first description of the complete deciduous dentition and dental eruption sequence for the early Oligocene anthracothere *Bothriogenys fraasi* (Figure 39). A detailed discussion concerning the pattern and timing of dental growth in *B. fraasi* is provided, and the ontogenetic sequence documented for B. fraasi is compared with those available for suoids and hippos, the two extant groups currently considered as possible sister taxa to anthracotheres. Results show that anthracotheres and suoids share a more similar dental emergence pattern, and one that may be close to the primitive condition for artiodactyls, while hippos have a very different dental eruption sequence as a consequence of their highly divergent life history pattern. As a growing body of life history research indicates that taxa in close phylogenetic proximity may be expected to share features of their dental developmental pattern, this finding suggests a useful test of competing hypotheses of a relationship between Anthracotheriidae and either Hippopotamidae or Suiformes can potentially be developed based on eruption patterns.

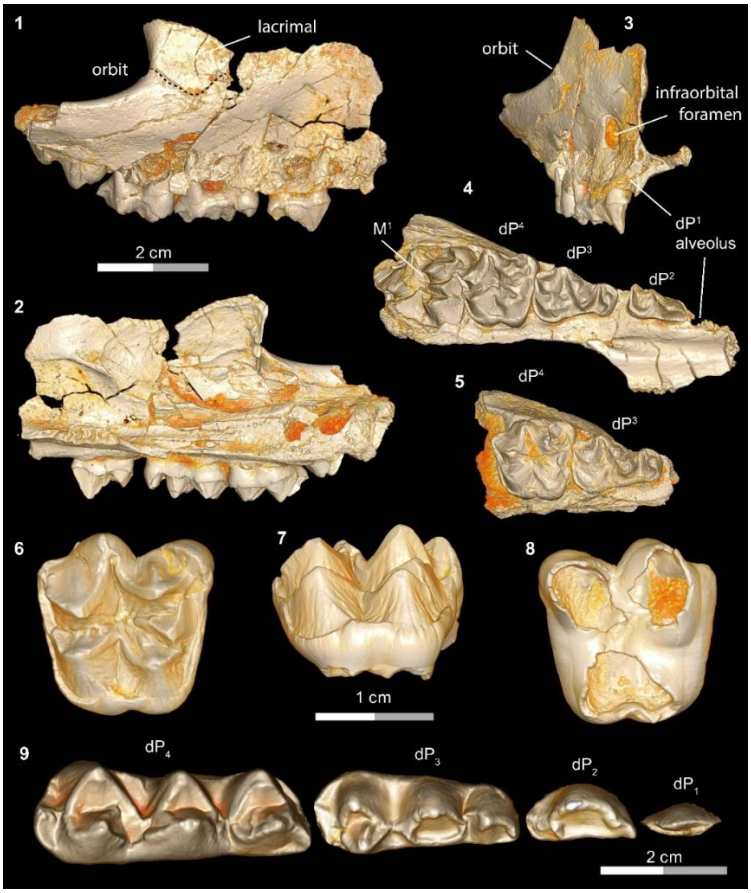

Figure 39. Micro-CT reconstruction of *Bothriogenys fraasi* : 1-4, right partial maxilla of DPC 5167 with dP2-M1, in (1) lateral, (2) medial, (3) anterior, and (4) occlusal views; 5, right partial maxilla of DPC 20439 with dP3- dP4, in occlusal view; 6-8, right dP4 of DPC 3224, in (6) occlusal, (7) lingual, (8) ventral views; 9, DPC 11416 with dP1- dP4, in occlusal view.

This research is published in *Palaeontologia Electronica* (Sallam et al., 2016).

4.1.25. Patterns of dental emergence in early anthropoid primates from the Fayum Depression, Egypt

The Fayum Depression of Egypt has produced a remarkable diversity of fossil anthropoids, and this, combined with advances in genetic analyses of living anthropoids, has led to establishment of a temporal and phylogenetic framework for anthropoids that is achieving some degree of consensus. Less well understood are the evolutionary mechanisms and selective factors behind the origin and early diversification of anthropoids. One area that has remained under explored is investigation into the life history patterns of early anthropoids, a major omission given that understanding patterns of growth and development is essential for interpreting the paleobiology of fossil species. Here we detail dental emergence sequences for five species in four families of early anthropoid primates from the Fayum, and use these data to test Schultz's Rule concerning the timing of emergence of molars versus premolars in mammals. Two important results are generated: (1) only the species *Aegyptopithecus zeuxis* had a dental eruption sequence identical to that observed among crown catarrhine primates (Figure 40); and (2) in all cases, the permanent canine was the last post-incisor dental element to fully erupt, a finding that may be significant for interpreting early anthropoid behavioral strategies.

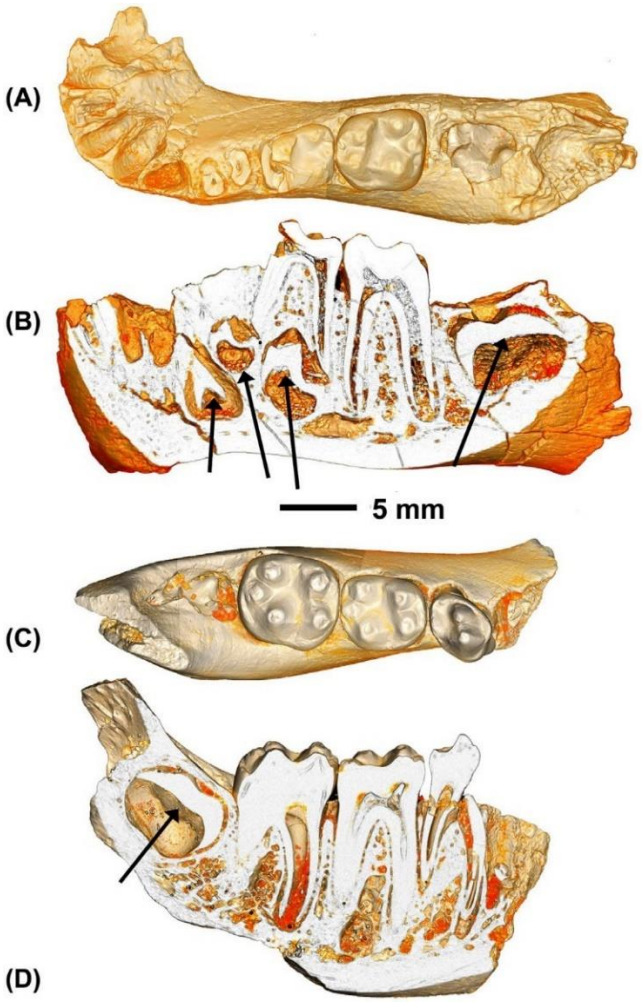

Figure 40. Juvenile *Aegyptopithecus zeuxis* from Fayum Quarry I. DPC 9866, left dentary dp4-m1fully erupted, m2 in crypt near alveolar margin, in occlusal (A) and lateral cutaway (B) views, arrows in B indicate positions of permanent canine, p3-4, and m2 embedded in the mandible. DPC 13599, right dentary p4-m2, m3 in crypt near alveolar margin, in occlusal (C) and lateral cutaway (D) views, arrow in D indicates m3 enamel cap still entombed in mandible while p4 is fully erupted.

This research is published in *Historical Biology* (Miller et al., 2017).

4.1.26. New data on the osteoglossid fishes (Teleostei, Osteoglossiformes) from the marine Danian (Paleocene) of Landana (Cabinda Enclave, Angola)

A caudal skeleton of a fish from the layer 3 of the marine Danian of Landana (Cabinda Enclave, Angola, Central Africa) is studied in details (Figure 41). Its general characters and its autogenous hypurals show that it is a primitive member of the family Osteoglossidae. The shape and the size of its two ventral hypurals strongly differ from what is known in other Osteoglossidae and even in other Osteoglossomorpha. That justifies the attribution of a peculiar generic status for this fish. Some chronological, stratigraphical and faunal criterions lead to think that it must be reported to the species *Ridewoodichthys caheni* of which the type material comes from the layers 4 and 5. The caudal skeleton of osteoglossid pattern from the layer 10 of the Danian of Landana previously ranged in *R. caheni* belongs to a younger and more evolved osteoglossid fish that has not yet received a scientific name.

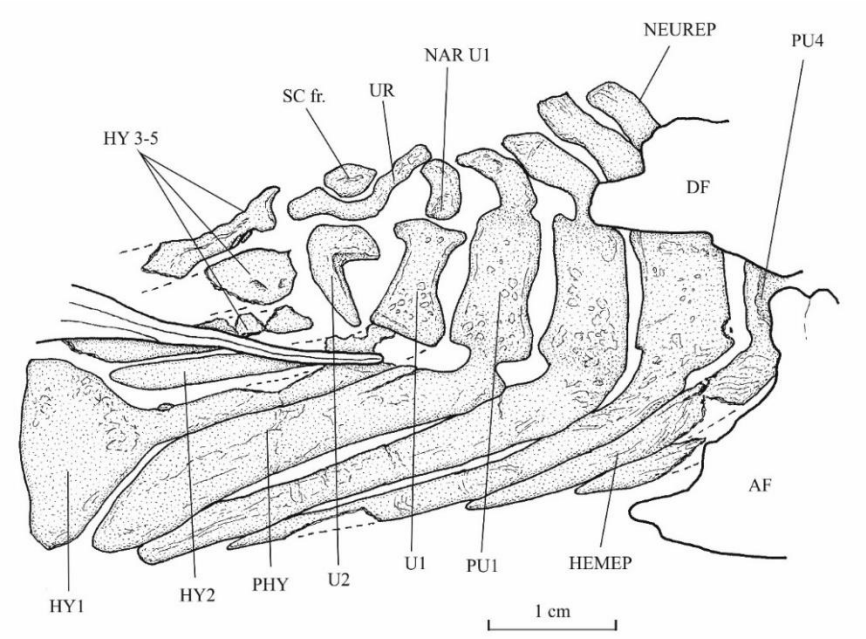

Figure 41. *Ridewoodichthys caheni*. Caudal skeleton of specimen MRAC RG 1275.

This research is published in *Geo-Eco-Trop* (Taverne, 2017).

4.1.27. The evolution of the European mesonychids (Mammal, Mesonychia), and their bearings on the European paleoecosystems and biostratigraphy

Mesonychids are an extinct group of primitive hoofed mammals, which possibly have had a scavenger-like diet similar to extant hyenas. Two years ago, the authors started a revision of the fossils of mesonychids that have been found in Europe in order to order their evolution on this landmass. The mesonychids are known from Thanetian and Ypresian localities (from MP6 to MP10 reference-levels). Only the genera *Dissacus* and *Pachyaena* were present in this continent. We can describe two new species, respectively from Palette (Ypresian, MP7) – *Dissacus rougierae* –, and from La Borie and Sézanne-Broyes (Ypresian, MP8+9) – *Dissacus raslanloubatieri* (Figure 42). The evolution of the geographic distribution of the European mesonychids is characterized by three phases: (1) the mesonychid *Dissacus* appeared in

Europe during the Thanetian (≈ 57-58 Mya), probably due to dispersal from North America; *D. europaeus* survived the PETM event (≈ 56 Mya) and possibly experienced a dwarfism; (2) the large mesonychid *Pachyaena* migrated into Europe shortly after the Paleocene-Eocene boundary (≈ 55 Mya), but it was restricted to Northwestern Europe, while *Dissacus* is recorded at this time only in southwestern Europe (Palette); and (3) *Pachyaena* rapidly disappeared from European environments, while *Dissacus* subsequently dispersed into Northwestern Europe (≈ 54-52 Myr ago). *Dissacus*, which has probably evolved endemically in Europe, reached very large size (close to 60-40 kg), especially in the Southern France and Northern Spain.

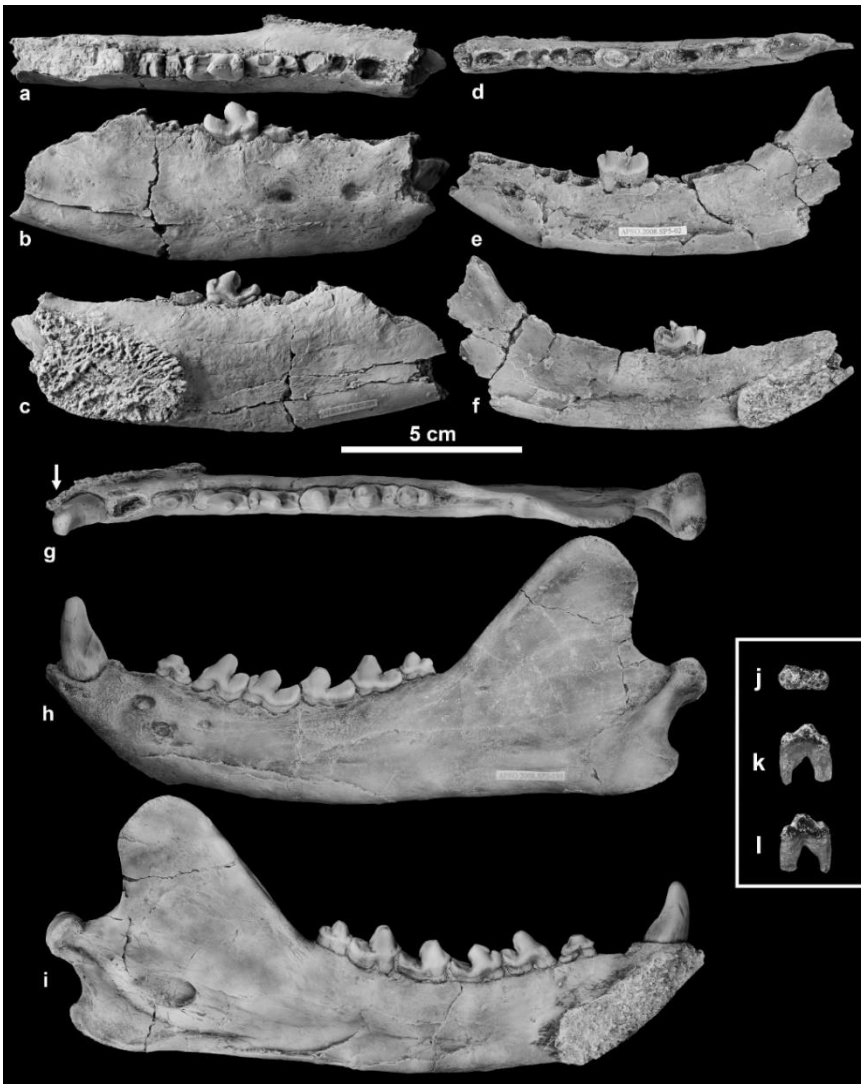

Figure 42. Specimens referred to the new species *Dissacus raslanloubatieri*.

The long presence in Europe of the mesonychids is possibly due to the few competitors in the European ecosystems. Finally; It seems that the mesonychids went through two radiative events: the first during the Paleocene, the second mostly during the early Eocene. The first one corresponds to the diversification of *Dissacus*, while the latter resulted in the appearance of the most specialized mesonychids, such as *Pachyaena* and *Mesonyx*.

This research is published in *Journal of Mammalian Evolution* (Solé et al., 2017).

4.1.28. 33 million year old *Myotis* (Chiroptera, Vespertilionidae) and the rapid global radiation of modern bats

The bat genus *Myotis* is represented by 120+ living species and 40+ extinct species and is found on every continent except Antarctica. The time of divergence of *Myotis* has been contentious as has the time and place of origin of its encompassing group the Vespertilionidae, the most diverse (450+ species) and widely distributed extant bat family. Fossil *Myotis* species are common, especially in Europe, beginning in the Miocene but earlier records are poor. Recent study of new specimens from the Belgian early Oligocene locality of Boutersem reveals the presence of a relatively large vespertilionid. Morphological comparison and phylogenetic analysis confirms that the new, large form can be confidently assigned to the genus *Myotis*, making this record the earliest known for that taxon and extending the temporal range of this extant genus to over 33 million years. This suggests that previously published molecular divergence dates for crown myotines (*Myotis*) are too young by at least 7 million years.

Additionally, examination of first fossil appearance data of 1,011 extant placental mammal genera indicates that only 13 first occurred in the middle to late Paleogene (48 to 33 million years ago) and of these, six represent bats, including Myotis. Paleogene members of both major suborders of Chiroptera (*Yangochiroptera* and *Yinpterochiroptera*) include extant genera indicating early establishment of successful and long-term adaptive strategies as bats underwent an explosive radiation near the beginning of the Early Eocene Climatic Optimum in the Old World. A second bat adaptive radiation in the New World began coincident with the Mid-Miocene Climatic Optimum (Figure 43).

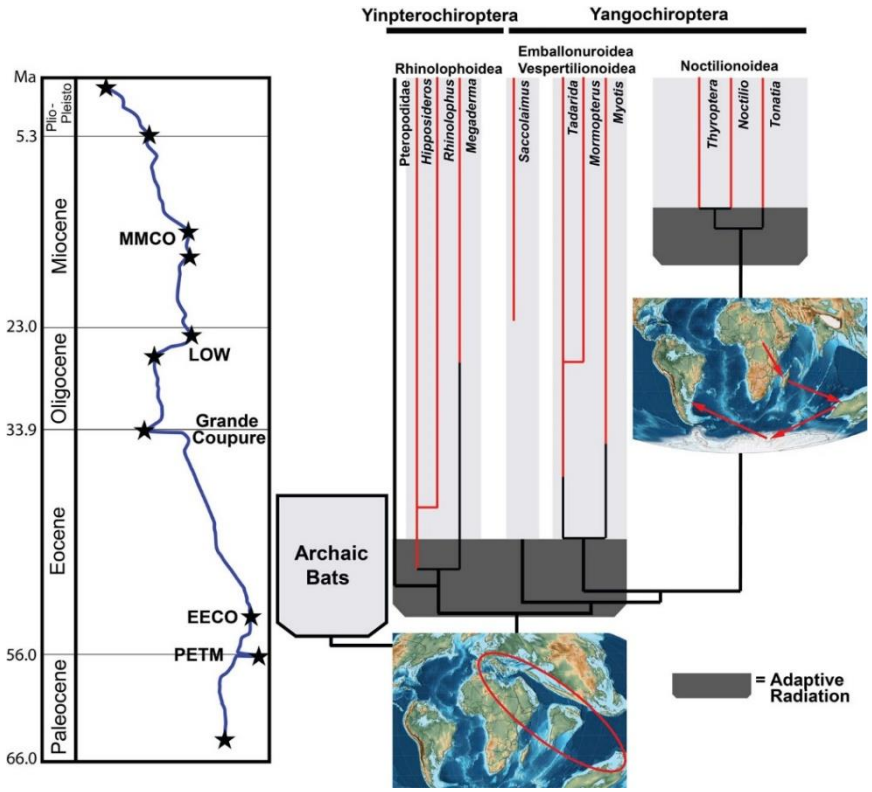

Figure 43. Proposed trajectory of bat evolutionary history.

This research is published in *PLOS ONE* (Gunnell et al., 2017).

4.1.29. Estimating body size in early primates: The case of *Archicebus* and *Teilhardina*

Obtaining accurate estimations of the body mass of fossil primates has always been a subject of interest in paleoanthropology because mass is an important determinant for so many other aspects of biology, ecology, and life history. This paper focuses on the issues involved in attempting to reconstruct the mass of two early Eocene haplorhine primates, *Teilhardina* and *Archicebus*, which pose particular problems due to their small size and temporal and phylogenetic distance from extant primates (Figure 44). In addition to a ranking of variables from more to less useful, the effect of using models of varying taxonomic and size compositions is examined. Phylogenetic correction is also applied to the primate database. Our results indicate that the choice of variable is more critical than the choice of model. The more reliable variables are the mediolateral breadth across the femoral condyles and the area of the calcaneocuboid facet of the calcaneus.

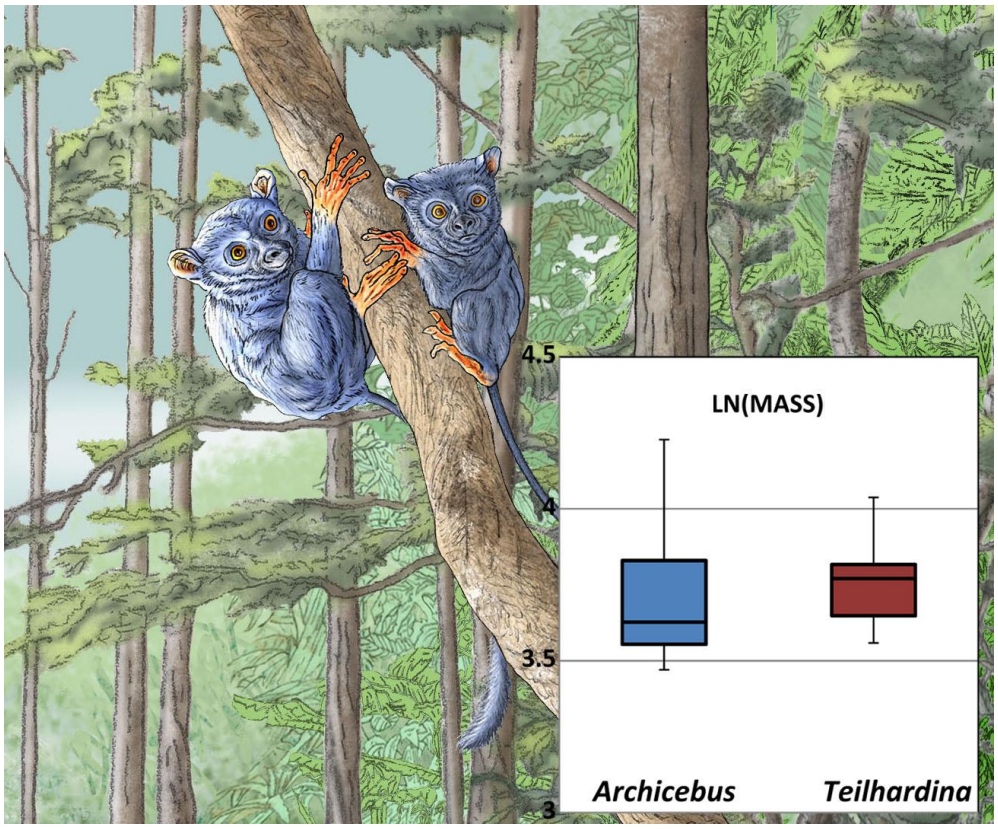

Figure 44. Body mass (in natural log) of early Eocene Chinese *Archicebus* and Belgian *Teilhardina* from conventional ordinary least squares regression models. The drawing illustrates the reconstruction of *Teilhardina* from Dormaal, Belgium (credit to Pascale Golinvaux, RBINS).

These variables suggest a body mass of 39 g (range 33-46 g) for *Archicebus* and 48 g (range 44-56 g) for *Teilhardina*. The width of the distal femur is found to be the most consistent estimator across models of various composition and techniques. The effect of phylogenetic correction is small but the choice of branch length assumption affects point estimates for the fossils. The majority of variables and models predict the body mass of *Archicebus* and *Teilhardina* to be in the range of the smaller extant mouse lemurs, as expected.

This research is published in *Journal of Human Evolution* (Dagosto et al., 2017).

4.1.30. A turtle of the African–European *Erymnochelys* group (Pleurodira, Podocnemididae) in the Belgian fossil record

An almost complete plastron, as well as several peripherals and a costal plate of a turtle from the middle Eocene of Saint-Gilles (Brussels), is presented here (Figure 45). Although this turtle specimen was donated to the Institut royal des Sciences naturelles de Belgique (Brussels, Belgium) more than a century ago, it remained undescribed. Its study allows us to recognize the second pleurodiran in the Belgian fossil record, where, until now, the Eocene *Neochelys* was the only one known. The Belgian material of *Neochelys* is known in lower Eocene (early Ypresian) levels, but the new pleurodiran specimen comes from the middle Eocene (early Lutetian, NP14 biozone, 46 to 48 Ma). It is the first partial articulate shell of a pleurodiran turtle recognized in Belgium, and the only member of this clade recognized in this country at specific level. The new specimen is a representative of the so-called *Erymnochelys* group, this lineage being known in Africa from the Upper Cretaceous to the present but in Europe only during the Eocene. It represents the first specimen of *Eocenochelus eremberti* identified outside its type locality, the French region of Saint-Germain-en-Laye (Yvelines, Île-de-France), where only one specimen was found. The plastron of the Belgian individual corresponds to the most complete for this species. Its analysis allows us not only to broaden the range of paleobiogeographical distribution of *Eocenochelus eremberti* but also to improve the knowledge about the anatomy and variability of this taxon.

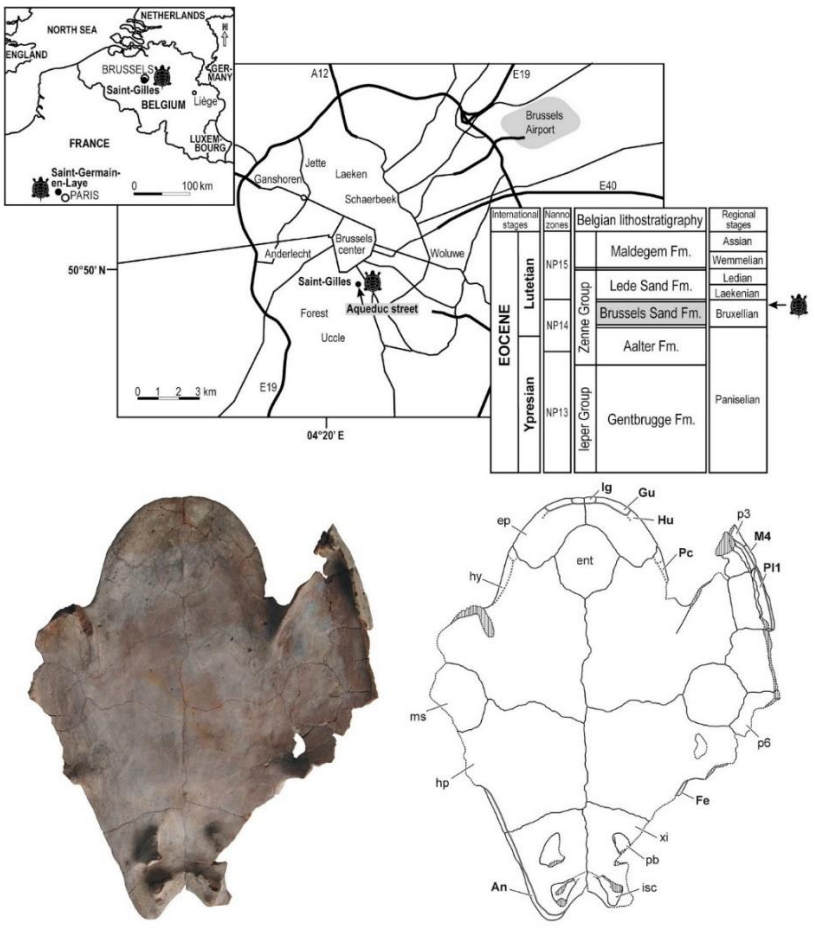

Figure 45. Location of Aqueduc Street in Saint-Gilles (Brussels municipality, Belgium) where the specimen IRSNB R356 of *Eocenochelus eremberti* was discovered (a plastron and articulated right bridge peripherals in dorsal view), in the lower Lutetian Brussels Sand Formation (middle Eocene).

This study is published in *Fossil Record* (Perez-Garcia & Smith, 2017).

4.1.31. Dispersal of the earliest European crocodyloids before the Paleocene-Eocene Thermal Maximum

Crocodyloid remains from the late Paleocene of Mont de Berru (France) hosted in the collections of the Muséum National d'Histoire Naturelle (Paris, France) and in the Institut royal des Sciences naturelles de Belgique (Brussels, Belgium) are described for the first time. This material, although fragmentary, can be clearly referred on a morphological basis to *Asiatosuchus depressifrons* (Blainville, 1855), a species previously reported from several Eocene Belgian localities thanks to abundant material including a nearly complete skeleton. The Paleocene material shares with *A. depressifrons* the number of alveoli involved in the dentary symphysis, the exclusion of the splenials from the symphysis (Figure 46), and the presence of a distinct depression on the jugal. The fossil remains from Berru represent the oldest European crocodyloid. Along with the alligatoroid *Diplocynodon remensis* Martin, Smith, de Lapparent de Broin, Escuillié and Delfino, 2014, previously reported from the same locality, the crocodyloid *A. depressifrons* indicates that these genera reached Europe before the Paleocene-Eocene Thermal Maximum. Although more complete remains from outside Europe are needed to refine phylogenetic hypotheses, according to the currently established fossil record the forerunners of diplocynodontids likely dispersed from North America, whereas those related to *Asiatosuchus* likely dispersed from Asia.

Figure 46. Right dentary of *Asiatosuchus depressifrons* (Blainville, 1855) from the late Paleocene of Berru (specimen IRSNB R358 in lateral view).

This study is published in *Historical Biology* (Delfino et al., 2017).

4.1.32. A gymnodont fish jaw with remarkable molariform teeth from the early Eocene of Gujarat, India (Teleostei, Tetraodontiformes)

The lower jaw of a gymnodont fish collected from the lower Eocene Cambay Shale Formation in Gujarat Province, western India, has fused dentaries without a beak and a remarkable series of teeth that are unique among all known fossil and living Tetraodontiformes (Figure 47). The teeth are molariform, with raised spokes radiating inward from the emarginated peripheral

edge of the crown. Tooth development is intraosseous, with new teeth developing in spongy bone before they erupt and attach to the dentary by pedicels. Although many of the 110 tooth loci in the fossil have lost their teeth, in life the teeth would have grown to fit tightly together to form a broad and continuous crushing surface. The estimated age of the Cambay Shale vertebrate fauna is ca. 54.5 Ma, making the jaw the second oldest confirmed gymnodont fossil. Preliminary comparisons with extant taxa of gymnodonts with fused dentaries (e.g., *Diodon*, *Chilomycterus*, and *Mola*) show detailed similarities in jaw structure, but further study of the dentition is needed to better understand the evolutionary position of the new fossil. We describe the new gymnodont as *Avitoplectus molaris*, gen. et sp. nov., in Avitoplectidae, fam. nov., and place the family as incertae sedis within Gymnodontes.

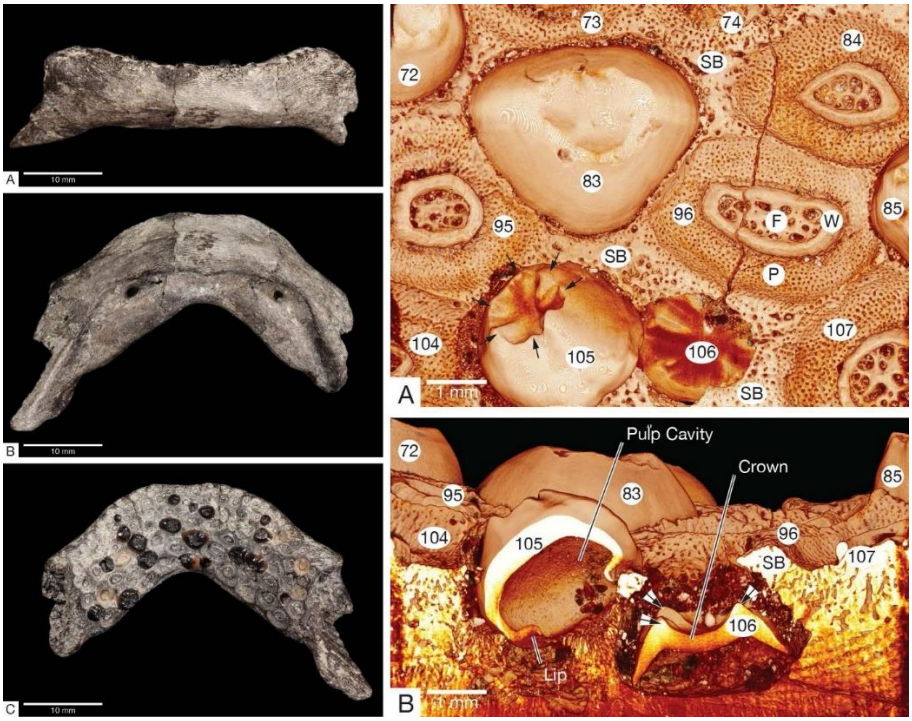

Figure 47. Left: the jaw of *Avitoplectus molaris* (WIF/A 2340) in anterior labial (A), ventral view (B), and dorsal views. Right: micro-CT reconstructions to show aspects of tooth replacement (A-B).

This study is published in *Journal of Vertebrate Paleontology* (Bemis et al., 2017).

4.1.33. First Old World record of the poorly known, swan-sized anseriform bird *Paranyroca* from the late Oligocene/early Miocene of France

A tarsometatarsus of a large anseriform bird from the late Oligocene/early Miocene of the Saint-Gérand-le-Puy area in France is assigned to the distinctive taxon *Paranyroca*, which was before only known from the early Miocene of North America (Figure 48). *Paranyroca* may be a stem group representative of Anatidae and its tarsometatarsus exhibits a peculiar character mosaic, with an Anhimidaelike hypotarsus and an Anatidae-like distal end. With regard to these features, the bone resembles the tarsometatarsus of another anseriform bird from Saint-Gérand-le-Puy, which was described as *Cygnopterus alphonsi* but has not yet been compared with *Paranyroca* in the original description. *C. alphonsi* was originally identified as a swan, but this classification has subsequently been contested and here it is proposed that the species is more closely related to *Paranyroca*.

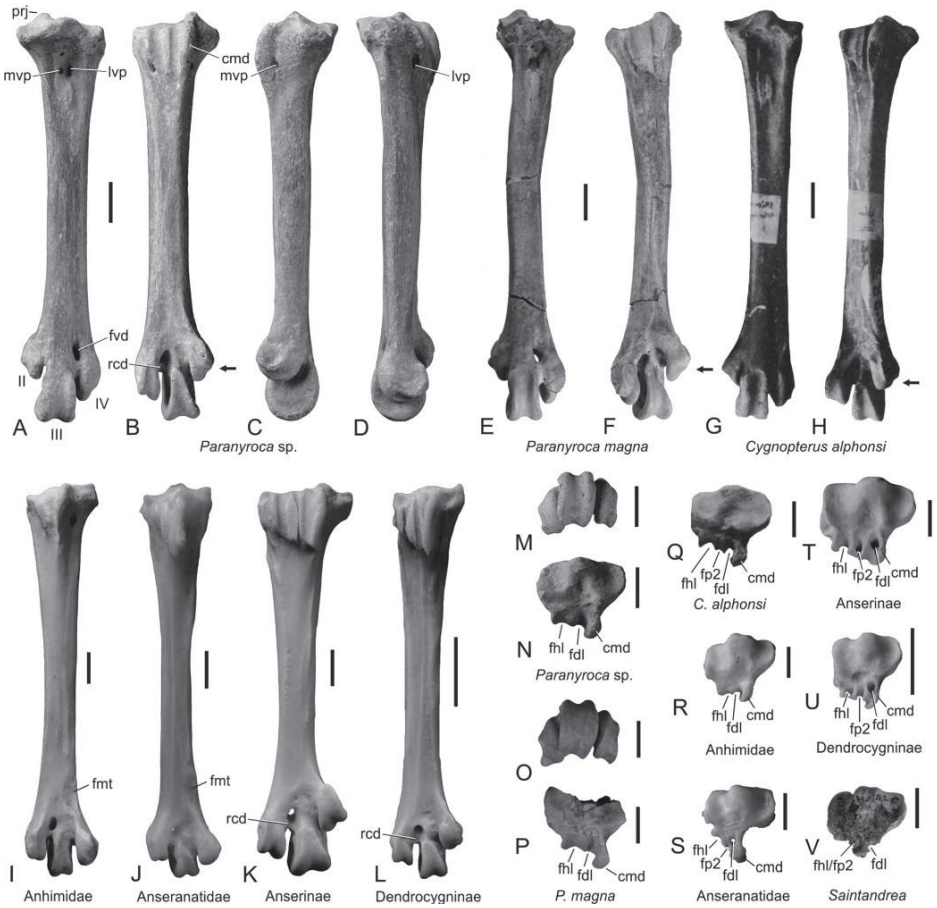

Figure 48. Tarsometatarsus of *Paranyroca* sp. from Saint-Gérand-le-Puy (PLV 1988/17-1, A-D, M-N) compared to *Paranyroca magna* from South Dakota, USA (E-F, O-P), *Cygnopterus alphonsi* (G-H, Q), *Chauna torquata* (Anhimidae, I, R), *Anseranas semipalmata* (Anseranatidae, J, S), *Cygnus olor* (Anatidae, K, T), *Dendrocygna viduata* (Anatidae, Dendrocygninae, L, U), and *Saintandrea chenoides* from the late Oligocene of France (V). Scale bars equal 10 mm.

This study is published in *Neues Jahrbuch für Geologie und Paläontologie* (Mayr & Smith, 2017).

4.1.34. A fossil heron from the early Oligocene of Belgium: the earliest temporally well-constrained record of the Ardeidae

We describe the earliest temporally well-constrained fossil that can be assigned to the Ardeidae (herons), from the lowermost Oligocene (32.0–33.0 million years ago) of Belgium. The specimen, a partial tarsometatarsus, belongs to a small species and is described as *Proardea*? *deschutteri* n. sp (Figure 49). It exhibits the characteristic tarsometatarsus morphology found in extant heron species, but a confident assignment to one of the ardeid subclades is not possible and even the assignment of the new fossil species to the crown group (the clade including the extant species) cannot be established. The fossil indicates a divergence of herons from their sister taxon by at least the earliest Oligocene, and current paleontological data suggest that herons arrived in Europe shortly after a major faunal turnover at the Eocene/Oligocene boundary. We consider that dispersal is the likely reason for the sudden appearance of herons in the earliest Oligocene of Europe but it is uncertain from where exactly this took place, with Asia and Africa being among the candidate areas.

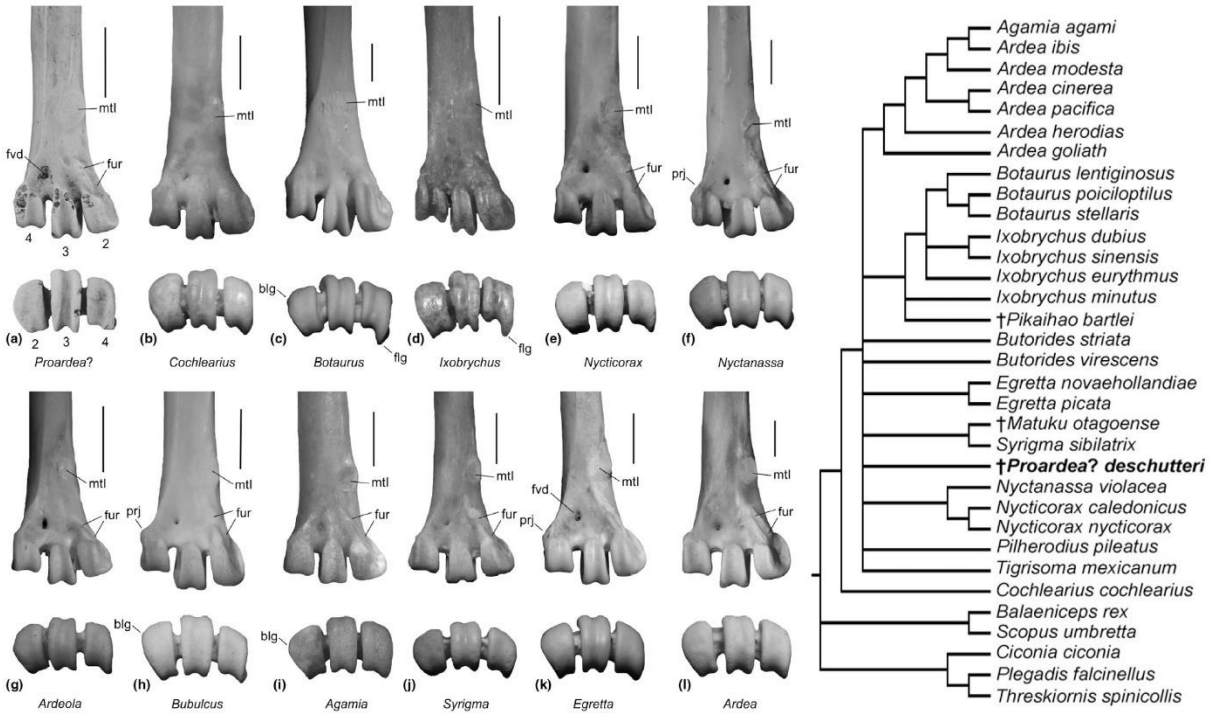

Figure 49. Distal end (plantar and distal view) of the tarsometatarsus of *Proardea*? *deschutteri* n. sp. from the earliest Oligocene of Belgium (IRSNB Av 129) in comparison with selected extant Ardeidae. Scale bars: 5 mm. Strict consensus tree of the analysis of the emended data matrices of Worthy et al. (2013) with *Proardea*? *deschutteri* n. sp. added.

This study is published in the journal *IBIS* (Mayr et al., 2018).

4.1.35. Evolution of the hypercarnivorous dentition in mammals (Metatheria, Eutheria) and its bearing on the development of tribosphenic molars

One major innovation of mammals is the tribosphenic molar, characterized by the evolution of the protocone and the talonid that occlude and provide shearing and crushing functions. This type of molar is an evolutionarily flexible structure that enabled mammals to achieve complex dental adaptations. Among carnivorous mammals, hypercarnivory is a common trend that evolved several times among therians (marsupials, placentals, and stem relatives). Hypercarnivory involves an important simplification of the carnassial molar pattern from the ancestral tribosphenic molar pattern, with the modification of the triangular tooth crown, and the loss of several cusps and cuspids typical of the tribosphenic molar. These losses confer to the molars of the hypercarnivorous mammals a plesiomorphic /paedomorphic morphology that resembles more the earliest mammaliaforms than the earliest therians. Here, we demonstrate that the modification of the molar morphology is fully explained by a patterning cascade mode of cusp development (Figure 50). Contrary to what was previously proposed, our study concludes that the metaconid (mesiolingual cusp of lower molars, associated with a puncturing function) does not influence cusp development of the talonid (distal crushing heel of lower molars). Moreover, it provides a new example of how heterochronic changes were crucial to the evolution of mammal dentition.

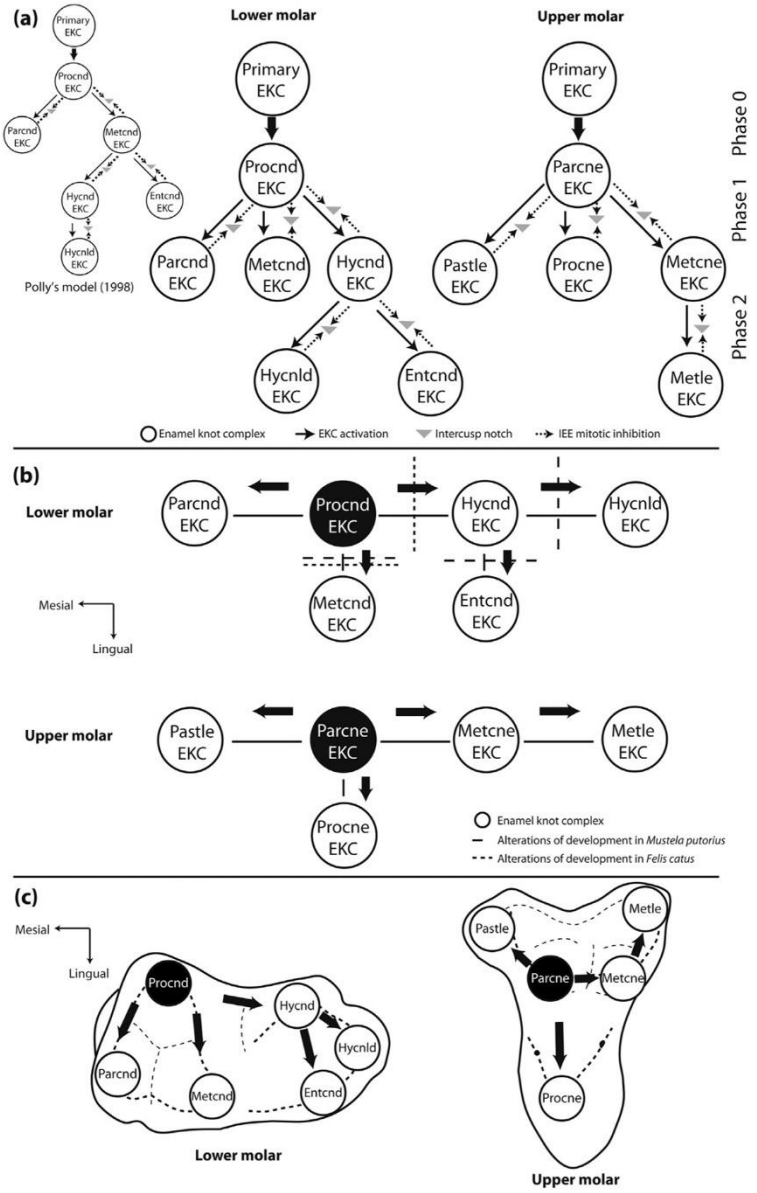

Figure 50. Modes of tooth crown morphogenesis of lower and upper tribosphenic molars. (a) Illustration of the cascade development model proposed by Polly (1998) (left) and hypothesis of cascade development proposed. (b) Directions of propagation of the cusp development. In black: first cusps to develop. (c) Directions of propagation mapped on a diagrammatic drawing in occlusal view of lower and upper molars.

This study is published in *Evolution & Development* (Solé & Ladevèze, 2017)

4.1.36. Incus facet morphology in carnivorous mammals from different ecosystems: Taxonomy vs. habitat

This study is prompted by the discovery of an incus of *Hyaenodon*, the first known auditory ossicle of this genus and thus of any hyaenodont mammal so far. The *Hyaenodon* incus is small, delicate and possesses an incudo-mallear facet of a general saddle-shape with two articulation facets, a large superior articulation area and a circular, inferior articulation area. Its general morphology and facet shape is most similar to the felid incus morphology. A large set of incus of recent Carnivora (felids, hyaenids, viverrids, herpestids, nandiniid and canids) of different ecosystems has been analysed. This study especially focuses on the incudo-mallear facet. The incudo-mallear facet is composed of: (1) three articular surfaces in felids, (2) a U-shaped surface in hyaenids and (3) four surfaces in canids (Figure 51). Both taxonomy (on family level) and habitat (open, closed or mixed habitat preference) might have an impact on the morphology of the incus facets, the former having a major impact in our sample.

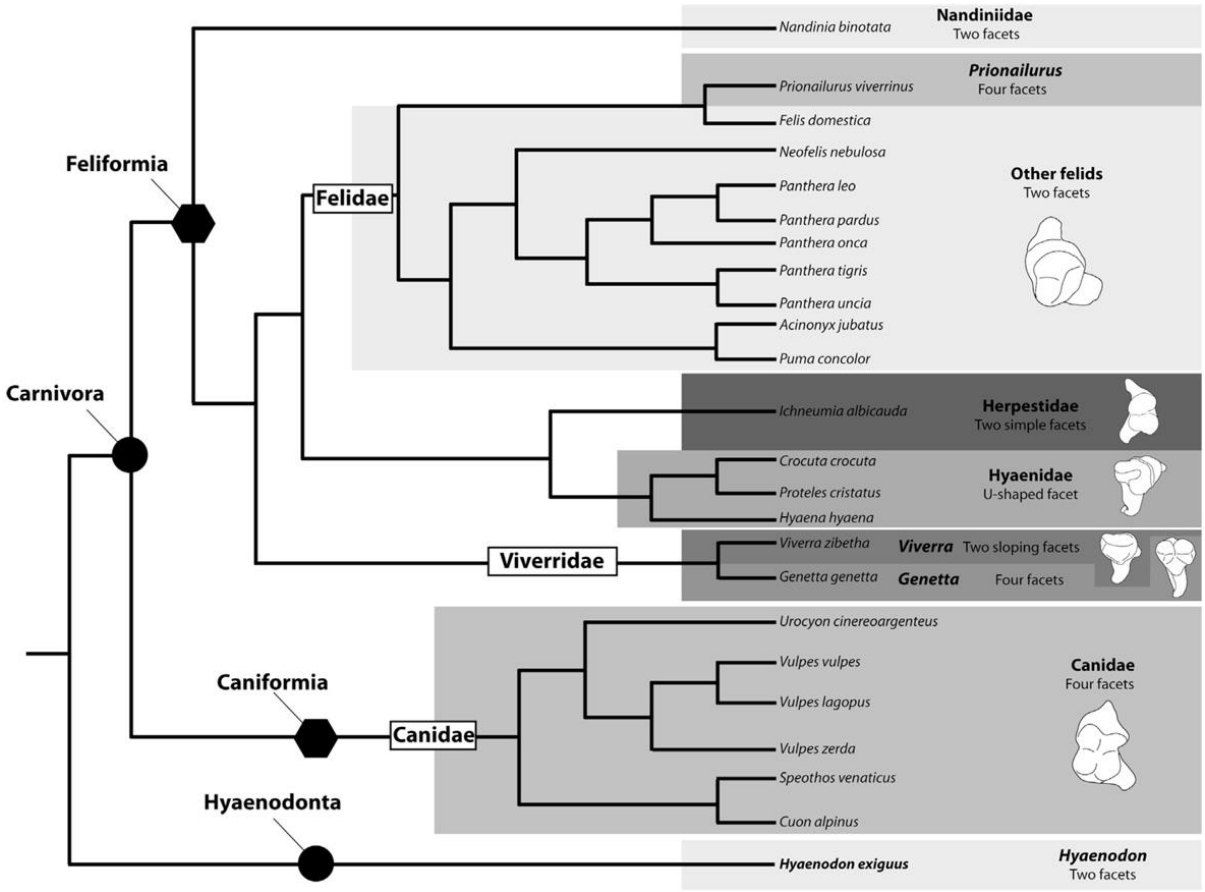

Figure 52. Simplified phylogenetic tree illustrating the relationships between the carnivorous mammals studied, with indication of their morphological incus types.

This study is published in *Geobios* (Bastl, Nagel & Solé, 2017)

4.1.37. The first hyaenodont from the late Oligocene Nsungwe Formation of Tanzania: Paleoecological insights into the Paleogene-Neogene carnivore transition

Throughout the Paleogene, most terrestrial carnivore niches in Afro-Arabia were occupied by Hyaenodonta, an extinct lineage of placental mammals. By the end of the Miocene, terrestrial carnivore niches had shifted to members of Carnivora, a clade with Eurasian origins. The transition from a hyaenodont-carnivore fauna to a carnivoran-carnivore fauna coincides with other ecological changes in Afro-Arabia as tectonic conditions in the African Rift System altered climatic conditions and facilitated faunal exchange with Eurasia. Fossil bearing deposits in the Nsungwe Formation in southwestern Tanzania are precisely dated to ~25.2 Ma (late Oligocene), preserving a late Paleogene Afro-Arabian fauna on the brink of environmental transition, including the earliest fossil evidence of the split between Old World monkeys and apes. Here we describe a new hyaenodont from the Nsungwe Formation, *Pakakali rukwaensis* gen. et sp. nov., a bobcat-sized taxon known from a portion of the maxilla that preserves a deciduous third premolar and alveoli of dP4 and M1. The crown of dP3 bears an elongate parastyle and metastyle and a small, blade-like metacone. Based on alveolar morphology, the two more distal teeth successively increased in size and had relatively large protocones.

Using a hyaenodont character-taxon matrix that includes deciduous dental characters, Bayesian phylogenetic methods resolve *Pakakali* within the clade Hyainailouroidea. A Bayesian biogeographic analysis of phylogenetic results resolve the *Pakakali* clade as Afro-Arabian in origin, demonstrating that this small carnivorous mammal was part of an endemic Afro-Arabian lineage that persisted into the Miocene (Figure 53). Notably, *Pakakali* is in the size range of carnivoran forms that arrived and began to diversify in the region by the early Miocene. The description of *Pakakali* is important for exploring hyaenodont ontogeny and potential influences of Afro-Arabian tectonic events upon mammalian evolution, providing a deep time perspective on the stability of terrestrial carnivore niches through time.

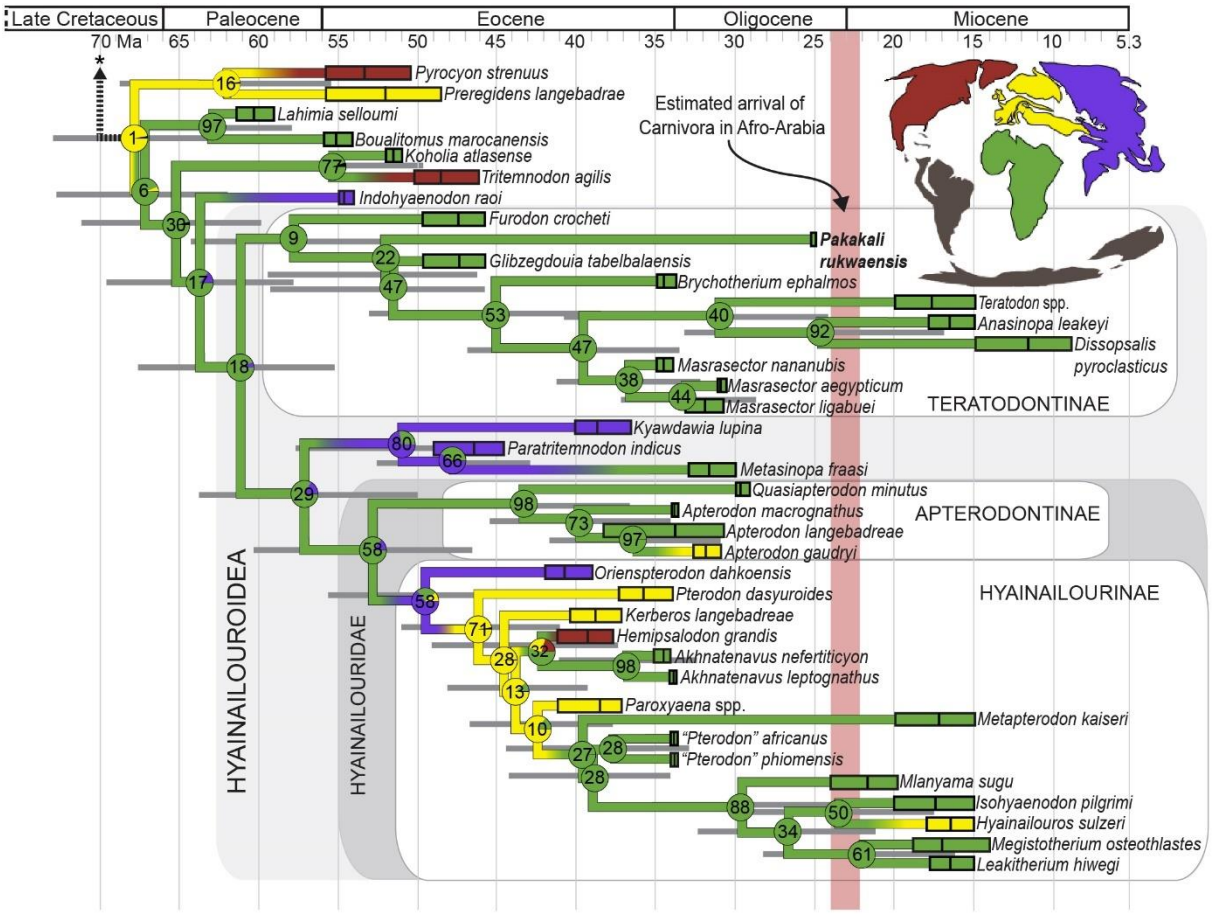

Figure 53. Phylogeny and biogeography of Afro-Arabian Hyaenodonta with *Pakakali* is nested within Hyainailouroidea and Teratodontinae.

This study is published in *PLOS ONE* (Borths & Stevens, 2017).

4.1.38. Geology, biostratigraphy and carbon isotope chemostratigraphy of the Palaeogene fossil-bearing Dakhla sections, southwestern Moroccan Sahara

New Palaeogene vertebrate localities were recently reported in the southern Dakhla area (southwestern Morocco). The Eocene sediment strata crops out on cliffs along the Atlantic Ocean coast. Vertebrate remains come from five conglomeratic sandstone beds and are principally represented by isolated teeth belonging to micromammals, selachians and bony fishes, a proboscidean assigned to ?*Numidotherium* sp. and many remains of archaeocete

whales (Basilosauridae). From fieldwork five lithostratigraphic sections were described, essentially based on the lithological characteristic of sediments.

Despite the lateral variations of facies, correlations between these five sections were possible on the basis of fossil-bearing beds (A1, B1, B2, C1 and C2) and five lithological units were identified. The lower part of the section consists of rhythmically bedded, chert-rich marine siltstones and marls with thin black phosphorite with organic matter at the base. The overlying units include coarse-grained to microconglomeratic sandstones interbedded with silts, indicating deposition in a shallow-marine environment with fluvial influence. The natural remanence magnetization of a total of 50 samples was measured; the intensity of most of the samples is too weak however, before or after the first step of demagnetization. The palaeomagnetic data from the samples are very unstable, except for eight from three similar sandstone levels which show a normal polarity. Matched with biostratigraphic data on rodents, primates, the selachian, sirenian and cetacean faunas, the new carbon isotope chemostratigraphy on organics (1) refines the age of the uppermost C2 fossil-bearing bed to earliest Oligocene time and (2) confirms the Priabonian age of the B1 to C1 levels (Figure 54).

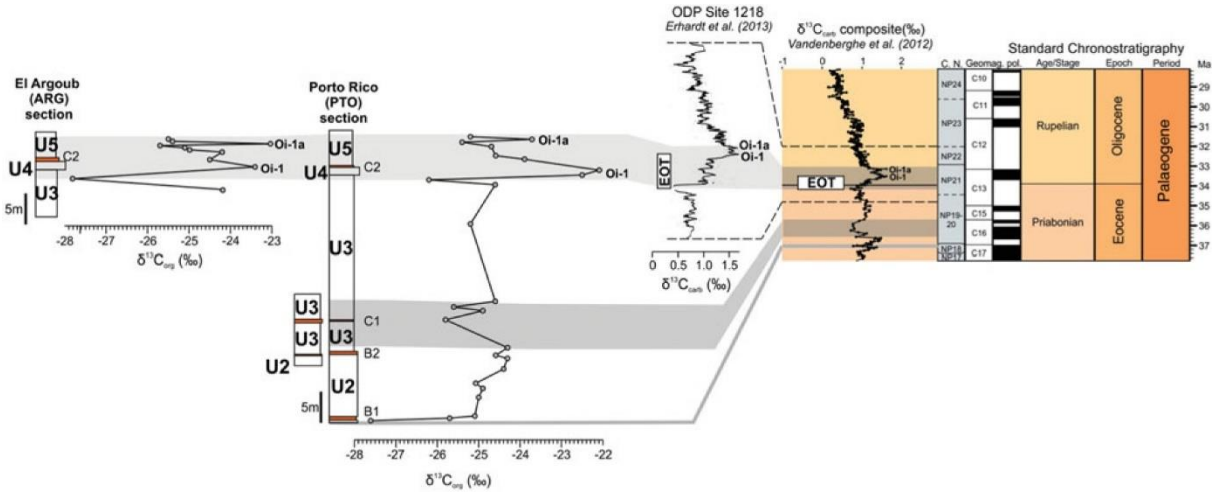

Figure 54. Carbon isotope values (‰ VPDB) of the Porto Rico and El Argoub sections, compared to $\delta^{13}C$ curves around the Eocene–Oligocene transition at ODP Site 1218 (Erhardt, Pälike & Paytan, 2013) and reference $\delta^{13}C$ composite curve (Cramer et al. 2009; modified by Vandenberghe, Hilgen & Speijer, 2012). EOT – Eocene–Oligocene Transition; U1–U5 – lithological units defined in the text; B1, B2, C1, C2 – fossil-bearing levels.

This study is published in *Geological Magazine* (Benammi et al., 2017).

4.1.39. Morphological diversification of ampullariid gastropods (Nsungwe Formation, Late Oligocene, Rukwa Rift Basin, Tanzania) is coincident with onset of East African Rifting

A new freshwater gastropod fauna is described from the late Oligocene Nsungwe Formation of the Rukwa Rift Basin, Tanzania (Figure 55). Six new species of ampullariids are established including five species of *Lanistes* (*L. microovum*, *L. nsungwensis*, *L. rukwaensis*, *L. songwellipticus* and *L. songweovum*) and one species of *Carnevalea* (*C. santiapillaii*). These taxa occupy a morphospace region comparable to nearly half of extant *Lanistes*, a common

and widespread genus in Africa and Madagascar. Palaeoecological evidence indicates that Nsungwe ampullariids inhabited fluvial, pond and paludal environments. Among these species are the oldest high-spired and fluvially adapated *Lanistes* taxa. We suggest that Nsungwe *Lanistes* rapidly diversified in concert with habitat heterogeneity associated with the initiation of rifting along the western branch of the East African Rift System (EARS). Taxonomy, evolution and the biogeographical affinities of Nsungwe Formation freshwater gastropods contributes significantly to expanding the undersampled Palaeogeneinvertebrate fossil record of continental Africa.

Figure 55. Depressed *Lanistes* morphotypes. A–D, *L. nsungwensis* sp. nov.; E, *L. carinatus* (Olivier, 1804), ANSP 367298-11; F–Q, *L. rukwaensis* sp. nov. Scale bars represent 10 mm.

This study is published in *Papers in Palaeontology* (Epa et al., 2018).

4.1.40. A Fossil Gekkotan (Squamata) from the Late Oligocene Nsungwe Formation, Rukwa Rift Basin, Tanzania

We describe the first record of a fossil gekkotan from the Late Oligocene Nsungwe Formation in the Rukwa Rift Basin, Tanzania (Figure 56). The specimen consists of an almost complete maxilla containing 23 tooth positions, with 10 teeth still in place. Typical gekkotan features include the tall facial process along with a posteriorly sloping angle, and the presence of unicuspid, pleurodont teeth with large resorption pits. Limited preservation does not allow for a more specific systematic assignment, which is why we refer the specimen to Gekkota incertae sedis. The material represents the second record of a Paleogene gekkotan from Africa and the first one from the central part of the continent.

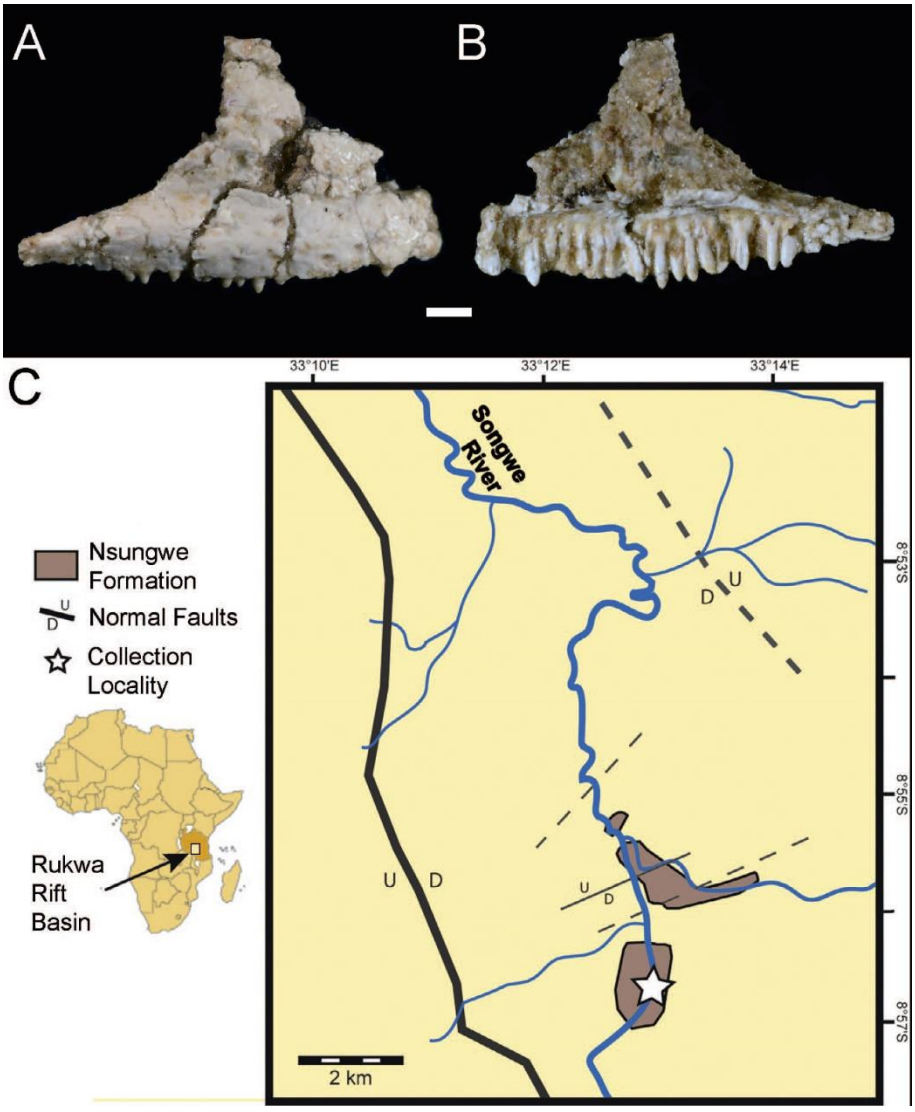

Figure 56. Specimen photograph and locality map. (A) RRBP 13002, gekkotan right maxilla in lateral view and (B) in medial view (scale bar = 1 mm); (C) map showing the Nsungwe Formation within the Rukwa Rift Basin (Tanzania) and the collection locality, including its relative position within Tanzania.

This study is published in *Journal of Herpetology* (Müller et al., 2018).

4.1.41. Plesiadapid mammals from the latest Paleocene of France offer new insights on the evolution of *Plesiadapis* during the Paleocene-Eocene transition

Plesiadapidae are among the most successful mammal families of the Paleocene, but in North America they disappear abruptly around the Paleocene-Eocene boundary. In contrast, in Europe, they survive a few million years into the Eocene, although only as the genus *Platychoerops*. The latest Paleocene deposits of Petit-Patis (Paris Basin, France) have produced three new plesiadapid species, one of each genus known in Europe: *Plesiadapis ploegi*, sp. nov., *Platychoerops boyeri*, sp. nov., and *Chiromyoides mauberti*, sp. nov (Figure 57). Each of these new species is represented by the very characteristic upper incisor, thus ascertaining their concomitant presence and in particular the spatial and temporal coexistence of *Plesiadapis* and *Platychoerops*. *Plesiadapis ploegi*, sp. nov., is morphologically intermediate between *Plesiadapis tricuspidens* and *Platychoerops russelli*, with a tricuspid I1 typical of *Plesiadapis* and a semimolariform p4 closer to *Platychoerops*. Its relatively high morphological variability is illustrated. *Platychoerops boyeri*, sp. nov., has the simple derived I1 of all *Platychoerops* and a p4 slightly more molariform than that of *Ples. ploegi*.

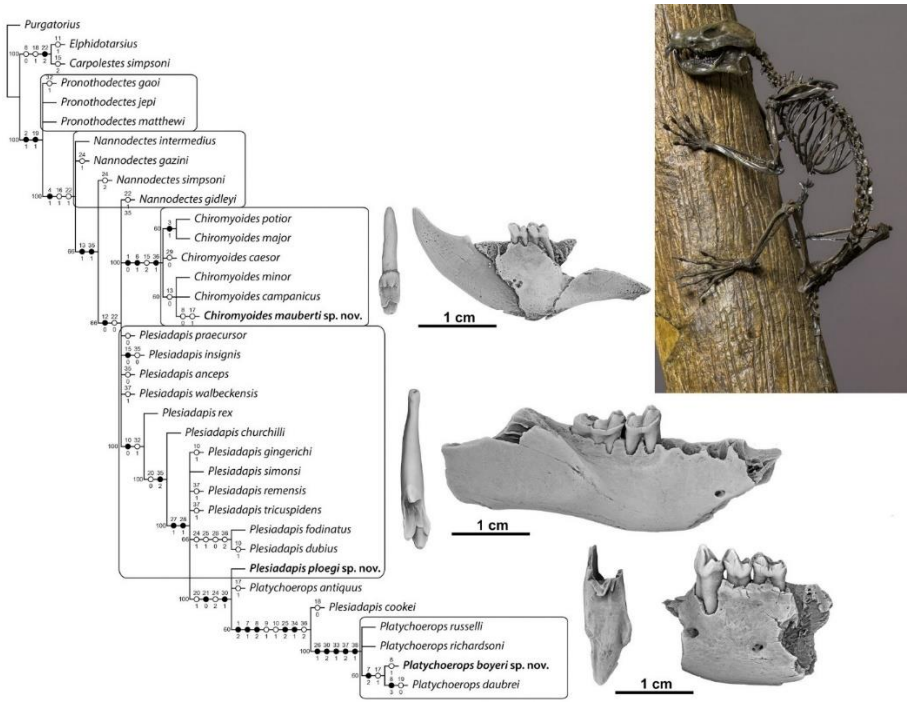

Figure 57. Phylogeny of plesiadapids, including the three new species and their dentition. Skeleton of *Plesiadapis*.

Chiromyoides mauberti, sp. nov., is closest to *Chiromyoides campanicus*, but it is smaller and has a particular I1 with multiple posterocones. The systematic position of '*Platychoerops*' *georgei* is discussed; this taxon is considered a chimera, and its type I1 belongs to either *Chiromyoides* or *Plesiadapis*. Cladistic analysis highlights the paraphyly or polyphyly of all genera of Plesiadapidae. Finally, there is some indication of morphological convergences between European and North American plesiadapids, which may be the result of similar environmental changes on both continents just before the Paleocene-Eocene boundary.

This study is published in *Journal of Vertebrate Paleontology* (De Bast et al., 2018).

4.1.42. New fossils from Tadkeshwar Mine (Gujarat, India) increase primate diversity from the early Eocene Cambay Shale

Several new fossil specimens from the Cambay Shale Formation at Tadkeshwar Lignite Mine in Gujarat document the presence of two previously unknown early Eocene primate species from India. A new species of *Asiadapis* is named based on a jaw fragment preserving premolars similar in morphology to those of *A. cambayensis* but substantially larger. Also described is an exceptionally preserved edentulous dentary (designated cf. *Asiadapis*, unnamed sp. nov.) that is slightly larger and much more robust than previously known Cambay Shale primates (Figure 58). Its anatomy most closely resembles that of Eocene adapoids, and the dental formula is the same as in *A. cambayensis*. A femur and calcaneus are tentatively allocated to the same taxon. Although the dentition is unknown, exquisite preservation of the dentary of cf. *Asiadapis* sp. nov. enables an assessment of masticatory musculature, function, and gape adaptations, as well as comparison with an equally well-preserved dentary of the asiadapid *Marcgodinotius indicus*, also from Tadkeshwar. The new *M. indicus* specimen shows significant gape adaptations but was probably capable of only weak bite force, whereas cf. *Asiadapis* sp. nov. probably used relatively smaller gapes but could generate relatively greater bite forces.

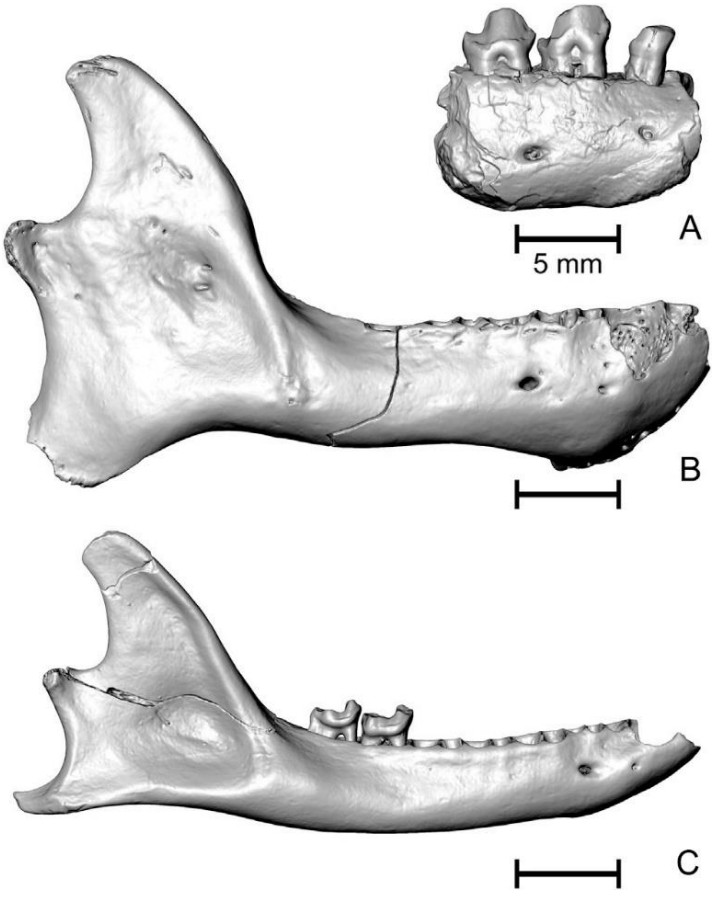

Figure 58. Lateral (buccal) views of lower jaws of primates from Tadkeshwar Lignite Mine, India. A, *Asiadapis tapiensis* sp. nov. B, cf. *Asiadapis* sp. nov. C, *Marcgodinotius indicus*.

This study is published in *Journal of Human Evolution* (Rose et al., 2018).

43. Mastication and enamel microstructure in *Cambaytherium*, a perissodactyl like ungulate from the early Eocene of India

The dentition of *Cambaytherium* was investigated in terms of dental wear, tooth replacement and enamel microstructure. The postcanine tooth row shows a significant wear gradient, with flattened premolars and anterior molars at a time when the last molars are only little worn. This wear gradient, which is more intensive in *Cambaytherium thewissi* than in *Cambaytherium gracilis*, and the resulting flattened occlusal surfaces, may indicate a preference for a durophagous diet. The tooth replacement (known only in *C. thewissi*) shows an early eruption of the permanent premolars. They are in function before the third molars are fully erupted. During the dominant phase I of the chewing cycle the jaw movement is very steep, almost orthal, with a slight mesiolingual direction and changes into a horizontal movement during phase II. The enamel microstructure shows Hunter-Schreger-bands (HSB) in the inner zone of the enamel. In some teeth the transverse orientation of the HSB is modified into a zig-zag pattern, possibly an additional indicator of a durophagous diet (Figure 59).

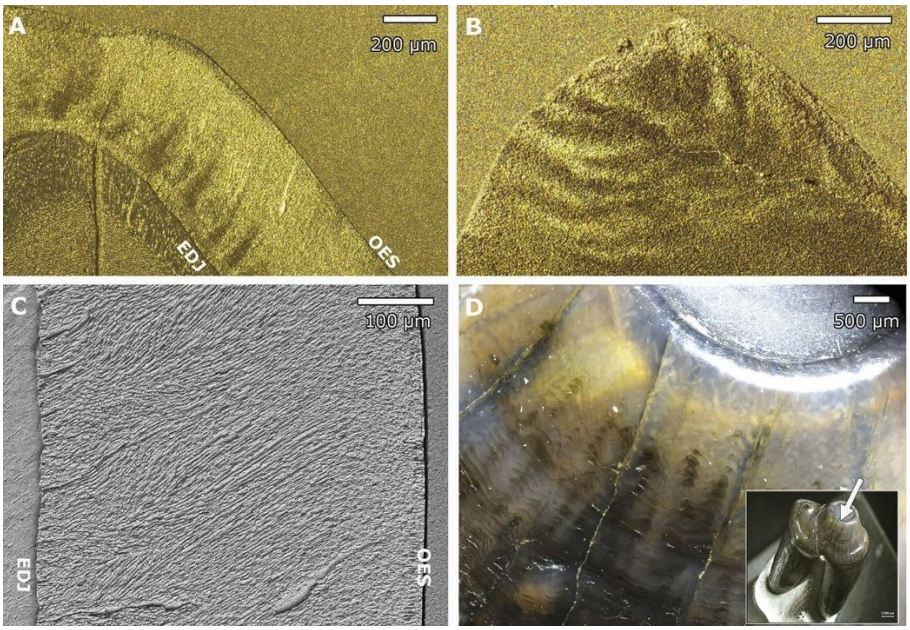

Figure 59. Hunter-Schreger bands in the enamel of *Cambaytherium thewissi* shown by different techniques.

This study is published in *Paläontologische Zeitschrift* (Koenigswald et al., 2018).

4.1.44. Shell anatomy of the African Paleocene bothremydid turtle *Taphrosphys congolensis* and systematic implications within Taphrosphyini

The bothremydid pleurodiran turtle *Taphrosphys congolensis* is a member of Taphrosphyina from the Paleocene of the Cabinda Province (Congo Basin, Angola). Very few specimens corresponding to elements of its shell have been so far figured. Abundant unpublished remains are analyzed in this paper. As a consequence, several regions of the shell are figured and characterized here for the first time, and intraspecific variability is recognized for several characters (Figure 60). Previous authors proposed some putative differences between the shells of *Taphrosphys congolensis* and the North American Paleocene *Taphrosphys sulcatus*.

The increase in the knowledge about the shell of this African form allows us to refute most of them, the shell of both forms being recognized as more similar than previously identified. Thus, the identification of the genus *Taphrosphys* as restricted to three forms (i.e. the skull taxon *Taphrosphys ippolitoi*, and the skull and shell forms *T. congolensis* and *T. sulcatus*) is supported, and the record unquestionably attributable to this genus is modified from the Upper Cretaceous–Eocene lapse of time to the Paleocene exclusively.

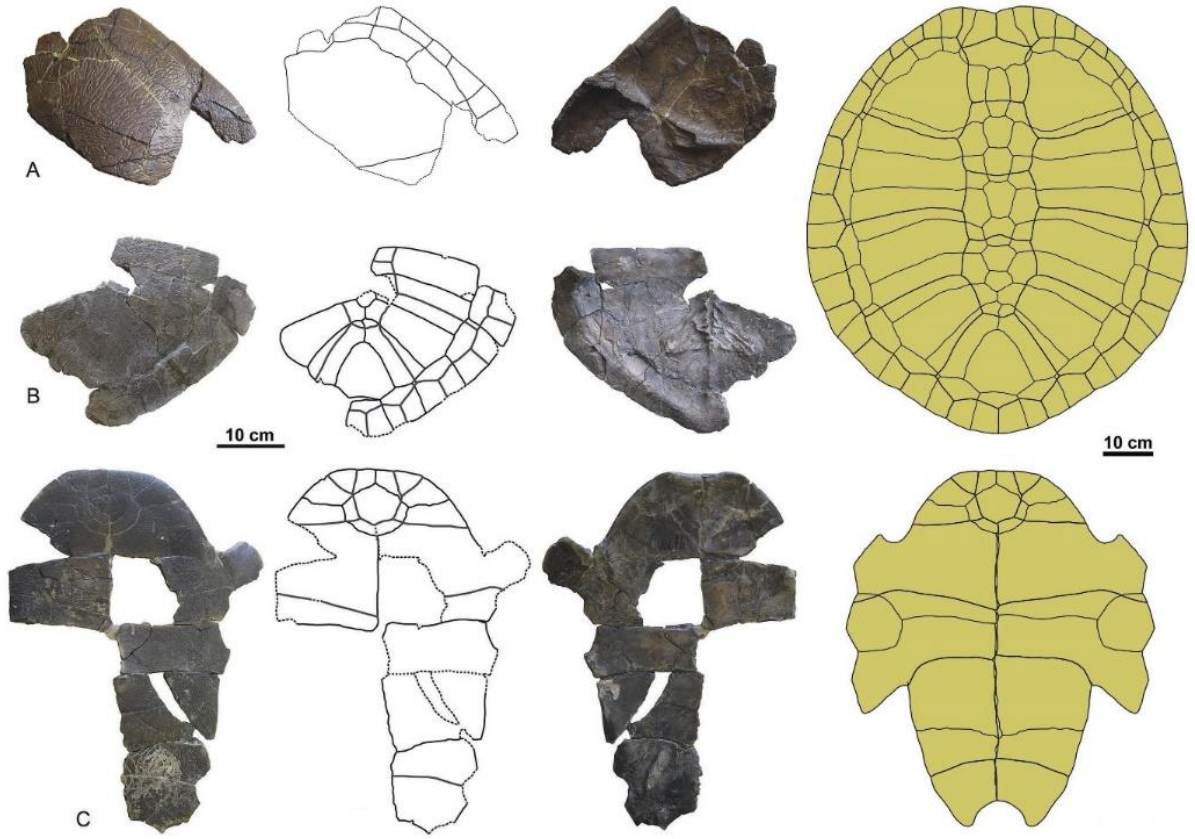

Figure 60. *Taphrosphys congolensis*, from Landana (Cabinda Province, Angola). Anterior (A) and posterior (B) regions of the carapace, and partial plastron (C). Reconstruction of the carapace in dorsal view and plastron in ventral view.

This study is published in *Historical Biology* (Pérez García et al., 2018).

4.1.45. Reassessment of historical sections from the Paleogene marine margin of the Congo Basin reveals an almost complete absence of Danian deposits

The early Paleogene is critical for understanding global biodiversity patterns in modern ecosystems. During this interval, Southern Hemisphere continents were largely characterized by isolation and faunal endemism following the breakup of Gondwana (Africa, Antarctica, India, Madagascar, South America, and Australia. Africa has been proposed as an important source area for the origin of several marine vertebrate groups but its Paleogene record is poorly sampled, especially from sub-Saharan Africa. To document the early Paleogene marine ecosystems of Central Africa, we revised the stratigraphic context of sedimentary deposits from three fossil-rich vertebrate localities: the Landana section in the Cabinda exclave (Angola), and the Manzadi and Bololo localities in western Democratic Republic of Congo.

We provide more refined age constraints based on invertebrate and vertebrate faunas, foraminiferal and dinoflagellate cyst assemblages, and carbon isotope records. We find an almost complete absence of Danian-aged rocks in the Landana section, contrary to prevailing interpretations over the last half a century (Figure 61).

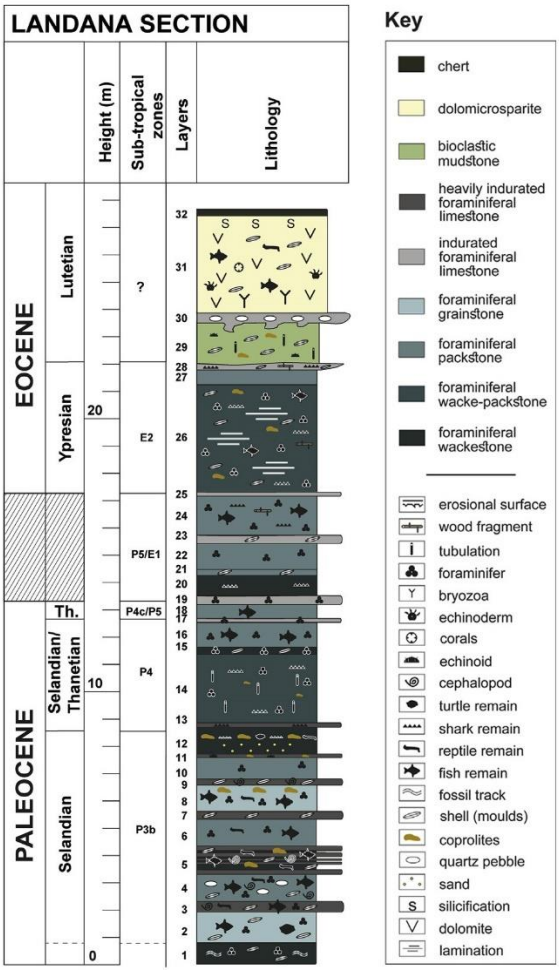

Figure 61. Stratigraphic log of the Landana section with ages estimated based on the identified sub-tropical zones of planktonic foraminiferans.

Refining the age of these Paleocene layers is indeed crucial for analyzing fish evolution in a global framework, with implications for the early appearance of Scombridae (tunas and mackerels) and Tetraodontiformes (puffer fishes). The combination of vertebrate fossil records from Manzadi and Landana sections suggests important environmental changes around the Cretaceous/Paleogene transition characterized by an important modification of the ichthyofauna. A dramatic faunal shift is the decrease in overall richness that lasts from the Selandian (middle Paleocene) to the Ypresian (early Eocene). The Lutetian (middle Eocene) of West Central Africa is characterized by the first appearance of numerous cartilaginous and bony fishes. Our analysis of the ichthyofauna moreover indicates two periods of faunal exchanges: one during the Paleocene, where Central Africa appears to have been a source for the European marine fauna, and another during the Eocene when Europe was the source of the Central Africa fauna. These data indicate that Central Africa has had connections with the Tethyian realm.

This study is published in *Geoscience Frontiers* (Solé et al., 2018).

4.1.46. New fossils, systematics, and biogeography of the oldest known crown primate *Teilhardina* from the earliest Eocene of Asia, Europe, and North America

Omomyiform primates are among the most basal fossil haplorhines, with the oldest classified in the genus *Teilhardina* and known contemporaneously from Asia, Europe, and North America during the Paleocene Eocene Thermal Maximum (PETM) 56 million years ago. Characterization of morphology in this genus has been limited by small sample sizes and fragmentary fossils. A new dental sample (n = 163) of the North American species *Teilhardina brandti* from PETM strata of the Bighorn Basin, Wyoming, documents previously unknown morphology and variation, prompting the need for a systematic revision of the genus. The p4 of *T. brandti* expresses a range of variation that encompasses that of the recently named, slightly younger North American species '*Teilhardina gingerichi*', which is here synonymized with *T. brandti*. A new partial dentary preserving the alveoli for p1-2 demonstrates that *T. brandti* variably expresses an unreduced, centrally-located p1, and in this regard is similar to that of *T. asiatica* from China (Figure 62).

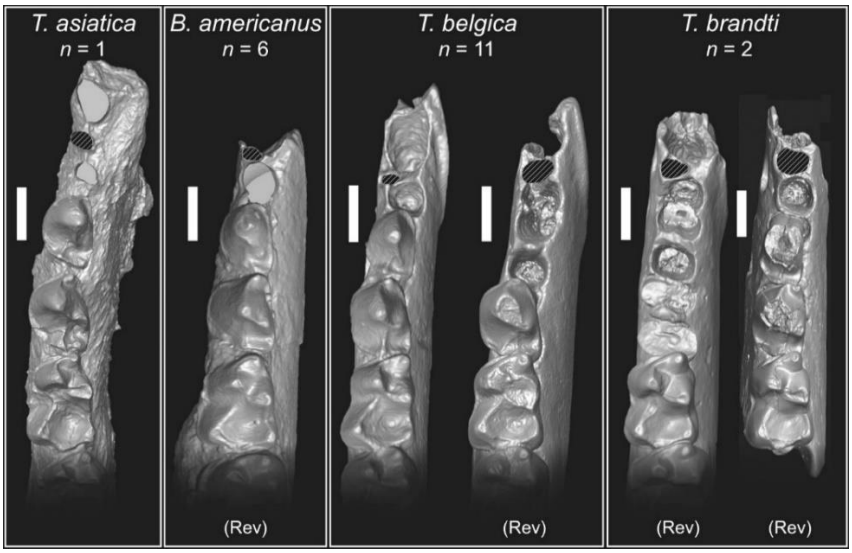

Figure 62. Comparative size of the p1 alveolus in *Teilhardina* and *Bownomomys*. n = sample size of specimens. (Rev) indicates = specimens reversed. Scale bars = 1 mm.

This observation, coupled with further documentation of variability in p1 alveolar size, position, and presence in the European type species *T. belgica*, indicates that the original diagnosis of *T. asiatica* is insufficient at distinguishing this species from either *T. belgica* or *T. brandti*. Likewise, the basal omomyiform '*Archicebus achilles*' requires revision to be distinguished from *Teilhardina*. Results from a phylogenetic analysis of 1890 characters scored for omomyiforms, adapiforms, and other euarchontan mammals produces a novel clade including *T. magnoliana*, *T. brandti*, *T. asiatica*, and *T. belgica* to the exclusion of two species previously referred to *Teilhardina*, which are here classified in a new genus (*Bownomomys americanus* and *Bownomomys crassidens*). While hypotheses of relationships and inferred biogeographic patterns among species of *Teilhardina* could change with the discovery of more complete fossils, the results of these analyses indicate a similar probability that the genus originated in either Asia or North America.

This study is published in *Journal Human Evolution* (Morse et al., 2018).

4.1.47. *Calcardea junnei* Gingerich, 1987 from the late Paleocene of North America is not a heron, but resembles the early Eocene Indian taxon *Vastanavis* Mayr et al., 2007

We revisit the holotype of *Calcardea junnei* Gingerich, 1987 from the latest Paleocene (Clarkforkian) of the Willwood Formation (Wyoming, USA). The species is based on a partial skeleton and was originally assigned to the Ardeidae (herons). As we show, this classification cannot be upheld and *Calcardea* Gingerich, 1987 more closely resembles the taxon *Vastanavis* Mayr et al., 2007 (Vastanavidae), a parrot-like bird from the early Eocene of India (Figure 63). Even though *C. junnei* is a large bird, its long wings and short tarsometatarsus argue against a predominantly terrestrial way of living, and the morphology of the tarsometatarsus and pedal phalanges instead suggest strong grasping feet. We conclude that an assignment of *Calcardea* to the landbird clade (Telluraves) is better supported than its classification into the waterbird clade (Aequornithes), which includes Ardeidae and other 'ciconiiform' and 'pelecaniform' taxa. *Calcardea junnei* is one of the oldest known representatives of Telluraves and its morphology shows plesiomorphic features, which contributed to its previous misidentification as a heron. *Calcardea* exhibits a distinctive osteology and affords a glimpse of a previously unknown late Paleocene avian morphotype.

Figure 63. Coracoid (above) and tarsometatarsus (below) of *Calcardea* from the late Paleocene of Wyoming (USA) compared to those of *Vastanavis* from the early Eocene of Gujarat (India) and *Berruornis* from the late Paleocene of France. Scale bars = 10 mm.

This study is published in *Journal of Paleontology* (Mayr et al., 2018).

4.1.48. *Cabindachanos dartevellei* gen. and sp. nov., a new chanid fish (Ostariophysi, Gonorynchiformes) from the marine Paleocene of Cabinda (Central Africa)

The osteology of *Cabindachanos dartevellei* gen. and sp. nov., a fossil fish from the marine Danian or early Selandian deposits of Landana (Cabinda Territory, Central Africa), is here studied in detail. This fish is known by only one partially preserved specimen that shows typical characters (Figure 64). The opercle is greatly hypertrophied. The preopercle has a very broad dorsal limb and a long narrower ventral limb. There is a wide plate-like suprapreopercle. The lower jaw is deep, with a well-marked coronoid process formed by the dentary. The articulation between the quadrate and the mandible is located before the orbit. The first supraneurals are enlarged. These characters indicate that *C. dartevellei* belongs to the family Chanidae (Teleostei, Gonorynchiformes). *Cabindachanos dartevellei* differs from all the other known fossil or recent chanid fishes by the gigantic development of its opercle and by the loss of the subopercle.

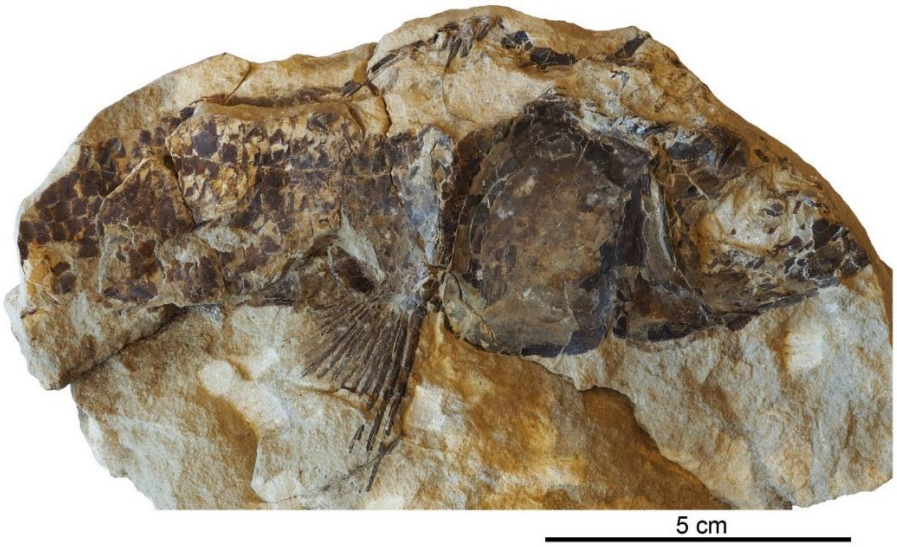

Figure 64. *Cabindachanos dartevellei* gen. and sp. nov. Holotype MRAC RG 4629; head, pectoral fin and beginning of the body (right side).

The straight angle formed by the two limbs of the preopercle and the well-developed posterior median crest of the supraoccipital indicate that *C. dartevellei* belongs to the subfamily Chaninae and the tribe Chanini.

This study is published in *Geologica Belgica* (Taverne et al, 2019).

4.1.49. New paroxyclaenid mammals from the early Eocene of the Paris Basin (France) shed light on the origin and evolution of these endemic European cimolestans

We describe four new species of an enigmatic family of mammals, which is endemic to Europe, the Paroxyclaenidae. The fossils described come from six localities of the Ypresian of the Paris Basin (France): Pourcy, Mutigny, Avenay, Condé-en-Brie, Grauves and Prémontré. They allow the description of three new genera and four new species belonging to the subfamilies Merialinae and Paroxyclaeninae. Two of these new species represent the earliest occurrence of each subfamily. Fossils from Mutigny, Avenay and Condé-en-Brie indicate that merialines

were more abundant than paroxyclaenines during the Ypresian. Surprisingly, merialines disappeared from the fossil record at the end of the Ypresian – the youngest records are close to the Ypresian/Lutetian boundary – while the paroxyclaenines were present in Europe until the end of the middle Eocene (Figure 65).

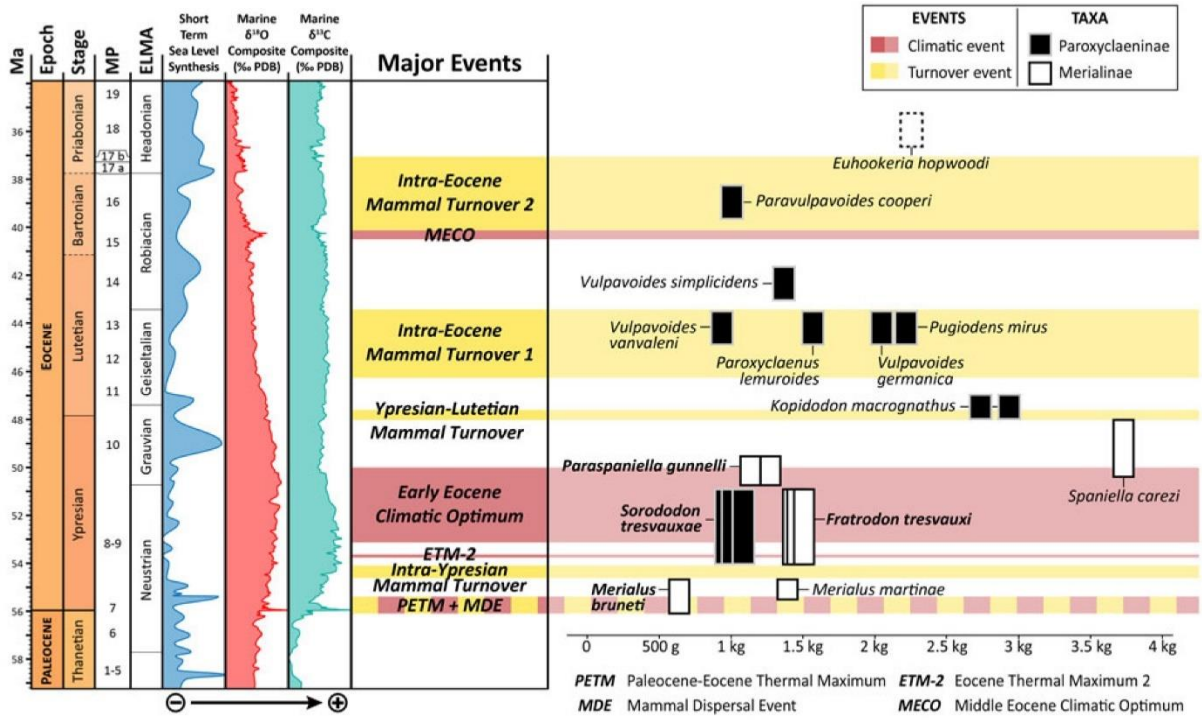

Figure 65. Temporal distribution and the evolution of body mass in paroxyclaenids. The four new paroxyclaenids described in the present paper are in bold.

Based on comparison with the data presently available for European mammals during the Ypresian, we suggest the existence of two periods of faunal turnover that must be more extensively studied in the future in order to be fully characterized: the 'Intra-Ypresian Mammal Turnover' and the 'Ypresian–Lutetian Mammal Turnover'. Finally, because the oldest paroxyclaenids appear morphologically closer to cimolestids such as Procerberus than to pantolestans, it is suggested that similarities between paroxyclaenids and pantolestans could be due to convergence.

This study is published in *Journal of Systematic Palaeontology* (Solé et al, 2019).

4.1.50. A diverse bird assemblage from the Ypresian of Belgium furthers knowledge of early Eocene avifaunas of the North Sea Basin

We describe an assemblage of 54 avian bones from early Eocene marine sediments of the Ampe quarry near Egem in Belgium (Figure 66). The fossils belong to at least 20 species in more than 11 higher-level taxa. Well-identifiable specimens are assigned to the Odontopterygiformes, Galliformes, Messelornithidae, Apodiformes, Halcyornithidae, Leptosomiformes (cf. Plesiocathartes), and Coraciiformes (cf. Septencoracias). Further specimens are tentatively referred to the phaethontiform Prophaethontidae and to the Accipitridae, Masillaraptoridae, and Alcediniformes. The three-dimensionally preserved fossils from Egem provide new data on the osteology of taxa that are otherwise mainly known from

compression fossils with crushed bones. The material also includes specimens that further knowledge of the composition of early Eocene avifaunas of the North Sea Basin. The comparatively well-represented small galliform species is clearly distinguished from the early Eocene Gallinuloididae and most closely resembles Argillipes aurorum, a largely ignored galliform species from the London Clay.

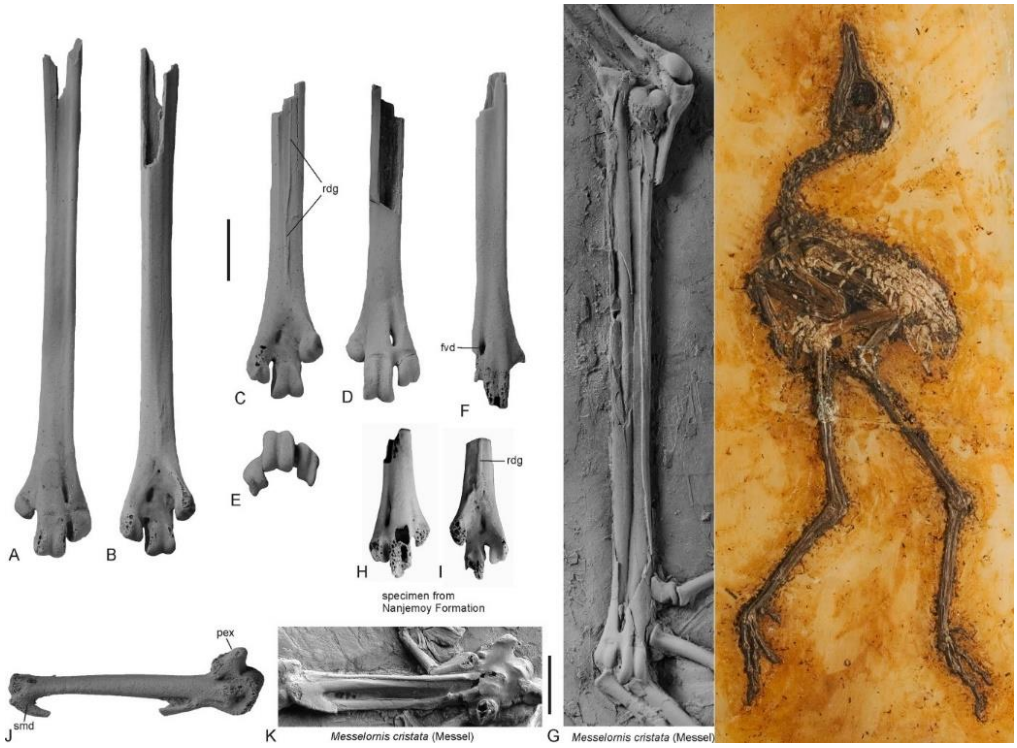

Figure 66. Fossil bones of a leg (tarsometatarsus) and a wing (carpometacarpus) of a Messelornithidae from the early Eocene of Egem (Belgium) compared to those of *Messelornis cristata* from the middle Eocene of Messel, Germany. Scale bar = 5 mm.

The tentatively identified fossils of Accipitridae and Alcediniformes would represent the earliest fossil records of these clades. The bird assemblage from Egem includes relatively few seabirds (Odontopterygiformes, cf. Prophaethontidae) and is dominated by remains of terrestrial species (Galliformes, Messelornithidae). Arboreal birds (Halcyornithidae, Leptosomiformes, cf. Alcediniformes, Coraciiformes) are less abundant and aerial insectivores (Apodiformes) very scarce, which either indicates a taphonomic bias in the composition of the avifauna or particular paleoenvironmental characteristics of the nearshore habitats in that area of the southern North Sea Basin.

This study is published in *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* (Mayr & Smith, 2019).

4.1.51. New Paleocene bird fossils from the North Sea Basin in Belgium and France

We describe new avian remains from Paleocene localities of Belgium and France (Figure 67). Four bones from the early to middle Selandian of Maret (Belgium) are among the earliest Cenozoic avian remains known from Europe and include the oldest temporally well constrained European records of the Gastornithidae, as well as tentative records of the palaeognathous

Lithornithidae and the Ralloidea. A more comprehensive fossil assemblage from the middle Thanetian of Templeuve (France) contains multiple bones of the Lithornithidae as well as a record of the Pelagornithidae. Specimens from the latest Thanetian of Rivecourt-Petit Pâtis (France) are tentatively assigned to the Ralloidea and Leptosomiformes (cf. Plesiocathartes). Because of the fragmentary nature of the fossils, the taxonomic identity of a number of other specimens remains uncertain. We note, however, that Paleocene avifaunas of Europe and North America appear to have had different compositions and only a few taxa, such as the palaeognathous Lithornithidae, are known from both continents. This suggests that the very similar early Eocene avifaunas of Europe and North America are the result of early Cenozoic dispersal events.

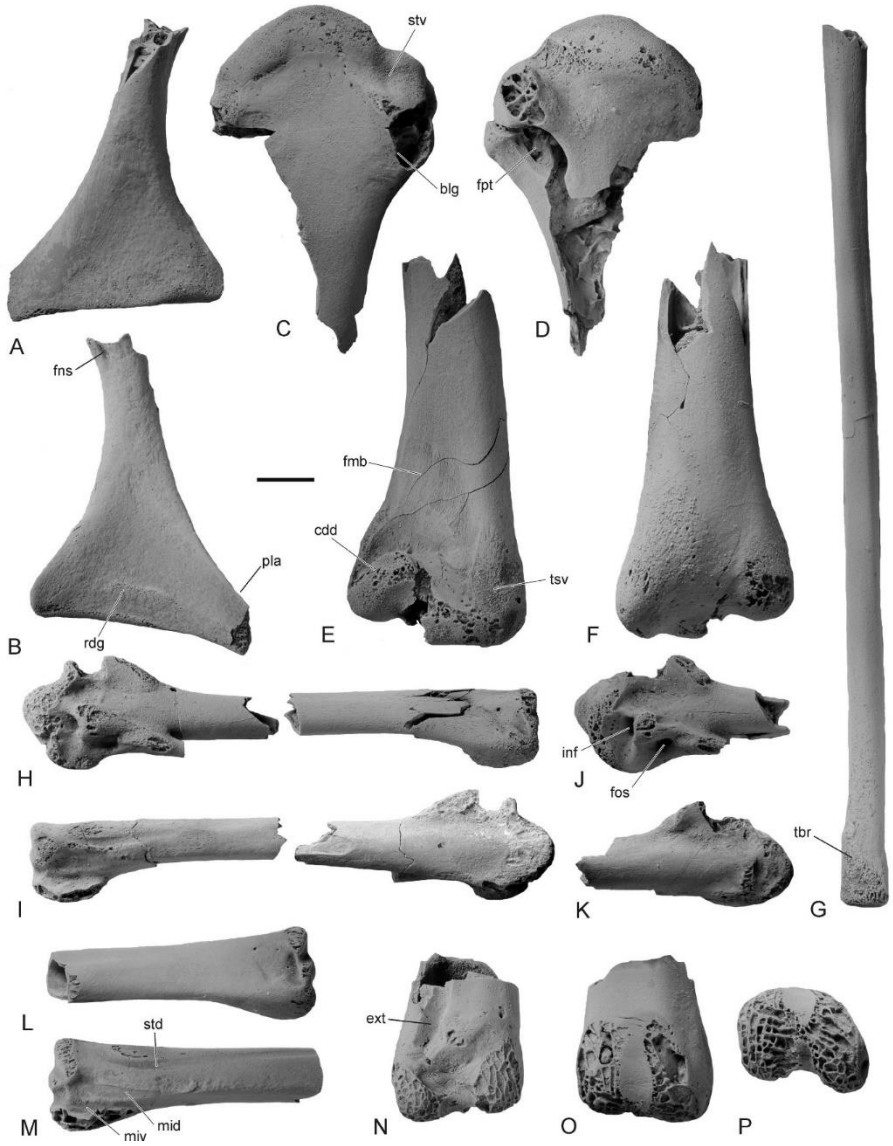

Figure 67. *Palaeognathous* lithornithid bird from the late Paleocene of Templeuve (France). A-B, coracoid. C-F, proximal and distal extremities of humerus from the same individual. G, radius lacking distal tip. H-I, carpometacarpus in two pieces. J-K, proximal end of carpometacarpus. L-M, distal portion of carpometacarpus. N-P, distal end of tibiotarsus. Scale bar = 5 mm.

This study is published in *Geologica Belgica* (Mayr & Smith, 2019).

4.1.52. Dinoflagellate cyst biostratigraphy and palaeoecology of the early Paleogene Landana reference section, Cabinda Province, Angola

Forty-four rock samples from the Landana section, belonging to the historical Dartevelle collection of the Royal Museum for Central Africa (RMCA) at Tervuren, Belgium, were palynologically processed and analysed. Systematic analysis of the samples from the Landana sea cliff locality has revealed 90 dinoflagellate cyst taxa spanning an interval that ranges at least from the middle Paleocene to the late Eocene/early Oligocene (Figure 68). This locality represents the first extensive sub-equatorial African Paleogene dinoflagellate cyst record. Dinoflagellate cyst occurrences were calibrated and evaluated against newly revised foraminiferal ranges. This novel dinoflagellate cyst biostratigraphic record was compared and correlated with contemporaneous records relatively close by in the Gulf of Guinea, as well as with records from more distant locations such as Antarctica, Australia and New Zealand.

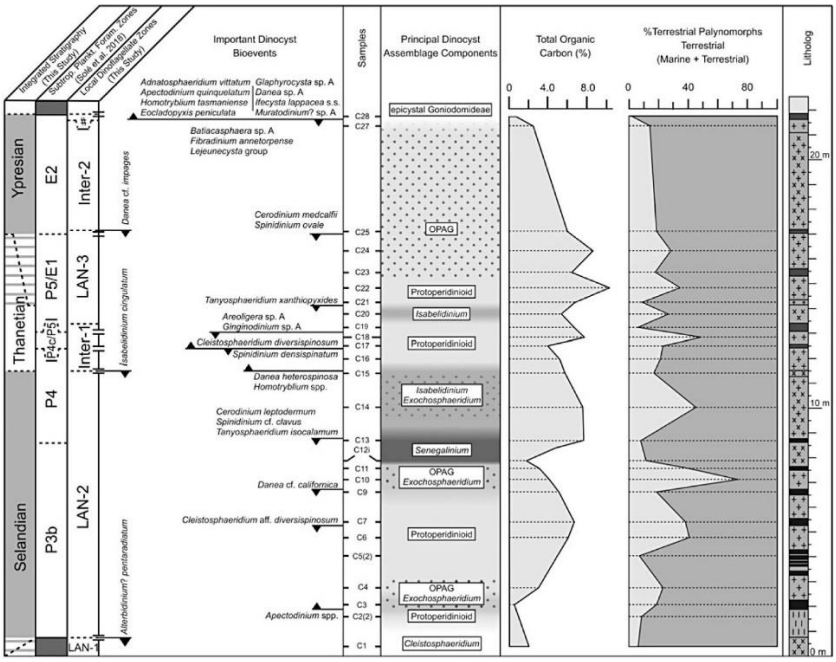

Figure 68. Landana stratigraphy, selected important dinoflagellate cyst bioevents and overall dinoflagellate cyst assemblage shifts next to total organic carbon (TOC) and %TP value changes.

A preliminary dinoflagellate cyst zonation is here proposed comprising three zones and five unzoned yet otherwise distinct intervals. The lower part of the Landana section records a large portion of the early to middle/late Selandian, which is made apparent by the presence of taxa such as *Isabelidinium cingulatum*, *Isabelidinium*? *viborgense*, and *Spinidinium densispinatum*. The Thanetian through Lutetian part of the section is more fragmentary and is devoid of any significant marker taxa normally typical for this time interval elsewhere. The upper part of the record is largely devoid of dinoflagellate cysts, with the few dinoflagellate cyst-bearing samples pointing to an Eocene to early Oligocene age. Dinoflagellate cyst assemblages are relatively variable and often largely dominated by a single particular taxon or complex. We record remarkably abundant peridinioid cysts signaling high palaeoproductivity for protracted periods of time, resulting from either heightened terrestrial influence or enhanced upwelling.

This study is published in *Palynology* (Steeman et al, 2019).

4.1.53. An enigmatic new ungulate-like mammal from the early Eocene of India

We report a new genus and species of herbivorous mammal, *Pahelia mysteriosa*, from the early Eocene Cambay Shale Formation, Tadkeshwar Lignite Mine, Gujarat, India (Figure 69). The new taxon, approximately the size of a small phenacodontid (e.g. *Ectocion parvus*), is represented by three mandibular fragments, the most complete of which documents nearly the entire symphysis and mandibular body plus P3–M3. *Pahelia* has incipiently selenolophodont molars with strong exodaenodonty, absent paraconids, weak but distinct entolophids, and prominent ectostylids. Molar size increases distally, but M3 does not develop a prominent third lobe. Premolars are simple, with prominent protoconids and short talonids but little development of other trigonid cusps. The mandibular symphysis is strongly fused, and there is an enlarged alveolus for an anterior tooth.

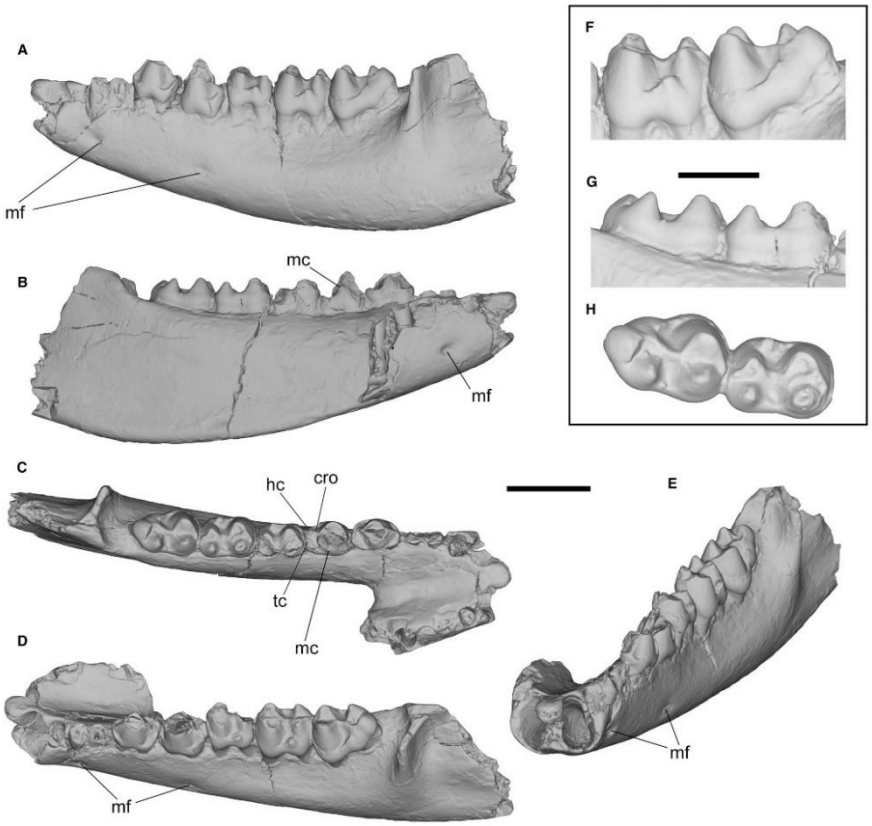

Figure 69. GU/RSR/TAD 9201, mandible with left dentary and P3–M3, holotype of *Pahelia mysteriosa* gen. et sp. nov. Scale bars represent 10 mm (A–E); 5 mm (F–H).

The combination of features present in the new taxon does not closely match that of any known mammal, but there are some similarities to a diversity of ungulates from Africa, Asia, Europe and North America. Preserved morphology is insufficient to assess the affinities of the new taxon with confidence, but a link to Quettacyonidae, also endemic to the Indian subcontinent, is morphologically and biogeographically plausible. If this scenario is correct, it suggests that *P. mysteriosa* could be a part of the endemic mammalian fauna of India prior to its initial faunal contact with Asia.

This study is published in *Papers in Palaeontology* (Zack et al, 2019).

4.1.54. Supergene manganese ore records 75 Myr-long Campanian to Pleistocene geodynamic evolution and weathering history of the Central African Great Lakes Region – Tectonics drives, climate assists

The southeastern part of the Democratic Republic of the Congo locally hosts Proterozoic manganese deposits. The deposits of Kisenge-Kamata are the most significant, but manganese ores are also known to occur at Kasekelesa (former Katanga Province) and Mwene-Ditu (former Kasai Province). For the present study, cryptomelane-rich samples from these two localities were dated, using the 40Ar/39Ar step-heating method with a CO_2 laser probe. The ages obtained are within a range of c. 77 Myr to c. 2 Myr (Figure 70).

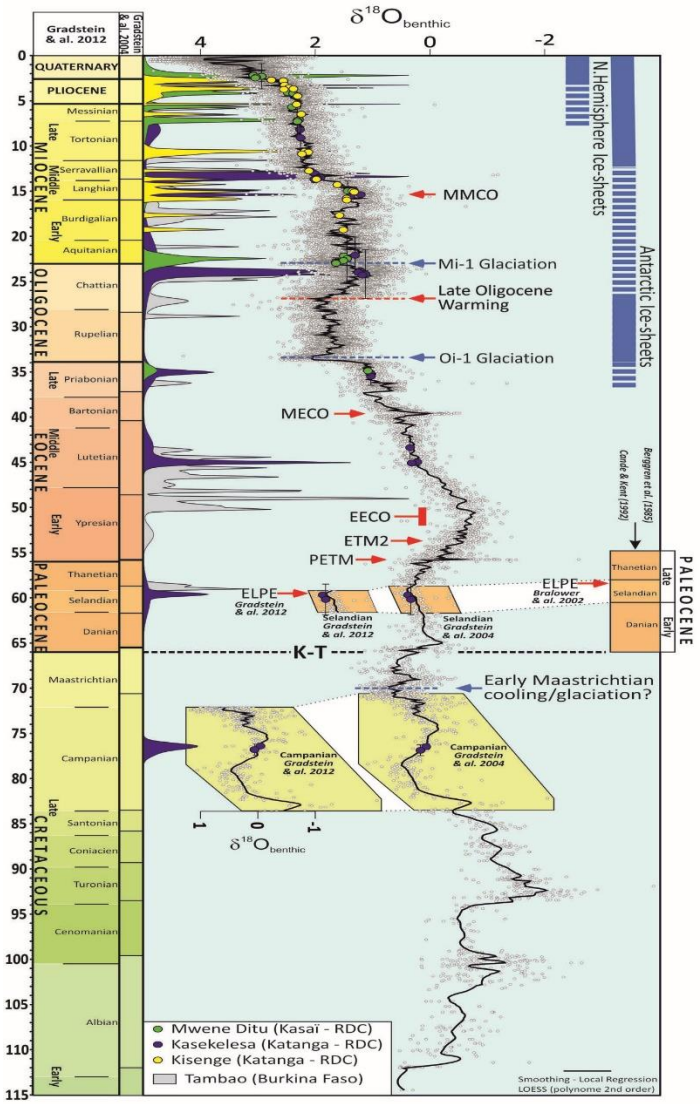

Figure 70. Validated ages and frequency diagrams of apparent ages (Kasekelesa (blue), Mwene-Ditu (green) and Kisenge (yellow)) vs. $\delta^{18}O$ benthic.

Cryptomelane formation took place at c. 76.4 Ma, c. 59.6 Ma, c. 45 Ma, c. 35 Ma, c. 23.8 Ma, c. 15.4 Ma, and c. 13.3 Ma at Kasekelesa, and it occurred at c. 35 Ma, c. 22.4 Ma, c. 15 Ma, c. 5.5–7.2 Ma, c. 3.6 Ma, and c. 2.1–2.3 Ma at Mwene-Ditu. The Campanian age (c. 76.4 Ma) recorded at Kasekelesa is the oldest 40Ar/39Ar age that has up to now been recorded for Mn ores from Africa. It documents the formation of oxidized ore along a Campanian or older erosion surface, which could be part of the 'African Erosion Surface'. The complete age record suggests that continent-wide tectonics accounts for most of the recognized supergene ore

formation episodes, controlled by vertical lithospheric movements that are ultimately responsible for alternating stages of landscape stability and erosion. Tectonics is thus regarded as the first-order control for secondary ore formation in Central Africa, over the last 80 Myr. Climate is a second-order control, because sufficient water supply is needed for supergene enrichment, whereby climatic conditions are recognized to have been favorable during some relatively cold Late Mesozoic and Paleogene periods, as well as during some humid and warm Neogene stages.

This study is published in *Gondwana Research* (De Putter et al, 2020).

4.1.55. Skeleton of a new owl from the early Eocene of North America (Aves, Strigiformes) with an accipitrid-like foot morphology.

We describe a partial skeleton of a large-sized owl from Wasatchian strata of the Willwood Formation (Wyoming, U.S.A.). The holotype of *Primoptynx poliotauros*, gen. et sp. nov., includes all major postcranial bones and is one of the most substantial Paleogene records of the Strigiformes. The fossil shows that owls exhibited a considerable morphological diversity in the early Eocene of North America and occupied disparate ecological niches. As in the protostrigid taxon *Minerva* from the late early to early middle Eocene of North America, but unlike in extant owls, the ungual phalanges of the hallux and the second toe of the new species are distinctly larger than those of the other toes (Figure 71).

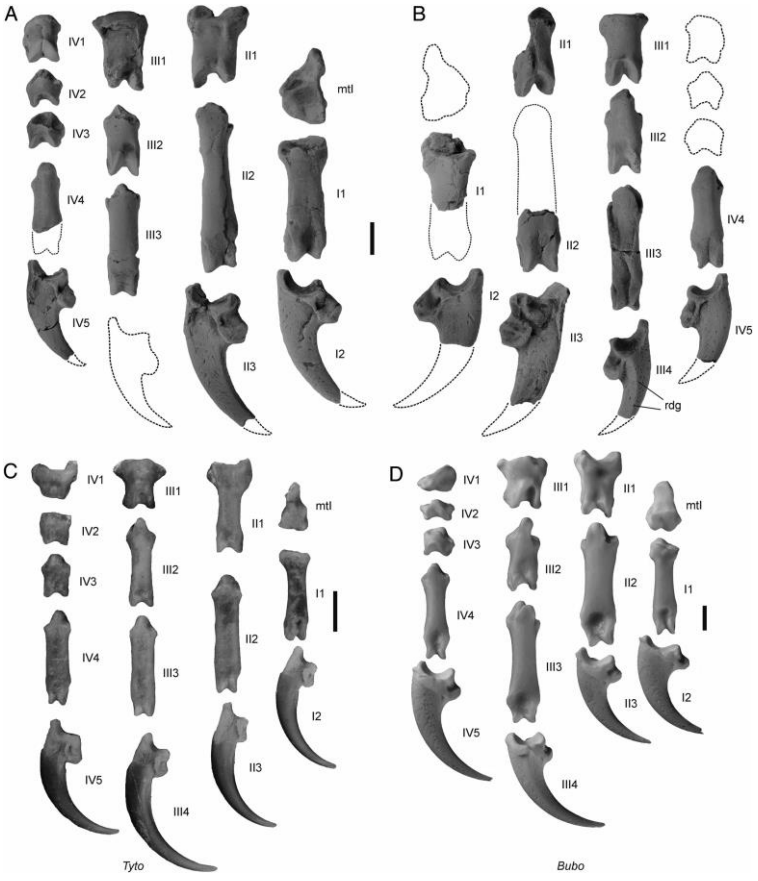

Figure 71. *Primoptynx poliotauros*, gen. et sp. nov., UMMP 96195, holotype, from the Willwood Formation of the northern Bighorn Basin, Wyoming, U.S.A., pedal phalanges in comparison with those of extant owls. Note the large ungual phalanges of the first and second toes of the fossil species. A, B, *P. poliotauros*, A, right and B, left feet. C, D, pedal phalanges of the right foot of C, *Tyto alba* (Tytonidae) and D, *Bubo scandiacus* (Strigidae); in C, the ungual phalanges bear the keratinous sheaths. Scale bars equal 5 mm.

Primoptynx poliotauros gen. et sp. nov., however, does not exhibit the derived tibiotarsus morphology of the Protostrigidae. Even though the new species may well be a stem group

representative of protostrigid owls, current data do not allow an unambiguous phylogenetic placement. Concerning the size of the ungual phalanges, the feet of *P. poliotauros* correspond to those of extant hawks and allies (Accipitridae). We therefore hypothesize that it used its feet to dispatch prey items in a hawk-like manner, whereas extant owls kill prey with their beak. *Primoptynx* and protostrigid owls were possibly specialized in foraging on prey items that required an accipitrid-like killing strategy, such as larger-sized or more defensive mammals. The extinction of these peculiar owls may have been related to the radiation of accipitrid diurnal birds of prey, which appear to have diversified in the late Eocene and early Oligocene.

This study is published in *Journal of Vertebrate Paleontology* (Mayr et al., 2020).

4.1.56. The upper Eocene-Oligocene carnivorous mammals from the Quercy Phosphorites (France) housed in Belgian collections

The Quercy Phosphorites Formation in France is world famous for its Eocene to Miocene faunas, especially those from the upper Eocene to lower Oligocene, the richest of all. The latter particularly helped to understand the 'Grande Coupure', a dramatic faunal turnover event that occurred in Europe during the Eocene-Oligocene transition. Fossils from the Quercy Phosphorites were excavated from the middle 19th century until the early 20th century in a series of sites and became subsequently dispersed over several research institutions, while often losing the temporal and geographical information in the process. In this contribution, we provide an overview and reassess the taxonomy of these barely known collections housed in three Belgian institutions: the Université de Liège, KU Leuven, and the Royal Belgian Institute of Natural Sciences (Figure 72).

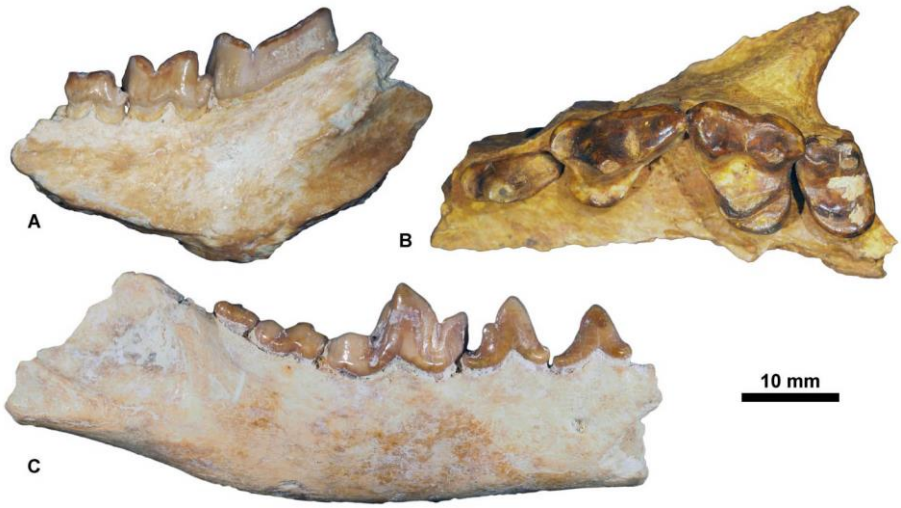

Figure 72. Carnivorous mammals from Pech du Fraysse (MP28) housed at the RBINS. A, *Hyaenodon leptorhynchus*, RBINS M 2326 (in labial view); B, *Cyonarctos dessei*, RBINS M 2327 (in occlusal view); C, *Phoberogale minor*, RBINS M 2328 (in labial view).

We focus our efforts on the carnivorous mammals (Hyaenodonta and Carnivoramorpha) and assess the stratigraphic intervals covered by each collection. These fossils are derived from upper Eocene (Priabonian), lower Oligocene (Rupelian), and upper Oligocene (Chattian) deposits in the Quercy area. The richness of the three collections (e.g., the presence of numerous postcranial elements in the Liège collection), the presence of types and figured

specimens in the Leuven collection, and some identified localities in the RBINS collection make these collections of great interest for further studies on systematics and the evolution of mammals around the 'Grande Coupure'.

This study is published in *Geologica Belgica* (Solé et al., 2021a).

4.1.57. Anatomy, Relationships, and Paleobiology of *Cambaytherium* (Mammalia, Perissodactylamorpha, Anthracobunia) from the lower Eocene of western India.

The anatomy of *Cambaytherium*, a primitive, perissodactyl-like mammal from the lower Eocene Cambay Shale Formation of Gujarat, India, is described in detail on the basis of more than 350 specimens that represent almost the entire dentition and the skeleton. *Cambaytherium* combines plesiomorphic traits typical of archaic ungulates such as phenacodontids with derived traits characteristic of early perissodactyls. *Cambaytherium* was a subcursorial animal better adapted for running than phenacodontids but less specialized than early perissodactyls (Figure 73). The cheek teeth are bunodont with large upper molar conules, not lophodont as in early perissodactyls; like perissodactyls, however, the lower molars have twinned metaconids and m3 has an extended hypoconulid lobe. A steep wear gradient with heavy wear in the middle of the tooth row suggests an abrasive herbivorous diet. Three species of *Cambaytherium* are recognized: *C. thewissi* (~23 kg), *C. gracilis* (~10 kg), and *C. marinus* (~99 kg). Body masses were estimated from tooth size and long bone dimensions. Biostratigraphic and isotopic evidence indicates an age of ca. 54.5 Ma for the Cambay Shale vertebrate fauna, the oldest Cenozoic continental vertebrate assemblage from India, near or prior to the initial collision with Asia. Cambaytheriidae (also including *Nakusia* and *Perissobune*) and Anthracobunidae are sister taxa, constituting the clade Anthracobunia, which is sister to Perissodactyla. We unite them in a new higher taxon, Perissodactylamorpha. The antiquity and occurrence of *Cambaytherium*—the most primitive known perissodactylamorph—in India near or before its collision with Asia suggest that Perissodactyla evolved during the Paleocene on the Indian Plate or in peripheral areas of southern or southwestern Asia.

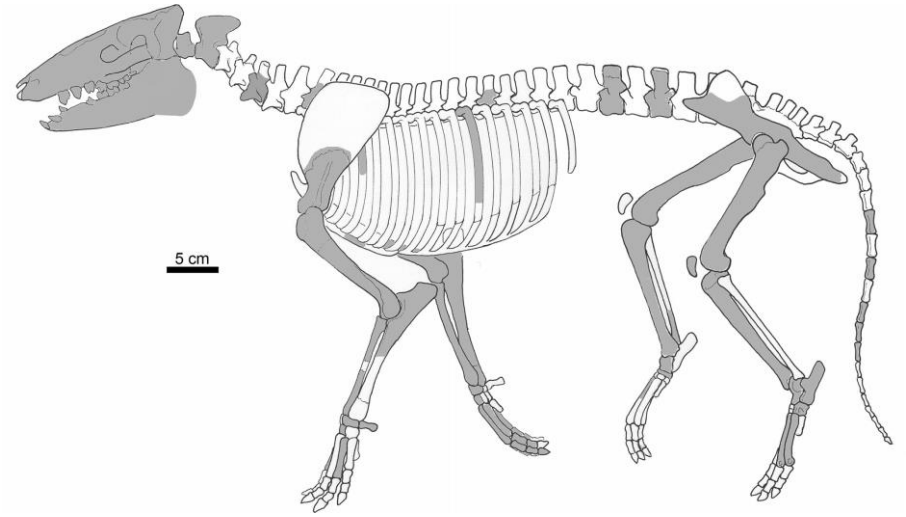

Figure 73. Skeletal reconstruction of *Cambaytherium thewissi*, with preserved elements shown in grey. Although much of the skeleton is represented, proportions should be regarded as approximate because

elements were found isolated and represent multiple individuals. Because phalanges cannot be assigned definitively to digit or limb, representative phalanges are shown only in one manus but likely represent both manus and pes.

This study is published in *Journal of Vertebrate Paleontology* (Rose et al., 2020).

4.1.58. New Specimens of *Frugivastodon* (Mammalia: Apatotheria) from the Early Eocene of India Confirm Its Apatemyid Status and Elucidate Dispersal of Apatemyidae

We here describe 18 new specimens of the sole apatemyid mammal known outside North America and Europe: *Frugivastodon cristatus* from the early Eocene Cambay Shale Formation of Vastan Lignite Mine, Gujarat, India. This mammal was previously represented by a single isolated lower molar, which hindered the establishment of its relationships among Apatemyidae. The new fossils show that the Indian apatemyid is unique and represents a new morphotype among this family. It is notably characterized by mesiodistally elongated lower molars with a reduced m3, a small hypocone on the upper molars, and a transversely wider M1 than in other apatemyids. The new data supports the inclusion of the enigmatic Uintan *Aethomylos* within Apatemyidae. The Indian *Frugivastodon* and the North American *Aethomylos* might represent a distinct clade of Apatemyidae that originated around the Paleocene-Eocene boundary. A paleobiogeographic analysis suggests that *Frugivastodon* dispersed from Europe into India during the early Ypresian. We also review the dispersal events that characterized the history of Apatemyidae (Figure 74).

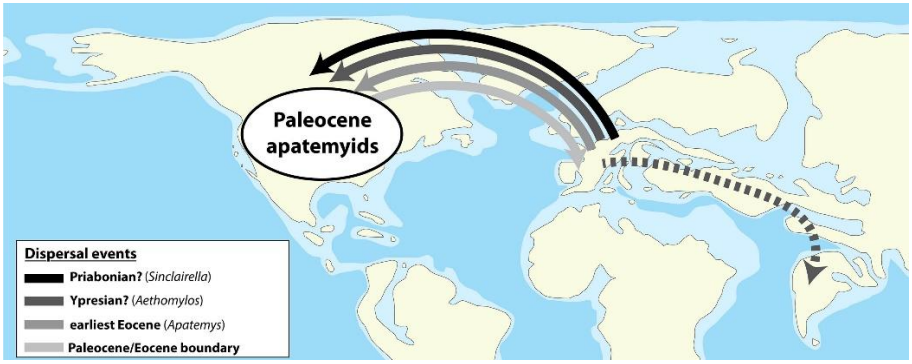

Figure 74. Schematic map showing the hypothetical geographic dispersion of apatemyids. Apatemyidae dispersed between North America and Europe via the Greenland Bridge and Thulean route; they dispersed from Europe to India probably through the Turgai Strait and/or along the Tethyan shore. Oldest apatemyids are recorded in the Paleocene of North America (Torrejonian) (Simpson 1940; McKenna 1963a; Szalay 1968; West 1973b). See text for explanations of the dispersal events. The exact timing of the dispersals of Apatemyidae in India is unknown but probably occurred in the Ypresian. Paleogeographic map adapted from Ron Blakey, Eocene (http://www2.nau.edu/rcb7/050Marect.jpg)

This study is published in Vertebrate Paleobiology and Paleoanthropology Series (Solé et al., 2020)

4.1.59. (U-Th)/He Dating of Supergene Iron (Oxyhydr-)Oxides of the Nefza-Sejnane District (Tunisia): New Insights into Mineralization and Mammalian Biostratigraphy

The mining district of Nefza-Sejnane (Tunisia) encloses numerous ores and raw material deposits, all formed in relation with successive Fe-rich fluids of meteoric and/or hydrothermal

origins. Here, for the first time in Tunisia, (U-Th)/He ages were obtained on supergene goethite from various localities/deposits of the district highlight direct dating of significant weathering episodes during late Tortonian and late Pleistocene. These weathering events are most likely associated with favorable conditions that combine (i) wet climate displaying sufficient meteoric water/fluid; and (ii) regional exhumation, due to large-scale vertical lithospheric movements enhancing the percolation of fluids. Matched with previous works, these results refine the stratigraphic frame for the polymetallic mineralization and clay deposits in the district, confirming the influence of meteoric fluids circulation during the late Cenozoic. As a consequence of the new (U-Th)/He data, we moreover propose a taxonomic and stratigraphic revision of the well-known mammalian fauna from the Fe-rich Douahria locality, suggesting an early Tortonian age for the fossils, i.e., prior to the first episode of meteoric event in the area (Figure 75).

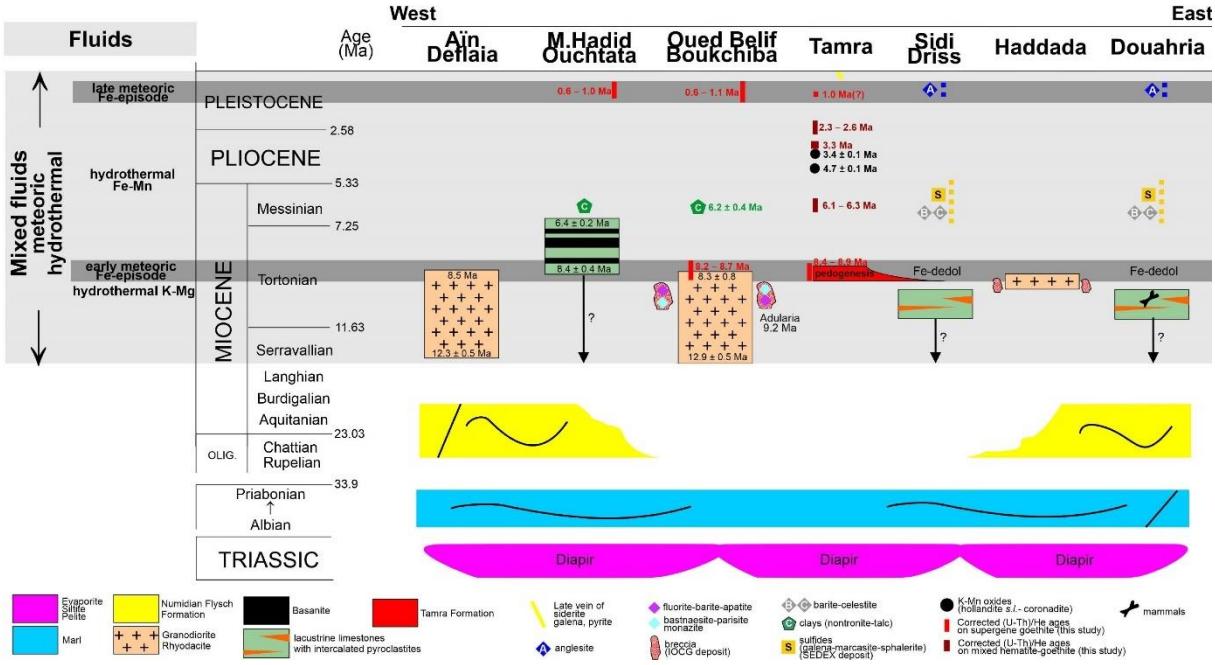

Figure 75. Stratigraphic frame of the Nefza-Sejnane district (Tunisia), including the new (U-Th)/He data on Fe (oxyhydr-)oxides. In red: data on supergene goethite; in red purple: data on mixed hydrothermal-meteoric hematite-goethite. Olig. = Oligocene. Questions marks (?) refer to potential larger stratigraphic extension.

This research is published in Minerals (Yans et al., 2021).

4.1.60. Additional vertebral material of *Thaumastophis* (Serpentes: Caenophidia) from the early Eocene of India provides new insights on the early diversification of colubroidean snakes

The Ypresian Cambay Shale Formation at Vastan, Mangrol, and Tadkeshwar lignite mines in Gujarat, western India, has yielded a rich vertebrate fauna including madtsoiid, palaeophiid, booid, and colubroidean-like snakes. The latter are particularly abundant, but their systematic affinities are difficult to resolve. Here we describe new specimens of the colubroidean-like snake *Thaumastophis missiaeni*, including anterior, middle, and posterior trunk vertebrae, as well as caudal vertebrae. The combination of primitive and derived caenophidian and

colubroidean vertebral characters confirms *Thaumastophis* as the earliest known stem-colubriform snake while *Procerophis*, from the same beds, is more derived and considered to represent a crown-Colubriformes. Additionally, *Thaumastophis* shares with *Renenutet enmerwer* from the late Eocene of Egypt a unique combination of vertebral characters that suggests an exchange with North Africa was possible along the southern margin of the Neotethys (Figure 76). We erect the new family Thaumastophiidae for *Thaumastophis* and *Renenutet* on the basis of their shared derived vertebral morphology.

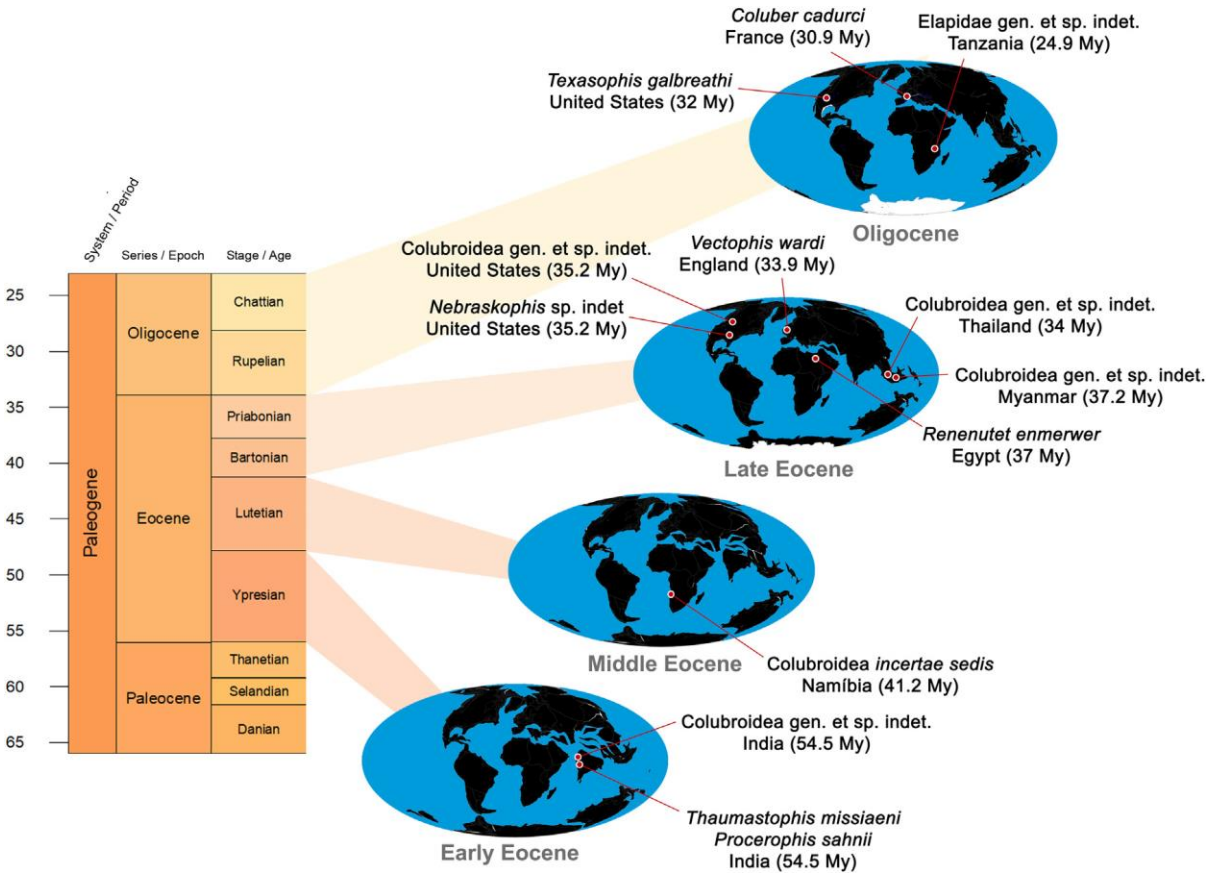

Figure 76. Distribution maps of colubroidean records in the Eocene and Oligocene. Early Eocene: *Thaumastophis missiaeni* and *Procerophis sahnii* (Ypresian of India; Rage et al., 2008); Colubroidea indet. (Ypresian of India; Rage et al., 2003). Middle Eocene: Colubroidea incertae sedis (Lutetian of Namibia; Rage et al., 2013). Late Eocene: *Renenutet enmerwer* (Priabonian of Egypt; McCartney and Seiffert, 2015); Colubroidea indet. (Bartonian of Myanmar; Head et al., 2005); Colubroidea indet. (Priabonian of Thailand; Rage et al., 1992); Colubroidea indet. (Priabonian of U.S.A.; Smith, 2013); *Vectophis wardi* (Priabonian of England; Rage and Ford 1980); *Nebraskophis* sp. (Priabonian of U.S.A.; Parmley and Holman, 2003). Oligocene: Elapidae indet. (Chattian of Tanzania; McCartney et al., 2014); *Coluber cadurci* (Rupelian of France; Rage, 1974); *Texasophis galbreathi* (Rupelian of U.S.A.; Holman, 1984).

This study is published in *Geobios* (Zaher et al., 2021).

4.1.61. Systematics and diversity of the giant soft-shelled turtles (Cryptodira, Trionychidae) from the earliest Eocene of Belgium

In 1909, the famous paleontologist Louis Dollo identified two putative new species of giant soft-shelled turtles from the lowest Eocene record of Belgium, '*Trionyx erquelinnensis*' and '*Trionyx*

levalensis', from Erquelinnes and Leval, respectively. However, these proposals did not meet the requirements of The International Code of Zoological Nomenclature, so they were considered as nomina nuda. The information on these specimens or about any other specimen of this lineage of giant turtles from the Belgian record is currently extremely limited. Relatively scarce material from giant trionychids has been described for the lower Eocene record of other European regions. Considering the available information, all the European material has recently been recognized as belonging to the genus *Axestemys*, which has a North American origin, and possibly attributable to a single species, *Axestemys vittata*, which currently lacks a diagnosis. Numerous and well-preserved Belgian specimens are deposited in the Royal Belgian Institute of Natural Sciences. In addition to the cited individuals from Erquelinnes and Leval, additional specimens from both localities, as well as others from Orp-le-Grand, are part of this collection. These specimens, found between the decades of 1910 and 1930, have been recently restored, and their study is carried out here.

The presence of *Axestemys vittata* in Belgium (in Leval and Orp-le-Grand) is confirmed (Figure 77). Knowledge about this species is significantly improved, and a diagnosis is proposed. However, the hypothesis proposed by Dollo is here confirmed, this species being not the only identified in the Belgian record. So, *Axestemys erquelinnensis* nov. sp. is defined based on the carapace from Erquelinnes known by Dollo, suggesting that the genus probably reached Europe during the Paleocene Eocene Thermal Maximum.

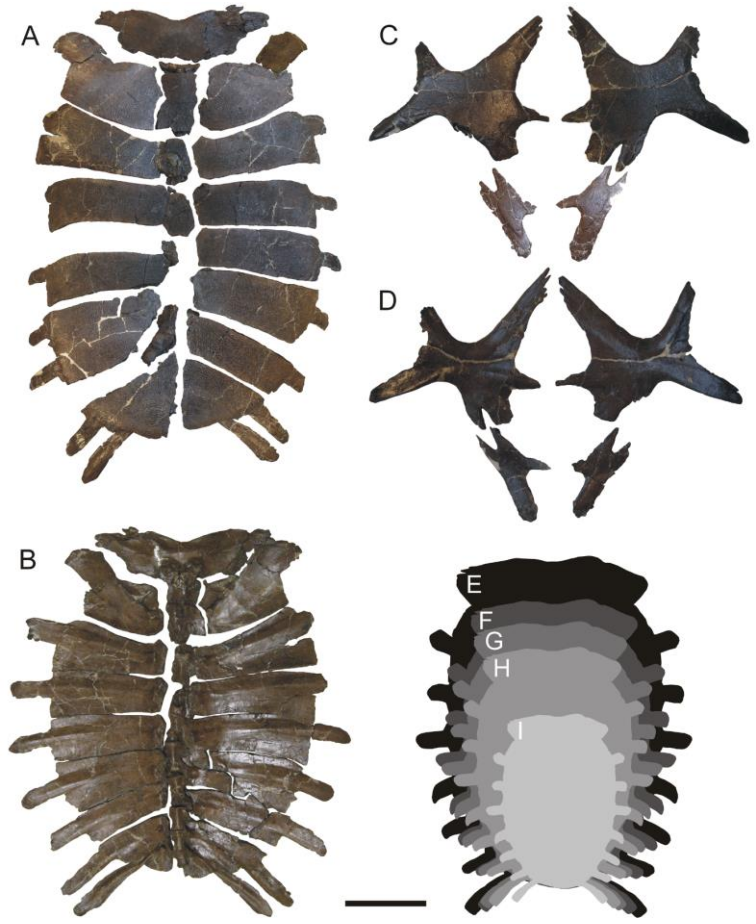

Figure 77. Shells of *Axestemys* (Cryptodira, Trionychidae), from the Tienen Formation (earliest Eocene) of Belgium. A–D. *Axestemys vittata* IRSNB R423, from Leval (Hainaut). A, B: carapace, in dorsal (A) and ventral (B) views; C, D: partial plastron, in ventral (C) and dorsal (D) views. E–I. Comparison of the length of the carapace of five Belgian specimens of *Axestemys*, using the profile of the individual of Erquelinnes IRSNB R86. E: IRSNB R423, *A. vittata*, from Leval; F: IRSNB R86, holotype of *A. erquelinnensis* nov. sp., from Erquelinnes (Hainaut); G: IRSNB R421, *A. vittata*, from Leval; H: IRSNB R420, *A. vittata*, holotype of '*Trionyx levalensis*', from Leval; I: IRSNB R428, *A. vittata*, from Orp-le-Grand (Walloon Brabant). Scale bar: 20 cm.

This study is published in *Geobios* (Pérez-García and Smith, 2021).

4.1.62. Presence of the large aquatic snake *Palaeophis africanus* in the middle Eocene marine margin of the Congo Basin, Cabinda, Angola

Ten isolated snake vertebrae from Landana and Sassa-Zao, Cabinda Exclave, Angola, present a “primitive” grade morphology with a weak lateral compression and do not belong to *Palaeophis* aff. *typhaeus* as originally referred to. They well belong to a single taxon and are here attributed to *Palaeophis africanus* for which the intracolumnar variation is described and illustrated (Figure 78). This species is Lutetian (middle Eocene) in age and originates from a marine coastal environment confirming again the aquatic capabilities of palaeophiid snakes. It represents the third largest species of *Palaeophis* with *P. colossaeus* and *P. maghrebianus* to which it is closely related in our tentative phylogenetic analysis, indicating that these three taxa could belong to an African clade. This study also contributes to the debate on the existence of primitive and advanced grades among palaeophiid snakes. *Palaeophis* presents laterally compressed anterior trunk vertebrae that could have been often erroneously considered as representing advanced grade species and potential parataxonomy.

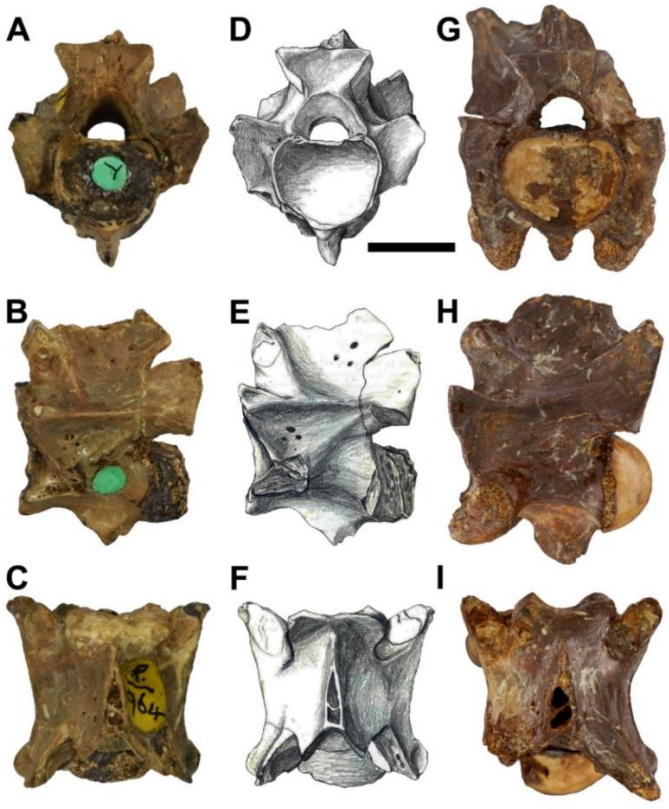

Figure 78. Comparison between the *Palaeophis africanus* vertebrae from Cabinda and Nigeria. A–C. NHMUK PV R 4964, trunk vertebra, holotype, in anterior (A), lateral (B) and dorsal (C) views. D–F. Drawings of NHMUK PV R 4964, trunk vertebra, holotype, in anterior (D), lateral (E) and dorsal (F) views. G–I. RMCA-RGP 16031a, anterior trunk vertebra in anterior (G), (reversed) lateral (H) and dorsal (I) views. Scale bar: 1 cm.

This study is published in *Geobios* (Folie et al., 2021).

4.1.63. A new basal raoellid artiodactyl (Mammalia) from the middle Eocene Subathu Group of Rajouri District, Jammu and Kashmir, northwest Himalaya, India

A new artiodactyl of moderate size, *Rajouria gunnelli* gen. et sp. nov., is described based on several dentaries, maxillae and isolated teeth from the middle Eocene Subathu Group of the Kalakot area, Rajouri District, Jammu and Kashmir, India (Figure 79). Despite its general resemblance with the family Dichobunidae by the retention of a paraconid on m1-2 and a

simple P4 where endocristids do not form an anterior loph, this taxon shares with Raoellidae two unambiguous characters: the presence of a hypoconid on p4, and an asymmetrical P4. The phylogenetic position of the new taxon within the Cetacea / Raoellidae clade is strongly supported by eight seven non ambiguous synapomorphies, among which a cristid obliqua on lower molars anteriorly pointing towards the postectoprotocristid, and a P3 with only two roots. The presence of a new basal raoellid in the middle Eocene Subathu Group sheds new light on the phylogeny and paleobiogeography of raoellid artiodactyls.

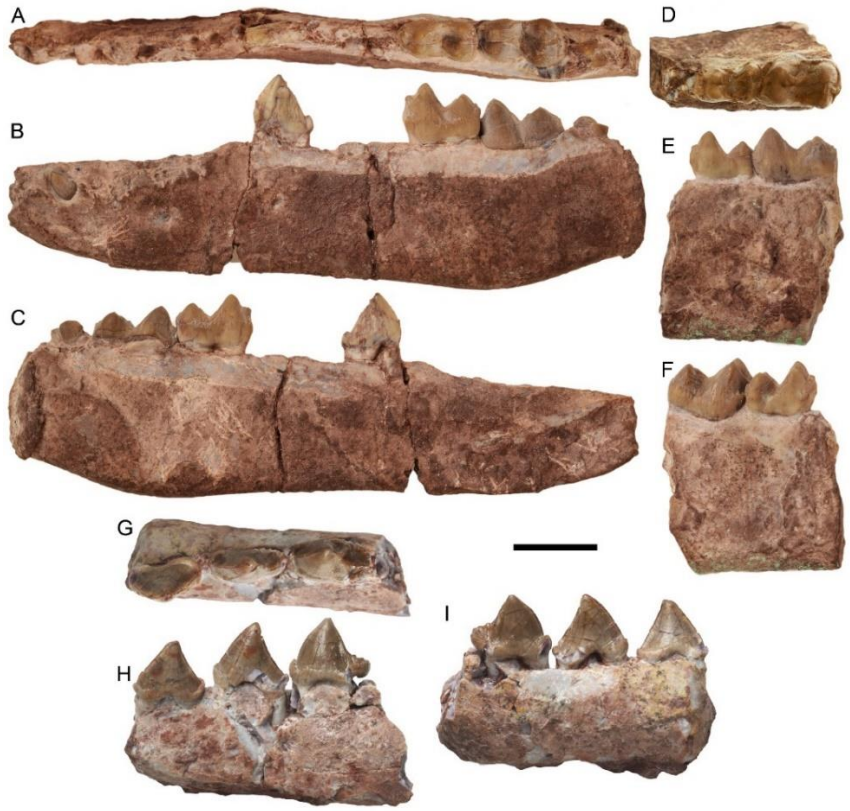

Figure 79. Lower dentition of *Rajouria gunnelli* gen. nov. sp. nov. A-C. GU/RJ/362, left dentary and holotype with i3 erupting, dp3, m1-2, trigonid part of m3 and alveoli of i1-2, c, p1-2, and p4 in occlusal (A), labial (B), lingual (C) views. D-F. GU/RJ/303, right dentary fragment with m1-2 in occlusal (D), labial (E), lingual (F) views. G-I. GU/RJ/144, left dentary fragment with p2-4 in occlusal (G), labial (H), lingual (I) views. Scale bar: 10 mm.

This study is published in *Geobios* (Rana et al., 2021).

4.1.64. New hyaenodonts (Mammalia) from the late Ypresian locality of Prémontré (France) support a radiation of the hyaenodonts in Europe already at the end of the early Eocene

We describe three new hyaenodonts from the late Ypresian locality of Prémontré (Aisne, France; close to MP 10 reference level). The new species – *Lesmesodon gunnelli* nov. sp., *Cynohyaenodon smithae* nov. sp., and *Eurotherium mapplethorpei* nov. sp. – represent the oldest occurrences of these three European genera. *Lesmesodon gunnelli* is also reported from the locality of Cuis (Marne, France; Ypresian, ≈MP 10). We further present the dentition of two specimens of *Lesmesodon edingeri* from Messel (Hessia, Germany; type locality of the genus) based on µCT scans (Figure 80). *Cynohyaenodon smithae* and *Lesmesodon gunnelli* support the presence of small (300-400 g) hyaenodonts in the late Ypresian of the Paris Basin. Estimation of dental indices indicates that these hyaenodonts had an insectivorous diet. The third species – referred to *Eurotherium* – may have weighed 4-5 kg and, based on dental indices, likely incorporated more vertebrate prey into its diet. We also performed a phylogenetic

analysis in order to test the relationships of these new taxa. These newly discovered species imply that the *Proviverra*/*Allopterodon*, *Cynohyaenodon*, and *Eurotherium* clades appeared in Europe earlier than previously known (i.e., Lutetian, MP 11). They reinforce the hypothesis that the hyaenodonts radiated during the middle-late Ypresian (MP 8/9-10) in Europe and adapted at that time to diverse ecological niches that they still occupied in the Priabonian (MP 13-14).

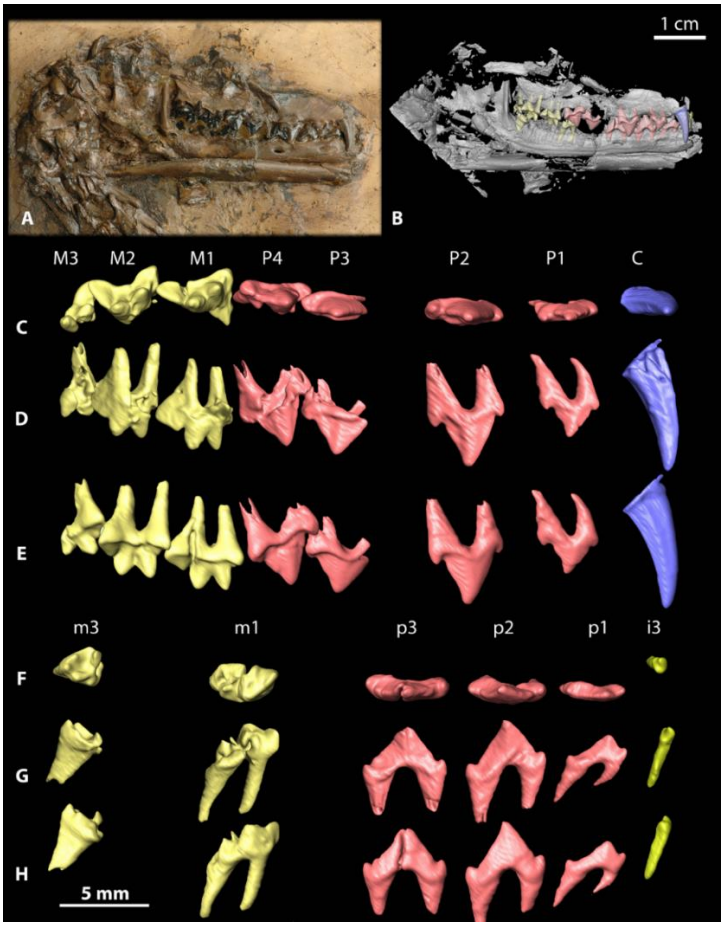

Figure 80. *Lesmesodon edingeri*, HLMD-Be 155. A, Original specimen in 1378 lateral view (right). B, Digitized specimen. C-E, right upper dentition; C, occlusal view; D, 1379 lingual view; E, labial view. F-H, right lower dentition; F, occlusal view; G, lingual view; H, 1380 labial view. Reversed views: D, G. Upper scale bar: A-B; lower scale bar: C-H.

This study is published in *Geobios* (Solé et al., 2021b).

4.1.65. New specimens of the mesonychid *Dissacus praenuntius* from the early Eocene of Wyoming and evaluation of body size through the PETM in North America

The Mesonychia is a group of archaic carnivorous mammals of uncertain phylogenetic affinities with a Holarctic distribution during the Paleogene. Intensive fossil collecting efforts in the Bighorn Basin, Wyoming, have resulted in recovery of the largest sample and most complete specimens yet known of the mesonychid *Dissacus praenuntius* from the second biozone of the Wasatchian North American Land Mammal Age (Wa-0). The Wa-0 biozone corresponds to the body of the Paleocene-Eocene Thermal Maximum (PETM), a brief but intense global warming event that occurred ~56 Ma ago that significantly impacted terrestrial mammal faunas, including dwarfing in many mammal lineages. To evaluate the potential response of this lineage to climate change, we compared the PETM sample of *D. praenuntius* with those recovered from just before the PETM in the last biozone of the Clarkforkian North American Land Mammal Age (Cf-3) and just after the PETM in the Wa-1 biozone (Figure 81).

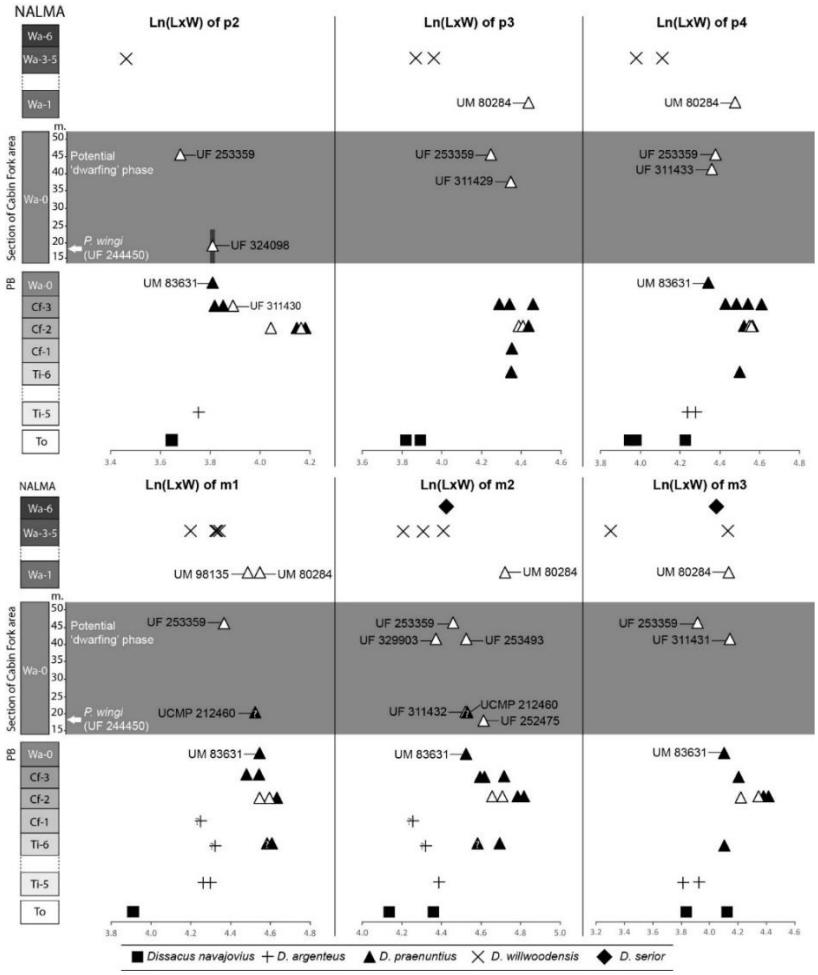

Figure 81. Sizes [ln (L × W) in millimeters] of lower premolars and molars of North American *Dissacus* species from the Torrejonian, middle Paleocene, through Wasatchian, early Eocene, strata. The range of variation expected in each sample is 0.40 units on a natural-log (ln) scale (mean ± two standard deviations, where s = 0.10; e.g., Gingerich, 1989, p. 25; Gingerich, 2019). Abbreviations: Cf = Clarkforkian; m = meter level in the Cabin Fork master section; PB = Polecat Bench; Ti = Tiffanian; To = Torrejonian; Wa = Wasatchian.

While the sample size is still too small to say with certainty, tooth size (as a proxy for body weight) of *D. praenuntius* appears to be smaller during the late PETM than during either the pre-PETM Cf-3, or post-PETM Wa-1 biozones, suggesting the possibility of a muted dwarfing response to the PETM. However, the pattern observed for *D. praenuntius* differs from that of many other PETM mammals, as the shift to smaller body size is less pronounced and may have only occurred in late Wa-0.

This study is published in *Geobios* (Solé et al., 2021c).

4.1.66. A reassessment of the Oligocene hyracoids from Malembo, Cabinda, Angola

The Oligocene Malembo locality, Cabinda exclave, Angola has yielded a rich vertebrate fauna represented by fragmentary remains. This fossiliferous locality is the only definite occurrence of Oligocene terrestrial mammals in sub-Saharan West Africa. The hyracoids from Malembo have only been very succinctly described and compared thus far, so that their systematic attribution is not consensual among specialists. A revision now allows the identification of three

(or four) medium to large-sized species represented by *Geniohyus dartevellei*, *Pachyhyrax* cf. *crassidentatus*, and two undetermined taxa (Figure 82). The species *G. dartevellei* is revived for the holotype of *Palaeochoerus dartevellei*; this species is unique to Malembo but appears close to *Geniohyus mirus*, a species only known from the early Oligocene of the Fayum, Egypt. Other species of *Geniohyus* and *Pachyhyrax crassidentatus* are also only known from the early Oligocene of the Fayum. The presence of *Geniohyus* and *Pachyhyrax* cf. *crassidentatus* at Malembo supports thus an early Oligocene age for the fauna.

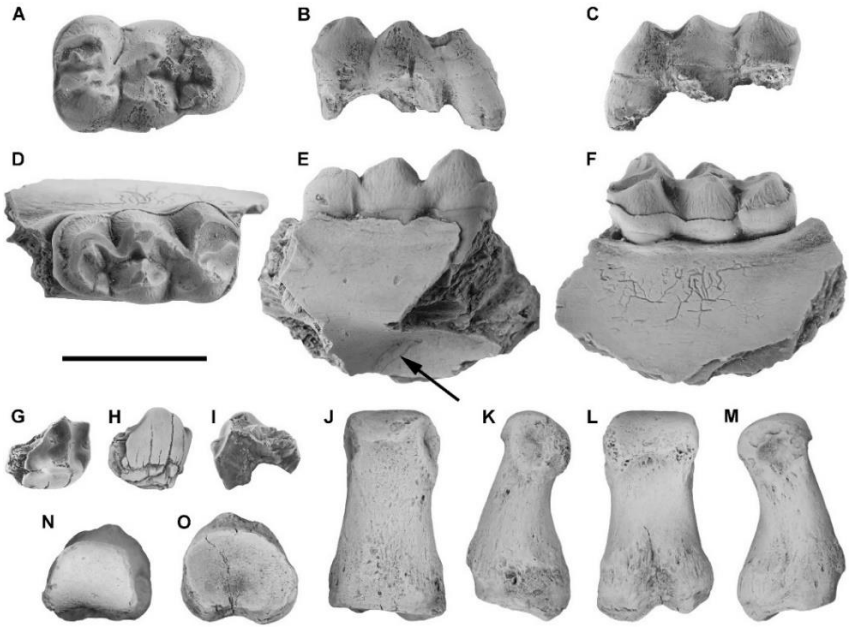

Figure 82. Hyracoids from Malembo, Angola: *Geniohyus dartevellei*, RMCA-RG6412, m3 in occlusal (A), lingual (B), and labial (C) views; *Pachyhyrax* cf. *crassidentatus*, RMCA-RG6423, m3 on a mandible fragment in occlusal (D), lingual (E), and labial (F) views (the arrow indicates the mandibular depression); Hyracoidea, gen. and sp. indet., RMCA-RG6416, fragment of m1 or m2 in occlusal (G), lingual (H), and labial (I) views; Hyracoidea, gen. and sp. indet., RMCA-RG6425, proximal phalanx in dorsal (J), plantar (K), and lateral (L, M), distal (N), and proximal (O) views. Scale bar = 1cm.

This study is published in *Geobios* (Tabuce et al., 2021).

4.2 Collateral Results

Together with eight field campaigns, 67 published papers, 72 communications at congresses, and organization of an international conference in Brussels, this project has also advanced :

- Recruitment of Dr. Floréal Solé as a postdoctoral researcher during 4 years at RBINS and 6 months at RMCA to specifically focus on the identification and comparison of mammal specimens. He successfully led 13 papers on Paleogene mammals, representing nearly 20% of the papers published in the framework of this project.

- Recruitment of Dr. Eric De Bast as postdoctoral researcher for 3 years at RBINS, thanks to a Belspo contract of additional researcher. This helped us to expand research activities on European Paleocene mammal faunas. Eric also helped with placing the type specimens and figured specimens of mammals from the RBINS collections on the web platform Virtual Collections (see below).

- Recruitment of Dr. Germain Bayon as postdoctoral researcher for 10 months at RMCA to focus on Paleogene geochemistry in order to understand the geodynamics of the Congo Basin.

- Recruitment of Shana De Clercq as researcher for 7 months at RMCA to realize thin section analysis, mineralogical analysis (XRD, calcimetry) and granulometry of the material from the sections of Landana, Bololo, Chiela, Kanzi, Manzadi and Sassa Zao. A bibliographic review on the geological setting of the wider Congo Basin has also been compiled.

- Recruitment and training of Dr. Thomas Steeman at the UGent to carry out a biostratigraphic study with dinoflagellate cysts in the framework of a PhD research. He brilliantly defended his thesis "*Paleocene-Eocene dinoflagellate cysts from Africa, India and Belgium. A taxonomic, stratigraphic and palaeoecological analysis*" on August 17th, 2020 and obtained the grade of Doctor in Science, Geology.

- Recruitment and training of Corentin Noiret at UNamur to carry out a PhD thesis on the chemostratigraphy of Paleocene-Eocene deposits of Europe and India. Unfortunately, due to personal issues, he had to postpone the public defense but this should take place in 2021.

- Training of Julie De Weirdt atUGent who completed a Master thesis in geology on Paleogene dinoflagellates of the Landana section in 2015.

- Recruitment and training of Ghéreint Devillet during 4 months at RBINS where he worked as a master student. His good results and ability to perform cladistic analysis were really helpful for several papers. Beside this, it was a good opportunity for G. Devillet to acquire several skills such as 3D segmentation and images processing for publications.

- Training of several students on the field such as Satish Gajwan, Waqaz Mirza, Raman Patel, Abhishek Pratap Singh (HNB Garhwal University, India) in order to collect fossils and learn screen-washing techniques (Figure 83). This contributed increased awareness of the paleontology at the local level.

Figure 83. Annelise Folie (RBINS) teaching Master student Abhishek Pratap Singh (HNB Garhwal University, India) for collecting microvertebrates by screen-washing technique (Photo: Thierry Smith, RBINS).

- Digitization of RMCA paleontological collections. More than two thousand records have been encoded by Florias Mees and Daniel Baudet in an Excel database for the early Paleogene sections excavated during the historical Belgian expeditions in DRC and Angola. Each specimen is catalogued together with its corresponding geological layer in order to study the stratigraphic distribution of the taxa.

- Digitization of important specimens housed at RBINS and made available for the public on the open access website http://virtualcollections.naturalsciences.be/virtual-collections/paleontology in the framework of a collaboration between projects DIGIT03 and PalEurAfrica. By this way, numerous type and figured specimens published in the framework of PalEurAfrica are now visible on "virtualcollections.be", including mammals from the Paleocene Belgian localities of Hainin (72 specimens), and Maret (5 specimens), as well as postcranial material of the primate *Teilhardina* (19 specimens) from the Eocene locality of Dormaal (Belgium, Figure 84).

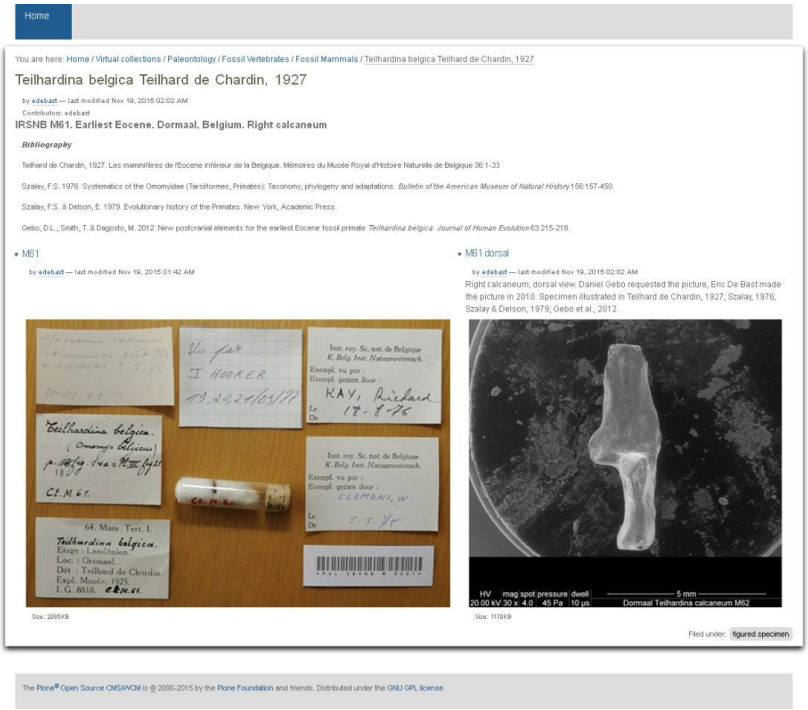

Figure 84. Overview of the digitization of a postcranial element of the early Eocene Belgian primate *Teilhardina belgica*

- Development and maintenance of excellent international collaborations. Among them, the Centre de Recherches Géologiques et Minières (CRGM) in DRC, and the HNB Garhwal University (Srinagar) and Wadia Institute of Himalayan Geology (Dehradun) in India. We hope to continue collaborations with these institutions, maybe in the scope of new discoveries in Kashmir. A first publication about an Eocene mammal from the Low Himalayas is in press (Rana et al., 2021).

- Development of an integrative and cooperative research network of 29 members + 117 collaborators (see 7.8.). This network is still very active and numerous collaborations continue independently from PalEurAfrica but have been initiated thanks to PalEurAfrica. It is obviously the thematic axis *3 Cultural, historical and scientific heritage* and more

specifically the research area *3.1 Cross- and interdisciplinary exploitation/valorisation of federal heritage resulting from scientific expeditions* that allowed the construction of this network. The starting point of this successful project is thanks to Belspo's choice to make a relatively open topic that corresponded perfectly with the historical missions of several Belgian federal institutions. This would have not been possible with a specific topic that would certainly have restricted the size of the scientific network.

5. DISSEMINATION AND VALORISATION

5.1. Results summary

The primary dissemination and valorisation of our results is evidenced by 67 full articles, 65 in impact factor journals (see point 6 of this report for details). Apart from this, 29 published abstract and 43 unpublished abstracts have been assembled in the framework of participation to international conferences, meetings and congresses where oral communications and posters were presented (see point 3.4 and 6 for details). In addition, our results have been disseminated through 34 interviews and press releases (see list below). Finally, we have demonstrated commitment to data sharing (results, expeditions, publications) on the website www.paleurafrica.be. Fossil specimens housed at the RBINS are also progressively available online through the platform http://virtualcollections.naturalsciences.be/virtual-collections/paleontology.

5.2. Media coverage

2014.03.10 Radio Campus ULB (radio) by Alexandre Wayenberg : "Science sans conscience" in the scope of the publication on the late Paleocene fauna from Rivecourt, France in the journal PLoS ONE (paper of Smith et al., 2014).

2014.11.20 11 press articles in the scope of the publication on the fossil mammal *Cambaytherium* and the origin of the perissodactyls in India in the scientific journal Nature Communication (paper of Rose et al., 2014). De Standaard (newspaper) : "Paarden ontstonden in India"; La Libre.be (web page) : "L'ancêtre du cheval, du tapir et du rhinocéros reconstitué en Inde » ; La Libre Belgique (newspaper) by Valentin Dauchot: « Voilà l'ancêtre du cheval et du rhinocéros », 2 full pages ; IFLScience (web page): "Mysterious 55 million years old rhino-horse relative found in India"; NBCNews.com (web page): "What horses and rhinos have in common: an ancestor in India"; Horses.nl (web page): "Paarden komen oorspronkelijk uit India"; Metro Fr (web page): "Les chevaux viennent d'Inde" ; National Geographic (journal) : "Fossil beast helps fill the backstory of horses, tapirs, and rhinos"; Sci-News.com (web page): "55-Million-year-old fossils suggest ancestor of rhinos, horses originated in India"; Tech Times (web page): "Ancestor of Horse and Rhino May Have Originated in India"; Discovery News (web page): "Ancient Rhino, Horse Relative Roamed 'Island' of India".

2014.11.20 News on the RBINS website in collaboration with Reinout Verbeke (RBINS Communication Survey): “Fossils Suggest Horses' Ancestors Originated in India” (“Les chevaux trouvent leur origine en Inde”). https://www.naturalsciences.be/en/news/item/2501

2015.02 Science Connection, volume 46: « Les chevaux trouvent leur origine en Inde » on the discoveries done in the Vastan Lignite Mine, Gujarat, India.

2016.06.27 News on the website published by Reinout Verbeke: “India was a Noah's Ark” (L’Inde était une arche de Noé”). https://www.naturalsciences.be/en/news/item/5984

2016.08.20 Deccan Herald: “Most ancient primate bone found”.

2016.07.01 Daily Science: “Gondwana's wildlife emerges from the ground” (« La faune du Gondwana surgit du sol »).

2016.08.23 News on the RBINS website in collaboration with Jonas Van Boxel (RBINS Communication Survey): “Discovery of the most primitive fossil primates” (“Découverte des fossiles de primates les plus primitifs”). https://www.naturalsciences.be/en/news/item/6149

2016.09.08 Science News: “Fossils hint at India’s crucial role in primate evolution”.

2016.09.12 IFLScience: “55-Million-Year-Old Fossils Hint That Primates First Evolved In India”.

2016.09.13 World News: “Fossil Discovery Hints That Primates First Evolved In India”.

2016.10.10 Science News for students: “Surprising primate fossils found in an Indian coal mine”.

2016.12.15 Discover Magazine: “Dawning of the Planet of the Apes”.

2017.06.09 News on the RBINS web site : “Bats appeared 7 million years before we expected” ("Des chauves-souris apparues 7 millions d’années plus tôt qu’on ne le pensait"). https://www.naturalsciences.be/en/news/item/6742

2017.06.28 Interview by Jean-Philippe De Vogelaere (Le Soir) in the scope of the special visit of the young authors of the book “The Maransart crocodile” ("Le crocodile de Maransart") at the RBINS.

2017.07.03 News on the RBINS web site: “The young authors of the book Basile, the Maransart crocodile” (“Les jeunes auteurs de Basile, le crocodile de Maransart”) on a private visit to the Museum”. https://www.naturalsciences.be/fr/news/item/6751/

2017.09.14 Development of exhibition “Apes” (« Singes ») press documentation in collaboration with Donatienne Boland and Reinout Verbeke (RBINS Communication Survey).

2017.10.10 Interview by Sophie Brems (RTBF) for the opening day of the exhibition “Apes” (“Singes”).

2017.10.11 News on the RBINS website “Where the apes come from ?” (“D’où viennent les singes ? »). https://www.naturalsciences.be/fr/news/item/9062/

2018.05.09 Video interview by Mr. Christopher Stern (Thomsonreuters) on the oldest bat of the genus *Myotis*, broadcast on RTBF channel in May 2018.

2019.04.04 News on the RBINS web site: “52 million years old birds found by palaeontology enthusiastics” (“Des oiseaux vieux de 52 millions d’années identifiés grâce à des amateurs”). https://www.naturalsciences.be/en/news/item/17614

2019.02.14 News on the RBINS web site: “Modern primates originated in Asia or North America”? (Les primates modernes originaires d’Asie ou d’Amérique du Nord?). https://www.naturalsciences.be/fr/news/item/17405/

2019.11.22 News on the RBINS web site: “Paleontologists discover mysterious hoofed animal that roamed India 54 million years ago” (“Des paléontologues découvrent un ongulé mystérieux qui vivait en Inde il y a 54 millions d’années”). https://www.naturalsciences.be/en/news/item/18404

2020.07.28 News on the RBINS web site: “Owl discovered that hunted like a hawk 55 million years ago” (“Découverte d’un hibou qui chassait comme un aigle il y a 55 millions d’années). https://www.naturalsciences.be/en/news/item/19165

5.3. Conclusions and perspectives

With eight field excavations (two in DRC and six in India), 67 publications (65 with impact factors), 29 published abstracts and 43 unpublished abstracts at international conferences, meetings and congresses, 34 interviews and press releases and a final international congress organised as a capstone for the project, we conclude that the PalEurAfrica project was efficient and successful. Our success results from a highly collaborative international research network. Partners at different institutions worked on different subjects at the same time in small groups of 2 or 3 partners. We also regularly engaged collaborators from outside PalEurAfrica (see list on point 7.8.). Importantly, some topics involved all partners together for more complex integrative works dealing with the paleontology and sedimentology of DRC and Angola. This system allowed our team to produce more publications and to broadly address the general theme of PalEurAfrica.

We anticipate that collaborations with the Centre de Recherches Géologiques et Minières (CRGM) in DRC (Figures 85 and 86), the HNB Garhwal University (Srinagar) and Wadia Institute of Himalayan Geology (Dehradun) in India will continue and that new joint projects will

be proposed to continue collaborative and complementary research in these countries (Figure 87).

Figure 85. The Centre de Recherche Géologique et Minière (CRGM) at Kinshasa, DRC, 2014 (Photo: Thierry Smith, RBINS).

Figure 86. The team is ready for the fieldwork. From left to right: Thierry Smith (RBINS), Patsy, Patrick & Nicole Kitambala Yaya (CRGM), Damien Delvaux & Daniel Baudet (RMCA), Elvis (CRGM) (Photo: Nancy Stevens, Univ. Ohio).

The project produced extraordinary and unexpected results, such as new tracks for primate origins (https://www.naturalsciences.be/fr/news/item/17405/), and the notion that perissodactyl origins involved India (Smith et al., 2015; https://www.naturalsciences.be/en/news/item/2501). Indeed, results on Paleogene vertebrates from India (several expeditions funded by grants from the National Geographic Society before 2015 and by the Leakey Foundation since 2015) have revealed a strong link with European and African faunas respectively. This hypothesis has been supported by the discovery of the early Eocene mammal assemblage from Tadkeshwar Lignite Mine (Smith et al., 2016). These important results supported our decision to include our studies on Indian vertebrates in the general results of PalEurAfrica.

Figure 87. Field crew in Tadkeshwar Lignite Mine, India, 2017. From left to right: Kenneth D. Rose (Johns Hopkins Univ.), Rachel Dunn (Des Moines Univ.), Rajendra S. Rana (Garhwal Univ.), Kishor Kumar (Wadia Inst.), Mohd Waqas (Garhwal Univ.), Imtiaz (local driver), Annelise Folie and Thierry Smith (RBINS) (Photo: Raman Patel, Garhwal Univ.).

A fruitful collaboration was developed with the CRGM of Kinshasa thanks to relationships with the RMCA. This helped to address obstacles concerned with organizing fieldwork in Central Africa, that would otherwise be problematic. However, no such scientific agreement exists between Belgium and Angola, hence permitting issues for fieldwork in Cabinda (Angola) hampered our ability to perform planned expeditions in 2015. Official procedures to develop a new cooperation program could take years to develop.

Another difficulty was the recruitment of researchers for UGent and RMCA that took a little longer than expected, due to the difficulty in identifying competent researchers in specific key domains. Taking our time on this matter was important in order to produce high quality, publishable results.

6. PUBLICATIONS

6.1. Peer reviewed papers

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6.4. Geobios special volume

A thematic doubled issue of the journal Geobios (issues 66-67) dedicated to the international congress PalEurAfrica and to the memory of our colleague Gregg L. Gunnell is published in 2021. It gathers 14 scientific articles and a foreword among which the following seven have already been cited here above as they have been published by partners of the PalEurAfrica project: Zaher et al. (2021), Pérez-García A. & Smith T. (2021), Folie et al. (2021), Rana et al. (2021), Solé et al. (2021a), Solé et al. (2021b), Tabuce et al. (2021). Next to these, the following seven other papers have been published by other participants of the congress:

Beard K.C., Métais G., Ocakoğlu F. & Licht A., 2021. An omomyid primate from the Pontide microcontinent of north-central Anatolia: Implications for sweepstakes dispersal of terrestrial mammals during the Eocene. *Geobios*. doi: 10.1016/j.geobios.2020.06.008.

Paepen M., Li H., Sun Y. & Smith T., 2021. A late early to early middle Eocene mammal assemblage from Bayan Ulan (Inner Mongolia, China): implication for the reassessment of the Arshantan Asian Land Mammal Age. *Geobios*. doi: 10.1016/j.geobios.2020.11.001.

McCartney J.A., Bouchard S.N., Reinhardt J.A., Roberts E.M., O'Connor P.M., Mtelela C. & Stevens N.J., 2021. The oldest lamprophiid (Serpentes, Caenophidia) fossil from the late Oligocene Rukwa Rift Basin, Tanzania and the origins of African snake diversity. *Geobios*. doi: 10.1016/j.geobios.2020.07.005.

Head J.J., 2021. A South American snake lineage from the Eocene Greenhouse of North America and a reappraisal of the fossil record of "anilioid" snakes. *Geobios*. doi: 10.1016/j.geobios.2020.09.005.

Claeson K.M., Ngasala S., Gottfried M.D., Roberts E.M., O'Connor P.M. & Stevens N.J., 2021. A new assemblage of Cenozoic lungfishes (Dipnoi: Lepidosirenidae) from the late Oligocene Nsungwe Formation, Rukwa Rift Basin, southwestern Tanzania. *Geobios*. doi: 10.1016/j.geobios.2020.09.004.

Boyer D.M., Miles L., Schaeffer, K. & Beard C., 2021. New dentaries of Chiromyoides (Primatomorpha, Plesiadapidae) and a reassessment of the "mammalian woodpecker" ecological niche. *Geobios*. doi: 10.1016/j.geobios.2021.03.002

Godinot M., Blondel C., Escarguel G., Lezin, Pélissié T., Tabuce R. & Vidalenc D., 2021. Primates and Plesiadapiformes from Cos (Eocene, Quercy, France). *Geobios*. doi: 10.1016/j.geobios.2021.03.004

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- REACHE collaborative network for the study of Tanzanian specimens (Blackburn et al., 2014).
- ONM, Tunis, Tunisia, project AC-1785 for the study of hyaenodontid mammals (Solé et al., 2016).
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