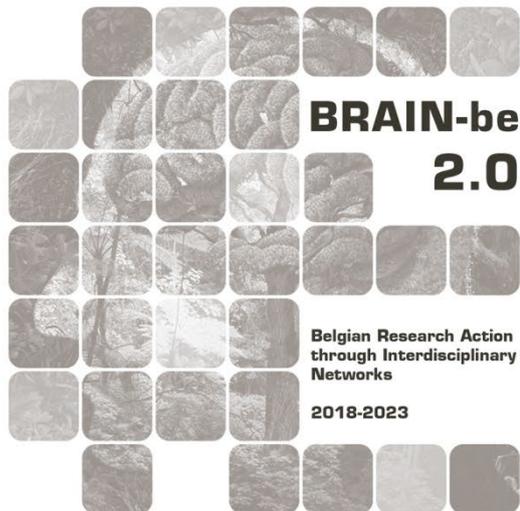


PERISSORIGIN

Origin and early radiation of perissodactyls based on precious fossil collections

Jérémy Tissier, Royal Belgian Institute of Natural Sciences (RBINS) – Thierry Smith, Royal Belgian Institute of Natural Sciences (RBINS)

Pillar 2: Heritage science



NETWORK PROJECT

PERISSORIGIN

Origin and early radiation of perissodactyls based on precious fossil collections

Contract - B2/233/P2/PERISSORIGIN

FINAL REPORT

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ABSTRACT

Perissodactyls (the odd-toed ungulates) comprise 17 extant species today, including horses, rhinoceroses and tapirs. Most species are greatly endangered and close to extinction. However, in the past, perissodactyls were one of the most diverse orders of large mammals, comprising iconic extinct creatures such as brontotheres or chalicotheres.

The project PERISSORIGIN aimed at understanding the origin and early radiation of perissodactyls. It proposed to reinvestigate these early perissodactyls and provide a new phylogenetic framework to discuss their paleobiogeography based on the RBINS collections.

The Collection objectives have been mostly fulfilled, since four specimens from Messel have been fully CT-scanned and segmented: a juvenile skull and two complete skeletons of *Eurohippus*, as well as the complete skeleton of *Hallensia* from the UNESCO world heritage Messel site (Middle Eocene). They have been partially described, and presented to congresses, and publications are in preparation. Surface scans of the four articulated perissodactyls specimens from the RBINS Messel collections have also been made. Other specimens from the RBINS collections (casts and originals) have been integrated in the phylogenetic analysis of early perissodactyls, and some have been reidentified.

The Scientific objectives have also been succeeded, since a comprehensive phylogeny of perissodactyls has been obtained and published. This phylogeny necessitated the creation of a new morphological character's matrix, and the scoring of 71 taxa (representing the largest sample of early perissodactyls, to date). This phylogeny is mostly based on dental characters, as well as a few cranial and mandibular ones. The phylogeny has also permitted to discuss the palaeobiogeography of early perissodactyls. It supports new hypotheses showing that early perissodactyls very quickly dispersed on the three continents from the Northern hemisphere (North America, Europe and Asia) during the Paleocene-Eocene Thermal Maximum (PETM; 56Ma), contrary to other scenarios that implied a strong endemism of early perissodactyls during the earliest Eocene. The topology suggests that contrary to previous hypotheses, Equoidea (horses) appeared later than previously expected, at around 49Ma rather than 56Ma, and were thus more derived than previously thought.

1. INTRODUCTION

Perissodactyls, or odd-toed ungulates, are a group of large mammals that comprise all extant species of rhinoceroses, horses and tapirs. Although they are mostly in danger of extinction today, they used to be a very diverse clade and include several lineages that are now fully extinct (e.g. brontotheres, chalicotheres and paleotheres).

The origin of this group in the fossil record remains poorly understood, since several different groups appear at the same time (during the earliest Eocene, around 56Ma), on three different continents: North America, Europe and Asia. In addition, almost all genera from this time period appear to be endemic to a continent, in contrast to almost all other modern mammal orders, that support the opposite view of large-scale distributions at the generic level, and thus of large-scale dispersals. For example, *Arenahippus* and *Cardiophus* were strictly North American, *Cymbalophus* and *Pliolophus* were strictly European, whereas *Erihippus* and *Orientalophus* were strictly Asian. The position of some major groups in the tree of perissodactyls also remains elusive, such as brontotheres and paleotheres, which makes the study of perissodactyls origin even more complex. Finally, even the closest sister-group of perissodactyls is still disputed. Some North American condylarths such as *Phenacodus* were

for a long time considered as the closest group to perissodactyls, but the discovery of Cambaytheridae from the Indian subcontinent has challenged this hypothesis. *Radinskya* from the Paleocene of China was also considered as a close sister group of perissodactyls. Finally, ancient collagen analysis has also suggested that some groups of endemic South American Native Ungulates (SANUs) could be sister groups of perissodactyls.

In addition, many species have been recently described in the last 10 years, that have not been included in large scale phylogenetic analyses yet. Including these taxa could greatly improve our understanding of perissodactyl's early evolution.

2. STATE OF THE ART AND OBJECTIVES

1. Data collection and specimen selection

The RBINS possesses a large collection of casts of perissodactyls from all over the world, that has been used as the main data source in the phylogenetic analysis. The specimens from Messel were also included in the sample, notably *Eurohippus messelensis*. Other specimens have been selected based on previous collection studies by the collaborators (Jérémy Tissier and Thierry Smith), particularly from the American Museum of Natural History (New York) and the Institute of Vertebrate Paleontology and Paleoanthropology (Beijing). Additional data have been collected in the Naturhistorisches Museum Basel during a collection visit to complete our sampling, in addition to the use of literature. The focus of the data sample has been to select holotype specimens, in addition to specimens found in their type locality, when the identification can be attested. Finally, another specimen from the RBINS has been integrated to this study, due to its very complete preservation and important stratigraphic age (earliest Eocene): the subcomplete mandible from Erquelinnes IRSNB M 167.



Lower jaw of Pliolophus quesnoyensis from Erquelinnes, Belgium (IRSNB M167), one of the oldest perissodactyls in the RBINS collections, alongside a skull of Eurohippus from Messel (Germany), preserved at RBINS.

The complete skeleton of an equoid displayed in the Belgian equine clinic Equitom in Lummen has also been investigated in this project, thanks to the work of a Master student (Charles Leriche).

2. Digitization of the collections

The RBINS possesses five exceptional specimens of perissodactyls from Messel, that were planned to be CT-scanned with X-ray tomography. The objective would be to make these specimens more accessible to researchers (since two of them are in exhibition at the RBINS and difficult to access), and to redescribe their anatomy, after segmenting and extracting 3D models of all bones and the dentition.

3. Phylogenetic analysis

Numerous studies have aimed to investigate the evolution of perissodactyls, but very few actually comprised a comprehensive taxonomic sample comprising all major groups of early perissodactyls. A table summarizing the focus points of those studies and their strengths is provided below (TABLE I). We have also noted the disadvantages of those matrices for the objective of the project PERISSORIGIN. Indeed, most of those matrices have focused on one or several particular groups, whereas our main objective is to understand the relationships and diversification of all groups of perissodactyls. We thus need to incorporate several representatives of all groups as well as all “problematic” taxa for which the position is uncertain. We also need to include as many as possible of the earliest representatives of all groups, and a good diversity of their geographic distribution in North America, Europe and Asia, to obtain a clear picture of their diversification.

TABLE I: COMPARISONS OF PUBLISHED MORPHOLOGICAL CHARACTER'S MATRICES WITH OUR NEW MATRIX

Study	N° of perissodactyls	N° of characters	Focus of the study	Strengths	Disadvantages for our study
Bai et al 2010	21	58	Chalicotheres	Good sample of chalicotheres	Low diversity
Bai et al 2017	19	73	Helaletidae	Good sample of helaletids	Low diversity
Bai et al 2018	33	70	Asian early perissodactyls	Good sample of Asian taxa (16 taxa)	Low representation of European (7 taxa) and North American taxa (9 taxa)
Bai et al. 2020	65	361	Ceratomorpha	Good sample of ceratomorphs and large number of characters	Low diversity
Bronnert et al. 2018	12	40	Isectolophidae	Good sample of isectolophids	Low diversity
Danilo et al. 2013	26	72	Palaeotheriidae	Good sample of palaeotheres	Low diversity
Froehlich 1999	36	125	Perissodactyla	Good diversity of perissodactyls	Very low representation of Asian taxa (1 taxon)
Froehlich 2002	29	121	Equidae	Good sample of early hippomorphs	Low diversity
Holbrook and Lapergola 2011				Same as Froehlich 1999	Same as Froehlich 1999

Hooker and Dashzeveg 2004	17	54	Early perissodactyls	Good diversity	Low number of taxa and characters
Kapur and Bajpai 2015	44	125	Early perissodactyls	Good diversity	Absence of brontotheres and chalicotheres
Missiaen and Gingerich 2014	22	60	Early perissodactyls	Good diversity	Low number of taxa and characters
Remy 2017	21	66	Palaeotheriidae	Good sample of palaeotheres	Low diversity
Remy et al 2019	25	66	Palaeotheriidae	Good sample of palaeotheres	Low diversity
Robinet et al. 2015	17	149	Lophiodontidae	Good sample of lophiodonts	Low diversity
Rose et al 2014	34	208	Early perissodactyls and Anthracobunia	Good diversity	Absence of recently described Asian taxa
Rose et al 2020	38	321	Early perissodactyls and Anthracobunia	Good diversity	Absence of recently described Asian taxa
Vautrin et al 2021	36	187	Early perissodactyls	Good sample of lophiodonts	Low diversity of Hippomorpha
Our study	65	101	Early perissodactyls		

Several recent taxa have also recently been described and have never been included in large scale phylogenetic analyses. Including these new taxa could potentially suggest new hypotheses on their identification or resolve some uncertain relationships.

4. Analysis of the evolutionary trends and diversity

The goal of this part of the project would be to interpret characters evolution based on the newly obtained phylogeny of early perissodactyls. This would allow us to study the evolution of important characters in perissodactyls evolution, such as molarization patterns, and finger reduction.

3. METHODOLOGY

WP 1: Data collection

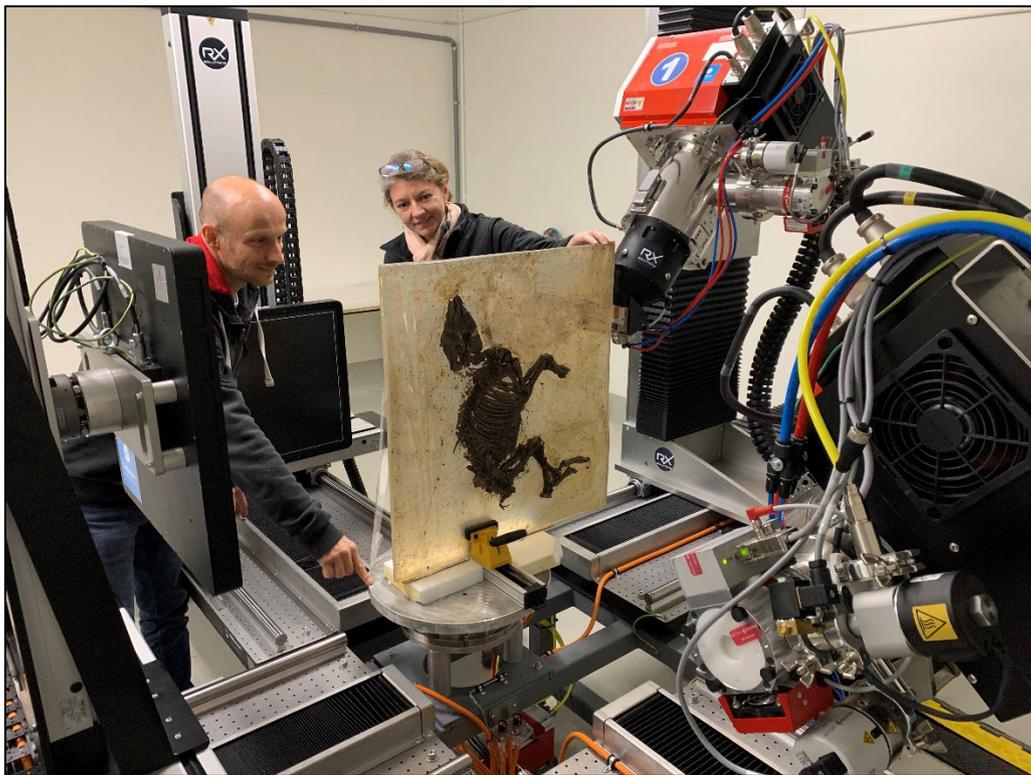
The project PERISSORIGIN has fully taken advantage of the large collection of high-quality casts of early perissodactyls of the RBINS collection (229 casts), which have been precious to score taxa the morphological data matrix and anatomical comparisons. This collection of casts has permitted to score 32 taxa in this matrix (about 50% of the total number of taxa). Some specimens have also been reidentified at the light of our new phylogenetic results.

Original specimens from the RBINS have also been included in this matrix, notably the perfectly preserved specimens of *Eurohippus messelensis* from Messel, as well as an almost complete lower jaw that was previously referred to as "*Cymbalophus*" but may finally belong to *Pliolophus* based on our new results.

In addition, a visit in the rich collections of the Natural History Museum in Basel (Switzerland) has also permitted to collect data for 6 additional taxa, and to enlarge the collection of casts of the RBINS thanks to mutual exchanges. Data gathered from previously developed projects were also used to score this matrix, as well as data obtained by collaboration with other researchers. Therefore, collection visits that were expected in the project proposal have been greatly reduced, reducing the cost and time necessary for this study.

WP 2: Digitization

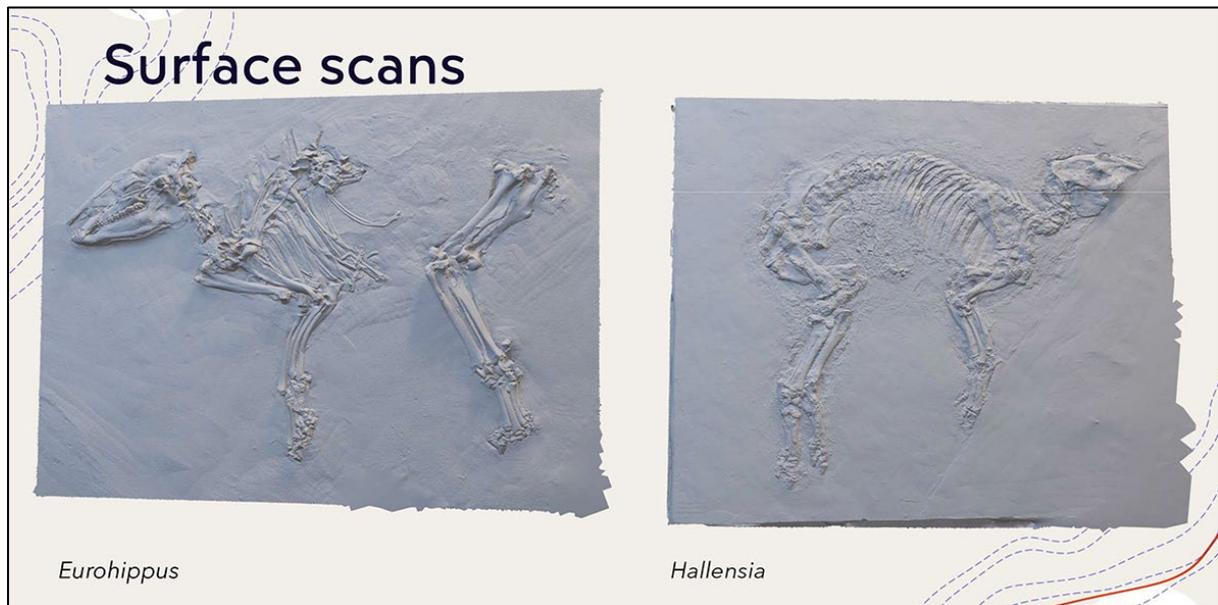
Four specimens from the Messel site at the RBINS have been CT-scanned during the project PERISSORIGIN. The first specimen selected was a juvenile skull of *Eurohippus messelensis* (IRSNB M 1852). This specimen was CT-scanned directly at the RBINS thanks to its small size and has permitted to confirm that X-ray microtomography could be successful to CT-scan this type of specimen, preserved on flat resin surface. Three other specimens have then been selected (two of *Eurohippus messelensis*, IRSNB M 1849 and 1841, each one complementary of the other for their anatomical parts; and one of *Hallensia*, IRSNB M 1465, the only available articulated skeleton in the world). However, due to their large size (more than 60x60cm), the RBINS microCT-scanner could not be used for this task. Very few microCT-scanners in Belgium, or Europe, could be used to scan such large specimen, with a very high resolution (less than 100 microns), necessary to extract the small teeth and smaller bones in three dimensions.



Installation of one of the RBINS Eurohippus specimens for micro Ct-scanning at Mateis lab, University of Lyon

The segmentation of these specimens was made with the software Avizo, and has permitted to extract most of the bones of these specimens, in good preservation. This work was also partially done by a Master student from UNamur (Charles Leriche), who was able to extract the tooth rows of one specimen of *Eurohippus*.

All four specimens have also been surface-scanned with a surface scanner, in addition to the last available specimen of perissodactyl from Messel, IRSNB M 1850 (*Eurohippus messelensis*). These scans do not permit access to any internal anatomy, but permit to visualize the surface as a photograph, with depth and height perception.



Two RBINS perissodactyl specimens surfaced scanned

All 3D models (individual bones and teeth in 3D obtained by segmentation, as well as surface 3D models) have been deposited on Morphosource and on the "Virtual Collections" platform (<http://virtualcollections.naturalsciences.be/>).

M 1465 *Hallensia matthesi*: [Showcase Media // MorphoSource](#) ply

M 1849 *Eurohippus messelensis*: [Showcase Media // MorphoSource](#) ply

M 1850 *Eurohippus messelensis*: [Showcase Media // MorphoSource](#) obj
[Showcase Media // MorphoSource](#) ply

M 1851 *Eurohippus messelensis*: [Showcase Media // MorphoSource](#) ply

WP 3: Study of the complete *Hallensia matthesi* housed at the RBINS

The study of the skeleton of *Hallensia matthesi* will mainly be carried out as part of a future project, funded by the Swiss National Science Foundation and developed in collaboration with the PERISSORIGIN project partners. All bones as well as the few preserved dental remains have been extracted in three dimensions by segmentation in Avizo and are thus ready for study. Preliminary results have been presented at the International Senckenberg Conference on the Messel Pit (8-12 December 2025) in Frankfurt.

WP 4: Description and valorization of the *Eurohippus* collection

The study of the four specimens of *Eurohippus* from the RBINS collection is in progress, after several months of segmentation in Avizo. Results have already been presented at the 2025 Congrès de l'Association Paléontologique Française (May 5-8) in Lille and at the International Senckenberg Conference on the Messel Pit (8-12 December 2025) in Frankfurt.

WP 5: Description of an intriguing anchitheriine from a private collection

This work has been principally undertaken by Charles Leriche, Master student from UNamur. We have been able to visit equine clinic Equitom of Lummen (Limburg Province) to observe an intriguing complete specimen of *Mesohippus* from South Dakota. This articulated skeleton supposedly possessed four well-developed forelimb fingers and three much longer hindlimb fingers, which is very unexpected for *Mesohippus*, a well-known Oligocene Equidae.

However, after careful inspection, the specimen was revealed to mostly consist of 3D printed elements (70% of the skeleton), especially the postcranial skeleton. The skull however is indeed real, and shows the classical morphology of *Mesohippus*. A report was thus made by the Master student, explaining which bones have been 3D-printed, and differentiating them from original ones. However, even though some bones were actually real, they did not belong to *Mesohippus*, or even to a perissodactyl, but to another kind of mammal.

This specimen is therefore not suitable for publication, but a future project could potentially focus on its very well-preserved skull, through CT-scanning methods. This would permit to observe the full dental morphology (hidden by the articulation of the lower and upper jaws), as well as other hidden characters, such as the bony labyrinth. Observing the teeth through CT-scanning could also permit to identify the species, which is yet unknown.

Therefore, contrary to what was hoped in the project proposal, no publication (excluding the report of Charles Leriche) will be dedicated to this specimen and it will not be integrated in the Virtual Collection.

WP 6: Creation of the phylogenetic matrix and analysis

It was necessary to create a new morphological character's matrix, specifically created for our objective, that would be able to recover the phylogeny of all groups of perissodactyls, including Isectolophidae, Tapiroidea, Rhinoceroidea, Lophiodontidae, Chalicotherioidea, Brontotherioidea, Palaeotheridae and Equidae. Specific characters had to be created to recover the relationships of each group, as each group possesses its own characteristics (e.g. the absence of hypocone on M3 in brontotheres, or the absence of metacone on M3 in rhinoceroses), as well as for the outgroups.

The resulting matrix comprises 101 characters: 7 on the skull, 42 on upper cheekteeth, 5 on the mandible, and 47 on the lower dentition. 71 taxa have been scored in this matrix, including 65 perissodactyls. It has been analysed with a parsimony algorithm in the TNT software, which resulted in 1254 equally parsimonious trees of 760 steps (retention index = 0.61 and homoplasy index = 0.85).

WP 7: Analyses of the phylogenetic topologies and of the evolutionary history of perissodactyls

After the phylogeny has been obtained, synapomorphies of the main clades of perissodactyls have been recovered in TNT, and traced on the topology in Mesquite. However, since our matrix only comprised craniodental characters, postcranial characters could not have been analyzed.

WP 8: Scientific communication

The main advances of the project PERISSORIGIN have been greatly communicated at local, national and international conferences: at the Young Researchers Overseas Day in Brussels, at the Annual Congress of the French Paleontological Association twice, and at the Annual Meeting of the Society of

Vertebrate Paleontology. Two other talks will also be presented during the International Senckenberg Conference on the Messel Pit in Frankfurt (December 2025).

A synthetic publication has been published in PNAS (*Earliest perissodactyls reveal large-scale dispersals during the PETM*) in January 2026.

At least one other paper will be dedicated to the analysis of the perissodactyls skeletons from Messel (in progress).

4. SCIENTIFIC RESULTS AND RECOMMENDATIONS

1. Data collection and specimen selection

The list of the taxa that have been scored in the matrix, and the source for characters observation is provided below in TABLE II.

TABLE II: TAXA SCORED IN THE NEW CHARACTER'S MATRIX WITH THEIR LOCALITIES AND SOURCES OF OBSERVATIONS (DIRECT AND/OR LITERATURE)

<i>Taxa</i>	<i>Direct observation</i>	<i>Locality</i>	<i>Reference</i>
<i>Arctocyon primaevus</i>	IRSNB (cast)	Cernay (France)	Russell 1964
<i>Arctocyonides arenae</i>	IRSNB (cast)	Cernay (France)	Russell 1964
<i>Bepitherium jordifusalbae</i> BMNH M36494	IRSNB (cast)	Les Vinyes and La Coma (Spain)	Checa and Colombo 2004
<i>Cambaytherium thewissi</i>	IRSNB (cast)	Ferry Cliff (UK)	Hooker 1984
<i>Cardiolphus europaeus</i>	IRSNB	Vastan (India)	Rose et al. 2014; 2019
<i>Cardiolphus laoshanensis</i>		Le Quesnoy (France)	Bronnert et al. 2018
<i>Cardiolphus radinskyi</i>	IRSNB (cast)	Wutu (China)	Tong & Wang 2006
<i>Cardiolphus semihians</i>	IRSNB (cast)	Bighorn Basin (USA)	Gingerich 1991
<i>Chasmotherium depereti</i>		Bighorn Basin (USA)	Gingerich 1991
<i>Cymbalophus hookeri</i>		Robiac (France)	Remy 2015
<i>Danjiangia pingi</i>	ISEM (cast)	Palette (France)	Godinot et al. 1987
<i>Desmatotherium guyoti</i>		Danjiangkou (China)	Wang 1995
<i>Eolophiodon laboriense</i>	NMB (Casts)	Bridger Basin (USA)	Scott 1883
<i>Eomoropus amarorum</i>	IRSNB (Cast of CM No. 3109)	La Borie (France)	Robinet et al. 2015
<i>Eotitanops borealis</i>	AMNH FM 14887	Washakie Basin and Uinta Basin (USA)	Radinsky 1964
<i>Epihippus uintensis</i>		Wind River Basin (USA)	Osborn 1913 ; Mader 2010
<i>Erihippus tingae</i>		southern California (USA)	Kelly and Murphey 2016
<i>Erihippus tingae</i>	IRSNB (cast)	Lingcha Formation (China)	Bai et al. 2018
<i>Eurohippus messelensis</i>	IRSNB	Messel (Germany)	Franzen 2006; 2017
<i>Gandheralophus minor</i>	IRSNB (cast)	Gandhera Quarry (Pakistan)	Missiaen and Gingerich 2012
<i>Gandheralophus robustus</i>	IRSNB (cast)	Gandhera Quarry (Pakistan)	Missiaen and Gingerich 2012
<i>Ghazijhippus talibhasani</i>		Kingri (Pakistan)	Missiaen & Gingerich 2014
<i>Grangeria anarsius</i>		Wind River Basin (USA)	Gazin 1956
<i>Hallensia matthesi</i>	IRSNB (cast)	Geiseltal (Germany)	Franzen & Haubold 1986; Franzen 1990
<i>Helaletes nanus</i>	AMNH FM 13124 AMNH FM 11635 NMB (Casts)	Bridger Basin (USA)	Radinsky 1963

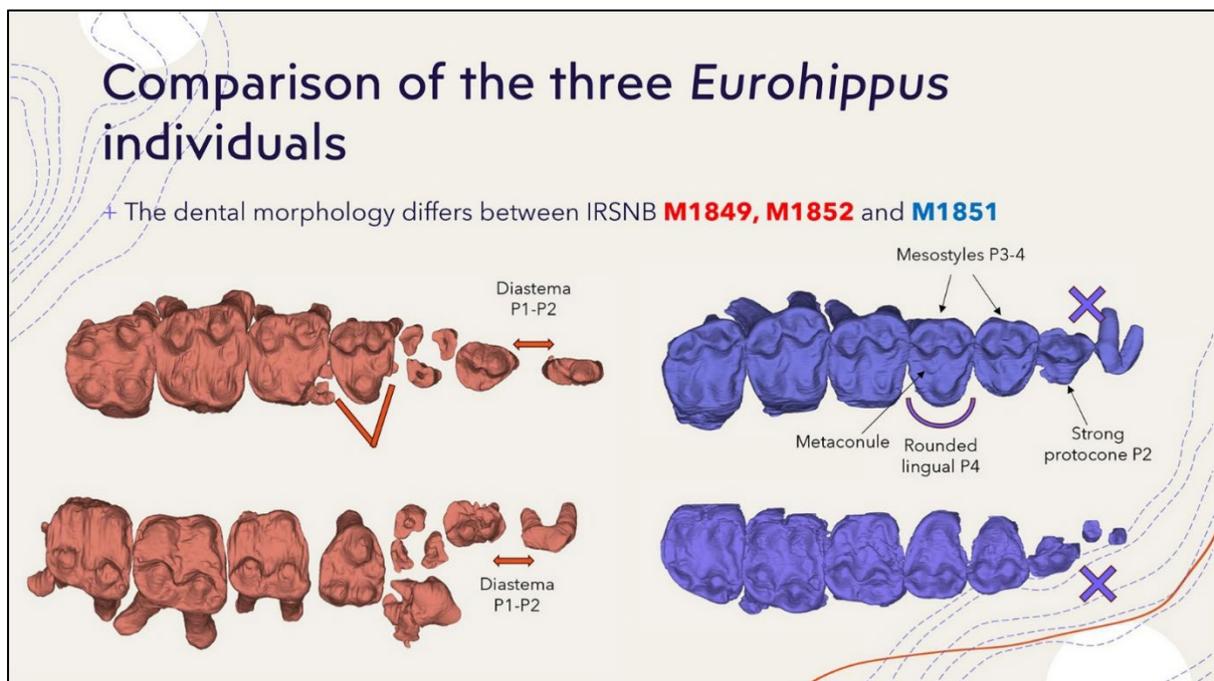
<i>Heptodon calciculus</i>	NMB (Cast of AMNH FM 14884)	Wind River Basin (USA)	
<i>Homogalax protapirinus</i>	AMNH, IRSNB (Cast)	Bighorn Basin (USA)	
<i>Hyrachyus modestus</i>		Bridger Basin (USA)	Bai et al. 2017
<i>Hyracotherium leporinum</i>	IRSNB (cast), NHM (photos)	Herne Bay (UK)	Owen 1841
<i>Irenolophus qii</i>		Huheboerhe (China)	Bai et al. 2019
<i>IRSNB M 167</i>	IRSNB	Erquelinnes (Belgium)	Missiaen et al 2013
<i>Isectolophus annectens</i>	AMNH	White River Basin (USA)	
<i>Isectolophus latidens</i>	AMNH FM 10640 AMNH FM 12221	Green River Basin (USA)	
<i>Kalakotia simplicidentata</i>	IRSNB (cast)	Kalakot (India)	
<i>Karagalax mamikhelensis</i>	IRSNB (cast)	Barbora Banda I (Pakistan)	Maas et al. 2001
<i>Lambdotherium popoagicum</i>	IRSNB (cast)	Bridger Basin (USA)	Bonillas 1936; Lucas and Holbrook 2004
<i>Litolophus gobiensis</i>	AMNH FM 26647	Nuhetingboerhe (China)	Bai et al. 2010
<i>Lophiaspis maurettei</i>		Palette (France)	Vautrin et al. 2021
<i>Lophiotherium cervulum</i>		Euzet les Bains (France)	Depéret 1917
<i>Mesohippus bairdi</i>	AMNH	White River Basin (USA)	
<i>Mesolambdolophus setoni</i>		Bridger Basin (USA)	Holbrook and Lapergola 2011
<i>Metanchilophus castrensis</i>	MHNT-PAL-2010-0-6	Castres (France)	Remy 2012
<i>Moropus elatus</i>	AMNH 11322	Harrison Formation or Upper Harrison Formation (USA)	Coombs 1978
<i>Orohippus pumilus</i>		Bridger Basin (USA)	Kitts 1957
<i>Pachynolophus eulaliensis</i>	IRSNB (cast)	St Eulalie (France)	Danilo et al 2013
<i>Pachynolophus livinierensis</i>	IRSNB (cast)	La Livinière (France)	Savage et al. 1965
<i>Palaeosyops paludosus</i>	NMNH (photos)	Bridger Basin (USA)	Gunnell and Yarborough 2000; Mader 2010
<i>Palaeotherium lautricense</i>	MHNT-PAL-2006-0-54	Montespieu (France)	Remy 1992
<i>Pappaceras meiomenus</i>	IVPP (Photos)	Huheboerhe (China)	Wang et al. 2016
<i>Perissobune intizarkhani</i>	IRSNB (cast)	Kingri (Pakistan)	Missiaen & Gingerich 2014
<i>Phenacodus intermedius</i>	IRSNB (cast)	Powder River, Bighorn, Wind River, Green River, Washakie, Laramie, Piceance, Huerfano, and San Juan Basins, and Big Bend National Park (USA)	Thewissen 1990
<i>Pliolophus barnesi</i>	IRSNB (cast)	Abbey Wood (UK)	Hooker 2010
<i>Pliolophus grangeri</i>	IRSNB (cast)	Bighorn Basin (USA)	Gingerich 1991
<i>Pliolophus quesnoyensis</i>	IRSNB (cast)	Le Quesnoy (France)	Bronnert et al. 2018
<i>Pliolophus sandrae</i>	IRSNB (cast)	Bighorn Basin (USA)	Gingerich 1989
<i>Pliolophus vulpiceps</i>	IRSNB (cast), NHM (photos)	Harwich (UK)	Owen 1858
<i>Propachynolophus gaudryi</i>		Indeterminate, "Ageian fauna", near Cuis (France)	Savage et al. 1965; Bronnert et al. 2023
<i>Propachynolophus levei</i>	IRSNB (cast)	Condé-en-Brie (France)	
<i>Propalaeotherium helveticum</i>	NMB	Egerkingen (Switzerland)	Savage et al. 1965
<i>Propalaeotherium isselanum</i>	NMB (Casts)	Geiseltal (Germany)	

<i>Propalaeotherium voighti</i>	NMB (Casts)	Geiseltal (Germany)	
<i>Protomoropus gabuniai</i>		Tsagan Khushu (Mongolia)	Hooker & Dashzeveg 2004
<i>Protorohippus venticolum</i>		Wind River Basin (USA)	Cope 1884; Wortman 1896
<i>Qianohippus magicus</i>		Shinao Basin (China)	Bai 2017
<i>Radinskya yupingae</i>	IVPP (3D model)	Datang (China)	McKenna et al. 1989; Holbrook 2014
<i>Systemodon tapirinus</i>	AMNH FM 55267	Castillo Pocket (USA)	
<i>Tetraclaenodon puercensis</i>	IRSNB (cast)	San Juan Basin (USA)	Kondrashov and Lucas 2012
<i>Thuliadanta mayri</i>		Ellesmere Island (Canada)	Eberle 2005
<i>Xenicohippus craspedotum</i>	AMNH FM 4831	Bighorn Basin (USA)	
<i>Xenicohippus osborni</i>		Huerfano Basin (USA)	Bown and Kihm 1981
<i>Yimengia magna</i>		Nomogen Formation (China)	Bai et al. 2020

2. Digitization of the collections

The CT-scan has permitted to reveal some unexpected details. Indeed, the adult teeth of the juvenile skull of *Eurohippus messelensis* were preserved below the decidual dentition, although not perfectly formed yet. In addition, its petrosal was also preserved, as well as a large part of the bony labyrinth inside of it. We have also been able to confirm the presence of a short metatarsal 5 on one specimen of *Eurohippus*, indicating that its hindlimb was still partly four-fingered. Finally, we have also observed that the specimen of *Hallensia* showed potential signs of decomposition by necrophagous insects, which is completely unexpected in comparison to the other specimens.

Interestingly, the teeth of the three individuals of *Eurohippus messelensis* show at least two different morphologies, indicating the possibility of two different species.



Dentition in 3D extracted from the RBINS *Eurohippus* complete skeletons

One individual shows the typical morphology of another species of *Eurohippus*, *E. parvulus*, which has not yet been identified in the locality of Messel, nor during this time period. This could thus indicate either a very large intraspecific variability in this genus, and the possible synonymy of those two species, OR a longer time range for the species *E. parvulus*, OR that the Messel locality might include some layers that are younger than expected. Further work is needed to test these hypotheses.

Two complete skeletons have been segmented representing 63 isolated 3D models of individual bones for IRSNB-M-1849, in addition to the four tooth rows, and 50 isolated 3D models for IRSNB-M-1851, in addition to the tooth rows as well. Finally, the teeth (decidua and adult), petrosal and bony labyrinth of the juvenile skull (IRSNB M 1852) have also been extracted. These specimens have also been used to score the morphological character's matrix used for the phylogenetic analysis.

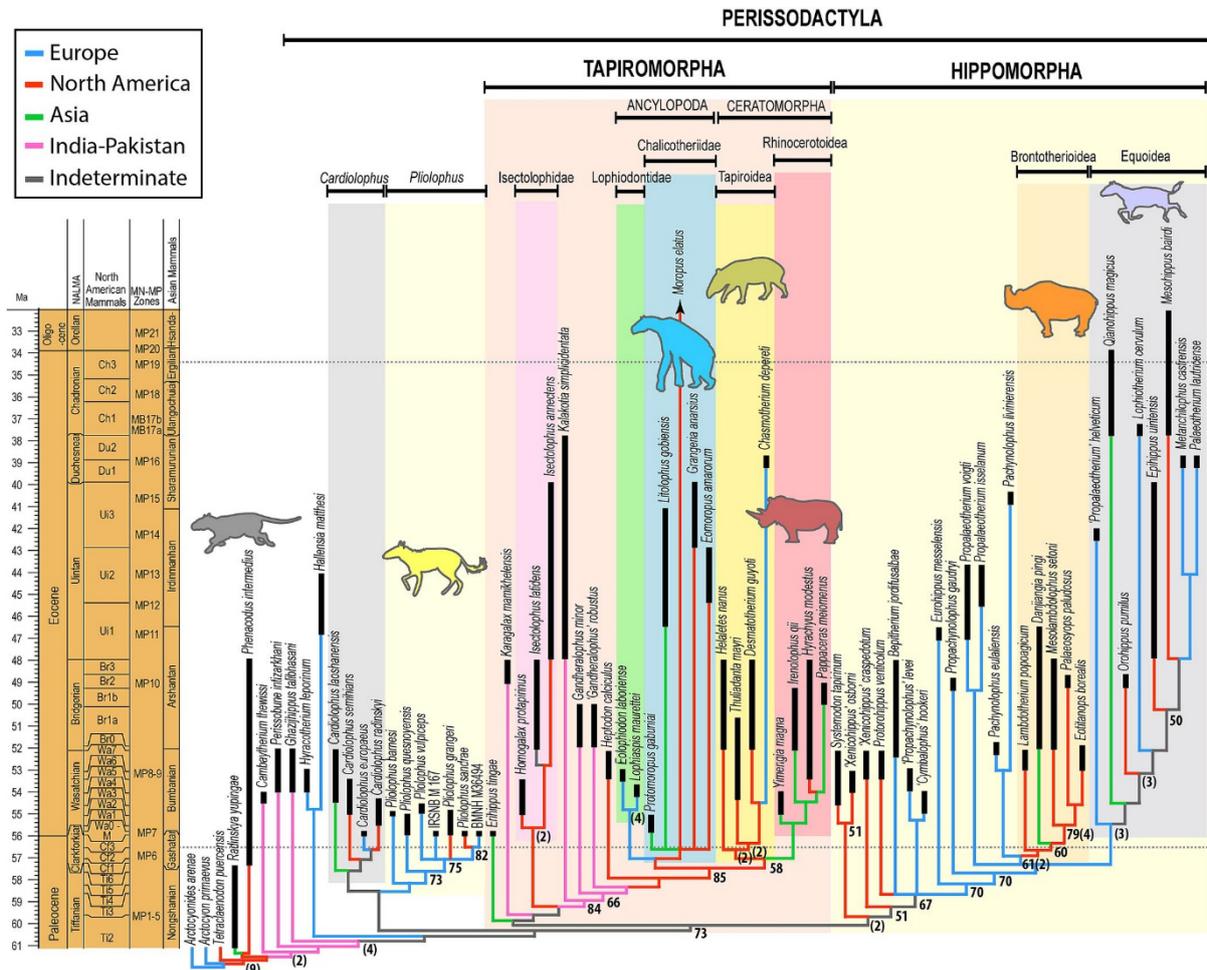
3. Phylogenetic analysis

The phylogenetic analysis, based on the new morphological characters matrix, have revealed interesting results, that have now been published in the *Proceedings of the National Academy of Sciences (PNAS)* in January 2026.

These major results can be summarized in several main points:

1. The number of early perissodactyls genera was overestimated in the past, and we propose to synonymize some of them. The Eurasian *Chowliia* should be considered as a junior synonym of the North American *Cardiophus* and the North American *Sifhippus* and *Arenahippus* should be considered as junior synonyms of the European *Pliolophus*. However, we still consider all species previously named within these genera as valid.
2. This new taxonomic configuration implies that all the species within these two genera (*Cardiophus* and *Pliolophus*) must have quickly dispersed on three continents (North America, Europe and Asia) where they have been found, rather than being the results of a local endemic speciation as previously suggested by their taxonomy.
3. These very fast dispersals may have happened around 56Ma, during the Paleocene-Eocene Thermal Maximum, a period of very high temperature, that drove migrations of many other mammals (Smith et al. 2006) or even before (Tabuce et al 2025).
4. We also show that contrary to previous identifications, *Hyracotherium* clearly differs from all other known perissodactyls, in particular those from North America, and that it is actually much more basal than previously thought, and should not be considered as an Equoid.
5. Likewise, we also show that many other taxa that were previously considered as Equoidea, or even Equidae, including taxa now included in *Pliolophus* (e.g. Secord et al. 2012), do not actually belong to these groups and thus should not be considered as horses. This is due to the fact that Brontotherioidea are now the sister-group of Equoidea according to our phylogeny, which had been suggested by other previous studies, but rarely tested (e.g. Holbrook and Lapergola 2011). This would imply that Equoidea, or "horses" (including some Palaeotheres) would have appeared later than previously thought, at around 50 Ma, rather than 56 Ma.
6. Finally, we also show that the bizarre gorilla-like chalicotheres can be considered as sister-group of Lophiodontidae (a group endemic to Europe), forming a clade called Ancylopoda, within the tapiromorphs and that Palaeotheriidae could be paraphyletic, and closely related to both Equoidea and Brontotherioidea, within hippomorphs. These relationships should be

further tested with a larger taxonomic sample, including more derived taxa of palaeotheres, brontotheres and equoids, which was out of the scope of this study.



Tree showing that horses (Equoidea; in the blue box on the right) are a group derived from perissodactyls, which appeared more recently than previously thought. Hyracotherium and other related species are now found at the very base of all perissodactyls (including rhinos, tapirs, and horses).

4. Analysis of the evolutionary trends and diversity

Thanks to the newly obtained phylogeny of early perissodactyls, we have been able to discuss all the synapomorphies of the main groups of perissodactyls, as well as additional morphological trends, such as the diastemas between the first and second premolars, as well as the direction of the cristid obliqua on lower molars, which is an important character distinguishing hippomorphs from most tapiromorphs. These characters are discussed in the paper “Earliest perissodactyls reveal large-scale dispersals during the PETM” published in PNAS, and its supplementary material.

5. DISSEMINATION AND VALORISATION

Dissemination:

- Participations in congresses (oral presentation):
 - Tissier J, Vautrin Q, Smith T. 2024. *PerissOrigin: phylogénie et diversification des premiers périssodactyles*. Congrès de l’association Paléontologique Française, Montauban, June 3-7, 2024. Award for the PeerJ prize.

- Tissier J, Smith T. 2024. *A new scenario for the diversification and dispersal of the very first perissodactyls around 56 million years ago*. 6th Young Researchers Overseas Day, Royal Academy for Overseas Sciences, Palace of the academies, Brussels, December 9th, 2024.
- Tissier J, Smith T. 2025. *PerissOrigin: re-examining the phylogeny of early perissodactyls reveals unnoticed dispersals of the first North American, European and Asian « horses »*. 85th Annual Meeting of the Society of Vertebrate Paleontology, Birmingham, November 12-15, 2025.
- Tissier J, Leriche C, Smith T. 2025. *Tomography of three articulated perissodactyl skeletons from Messel*. International Senckenberg Conference on the Messel Pit: The World at the Time of Messel: Back to the Future?, Frankfurt, December 8-12, 2025.
- Smith T, Tissier J. 2025. *Do diversification and dispersals of early Eocene perissodactyls differ from those of other modern mammals?* International Senckenberg Conference on the Messel Pit: The World at the Time of Messel: Back to the Future?, Frankfurt, December 8-12, 2025.
- Participations in congresses (poster presentation):
 - Tissier J, Smith T. 2025. *Première visualisation tridimensionnelle par tomographie d'un squelette de périssodactyle de Messel (Eurohippus messelensis)*. Congrès de l'Association Paléontologique Française, Lille, May 5-8, 2025.
- Report:
 - Leriche C. 2025. *Initiation aux recherches en paléontologie des vertébrés, en particulier en paléomammalogie du Paléogène*. Rapport de stage professionnel, UNamur.

Press coverage :

- Des paléontologues remettent en question l'arbre généalogique des chevaux. Belga. La Libre, Belgium, 13/01/2026.
- Des paléontologues redessinent l'arbre évolutif des chevaux ; par Reinout Verbeke, site Web de l'IRSNB, 13/01/2026.
- L'arbre généalogique des chevaux remis en question. Belga. Le Soir, Belgium, 14/01/2026.
- War das Urpferd gar kein Pferd? Süddeutsche Zeitung, Germany, 16/01/2026.
- „Urferd“ war gar kein Pferd. Wissenschaft.de, 12/01/2026.
- Les chevaux: des animaux plus récents qu'il n'y paraît. Radio Télévision Suisse, 28/01/2026
- « Ces découvertes chamboulent » : les origines des premiers chevaux passées à la loupe à Jurassica à Porrentruy. L'Est Républicain. Switzerland, 15/01/2026.
- Des paléontologues remettent en question l'arbre généalogique des chevaux. RTBF, Belgium, 16/01/2026.
- L'origine des chevaux rajeunit de 6 millions d'années ; par Laetitia Theunis, Daily Science, Belgium, 24/02/2026.

Collection valorization:

During the project PERISSORIGIN, several specimens from collections curated by partners have been molded and casted. Casts have been donated to the RBINS collections. Several RBINS specimens are now viewable on the RBINS platform Virtual Collections.

6. PUBLICATIONS

- Tissier J, Smith T. 2026. Earliest perissodactyls reveal large-scale dispersals during the PETM. *Proceedings of the National Academy of Sciences (PNAS)* 123(4): e2519690122.

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8. REFERENCES

- Bai, B., Wang, Y.Q., Meng, J. 2010. New craniodental materials of *Litolophus gobiensis* (Perissodactyla, "Eomoropidae") from Inner Mongolia, China, and phylogenetic analyses of Eocene chalicotheres. *American Museum Novitates* 2010.3688: 1-27.
- Bai, B., Wang, Y.Q., Mao, F.Y., Meng, J. 2017. New material of Eocene Helaletidae (Perissodactyla, Tapiroidea) from the Irdin Manha Formation of the Erlian Basin, Inner Mongolia, China and comments on related localities of the Huheboerhe area. *American Museum Novitates* 2017.3878: 1-44.
- Bai, B., Wang, Y.Q., Meng, J. 2018. The divergence and dispersal of early perissodactyls as evidenced by early Eocene equids from Asia. *Communications Biology* 1.1: 115.
- Bai, B., Meng, J., Zhang, C., Gong, Y.X., Wang, Y.Q. 2020. The origin of Rhinoceroidea and phylogeny of Ceratomorpha (Mammalia, Perissodactyla). *Communications Biology*, 3(1)
- Bronnert, C., Gheerbrant, E., Godinot, M., & Métais, G. 2018. First European 'Isectolophidae' (Mammalia, Perissodactyla): *Chowliia europea*, sp. nov., from the lower Eocene of Le Quesnoy, France. *Journal of Vertebrate Paleontology*, 38(4), 1-9.
- Danilo, L., Remy, J. A., Vianey-Liaud, M., Marandat, B., Sudre, J., & Lihoreau, F. 2013. A new Eocene locality in southern France sheds light on the basal radiation of Palaeotheriidae (Mammalia, Perissodactyla, Equoidea). *Journal of Vertebrate Paleontology*, 33(1), 195-215.
- Froehlich, D. J. 1999. Phylogenetic systematics of basal perissodactyls. *Journal of Vertebrate Paleontology*, 19(1), 140-159.
- Froehlich, D. J. 2002. Quo vadis eohippus? The systematics and taxonomy of the early Eocene equids (Perissodactyla). *Zoological Journal of the Linnean Society*, 134(2), 141-256.
- Holbrook, L. T., Lapergola, J. 2011. A new genus of perissodactyl (Mammalia) from the Bridgerian of

- Wyoming , with comments on basal perissodactyl phylogeny. *Journal of Vertebrate Paleontology* 31: 895–901.
- Hooker, J. J., & Dashzeveg, D. 2004. The origin of chalicotheres (Perissodactyla, Mammalia). *Palaeontology*, 47(6), 1363-1386.
- Kapur, V. V., & Bajpai, S. 2015. Oldest South Asian tapiromorph (Perissodactyla, Mammalia) from the Cambay Shale Formation, western India, with comments on its phylogenetic position and biogeographic implications. *The Palaeobotanist* 64: 95–103
- Missiaen, P., & Gingerich, P. D. 2014. New basal Perissodactyla (Mammalia) from the lower Eocene Ghazij formation of Pakistan. *Contributions from the Museum of Paleontology, University of Michigan*, 32(9), 139-160.
- Remy, J. A. 2017. Critical comments on the genus *Propachynolophus* Lemoine, 1891 (Mammalia, Perissodactyla, Equoidea). *Palaeovertebrata* 41 (1)-e3: 1–18.
- Remy, J. A., Krasovec, G., Lopez, É., Marandat, B., & Lihoreau, F. 2019. The Palaeotheriidae (Equoidea, Perissodactyla, Mammalia) from the Eocene fauna of Aumelas (Hérault department, France). *Geodiversitas*, 41(1), 525-585.
- Robinet, C., Remy, J. A., Laurent, Y., Danilo, L., & Lihoreau, F. 2015. A new genus of Lophiodontidae (Perissodactyla, Mammalia) from the early Eocene of La Borie (Southern France) and the origin of the genus *Lophiodon* Cuvier, 1822. *Geobios*, 48(1), 25-38.
- Rose, K.D., Holbrook, L.T., Rana, R.S., Kumar, K., Jones, K.E., Ahrens, H.E., Missiaen, P., Sahni, A. and Smith, T. 2014. Early Eocene fossils suggest that the mammalian order Perissodactyla originated in India. *Nature communications*, 5(1).
- Rose, K.D., Holbrook, L.T., Kumar, K., Rana, R.S., Ahrens, H.E., Dunn, R.H., Folie, A., Jones, K.E. and Smith, T. 2019. Anatomy, relationships, and paleobiology of *Cambaytherium* (Mammalia, Perissodactylamorphia, Anthracobunia) from the lower Eocene of western India. *Journal of Vertebrate Paleontology*, 39(sup1).
- Secord, R., Bloch, J.I., Chester, S.G.B., Boyer, D.M., Wood, A.R., Wing, S.L., Kraus, M.J., McInerney, F.A., Kribaum, J. 2012. Evolution of the earliest horses driven by climate change in the Paleocene-Eocene Thermal Maximum. *Science* 335: 959–962.
- Smith, T., Rose, K. & Gingerich, P. 2006. Rapid Asia-Europe-North America geographic dispersal of earliest Eocene primate *Teilhardina* during the Paleocene-Eocene Thermal Maximum. *Proceedings of the National Academy of Science, USA*, 103(30): 11223–11227.
- Tabuce, R., Marandat, B., Adnet, S., Gernelle, K., Girard, F., Marivaux, L., Solé, F., Schnyder, J., Steurbaut, E., Storme, J-Y., Vianey-Liaud, Yans, J. 2025. European mammal turnover driven by a global rapid warming event preceding the Paleocene–Eocene Thermal Maximum. *Proceedings of the National Academy of Science, USA*, 122(25): e2505795122.
- Vautrin, Q., Tabuce, R., Lihoreau, F., Bronnert, C., Gheerbrant, E., Godinot, M., Metais, G., Yans, J., Dutour, Y., Vialle, N. and Philip, J., 2020. New remains of *Lophiaspis maurettei* (Mammalia, Perissodactyla) from the early Eocene of France and the implications for the origin of the Lophiodontidae. *Journal of Vertebrate Paleontology*, 40(6), p.e1878200.