

September 10-13, 2019

Royal Belgian Institute of natural Sciences, Brussels, Belgium



International symposium

*Evolution and Paleoenvironment of Early Modern Vertebrates during the Paleogene*

Program and abstracts



Belgian Science Policy Office



## PalEurAfrica Meeting 2019



In the framework of the PalEurAfrica research project (see <http://www.paleurafrica.be>), we are happy to invite you to the Royal Belgian Institute of Natural Sciences (RBINS) for an international symposium related to the evolution and paleoenvironment of early modern vertebrates during the Paleogene. This allows us to gather specialists who work on macro- and micropaleontology, bio- and isotope stratigraphy, paleoenvironment, paleogeography, and geology of Paleogene vertebrate bearing sites.

This international meeting also celebrates the memory of one of our PalEurAfrica partners, Gregg Gunnell (1954-2017), who tragically died unexpectedly in the middle of his career, having made significant contributions to our understanding of research on Paleogene vertebrate evolutionary history.

### Host committee

Thierry Smith (Chair) – *Royal Belgian Institute of Natural Sciences, Brussels, Belgium*  
Thierry De Putter – *Royal Museum for Central Africa, Tervuren, Belgium*  
Stephen Louwye – *Universiteit Gent, Gent, Belgium*  
Johan Yans – *Université de Namur, Namur, Belgium*  
Matthew Borths – *Duke University Lemur center, Durham, NC, USA*  
Nancy Stevens – *Ohio University, Athens, OH, USA*

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Robert Speijer – *Universiteit Leuven, Leuven, Belgium*  
Rodolphe Tabuce – *Université de Montpellier, Montpellier, France*

### Symposium staff

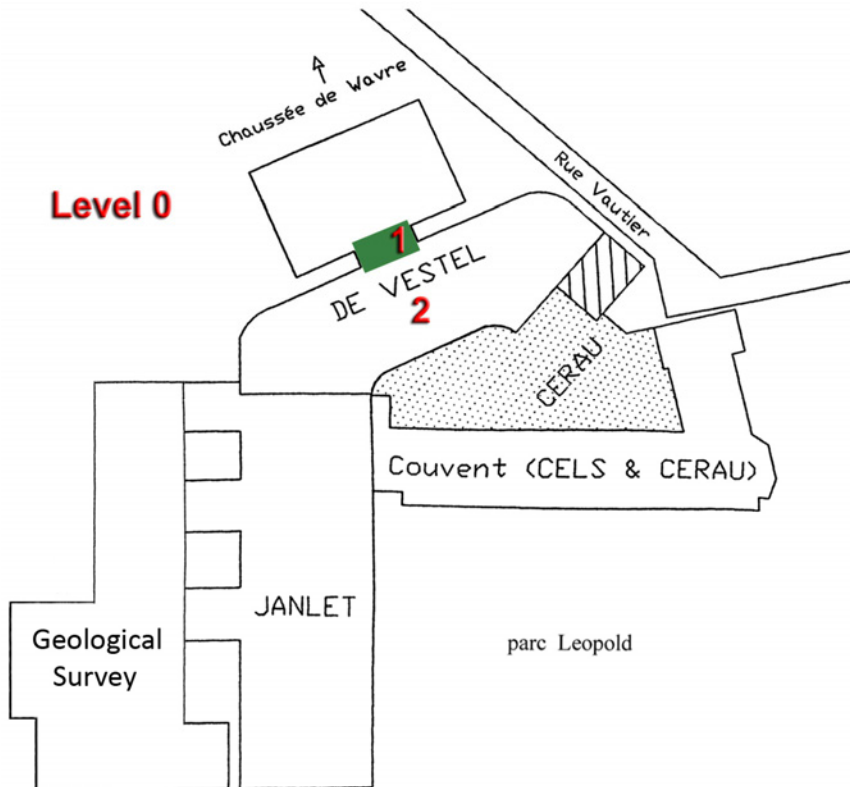
*Royal Belgian Institute of Natural Sciences, Brussels, Belgium*  
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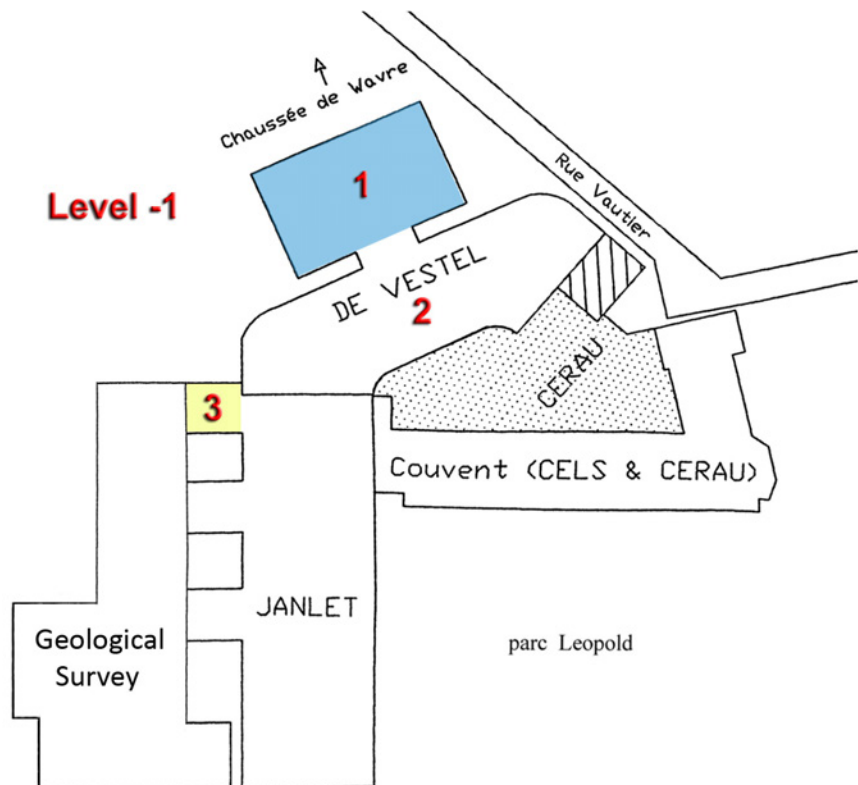
### Editors

Thierry Smith & Annelise Folie – *Royal Belgian Institute of Natural Sciences, Brussels, Belgium*

## Conference venue: Museum of Natural Sciences



1. Registration desk (Tuesday September 10, 2019)
2. Stairs reaching Level -1



1. Large auditorium (technical sessions)
2. Stairs reaching Level 0
3. VIP room (coffee breaks & poster sessions)

## Scientific Program

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.	Rabenstein et al.	Mayr G.	
9h30	Miller et al.	Čerňanský & Smith	Jouve et al.	
9h45	Borths et al.	Rabi et al.	Lambert et al.	
10h00	Gingerich et al.	Solé F.	Zouhri et al. (02)	
10h15				
10h30	Coffee Break & Posters (VIP room)	Coffee Break & Posters (VIP room)	Coffee Break & Posters (VIP room)	
10h45				
11h00	Speijer & Pälke	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			
12h30		Lunch Break (12:00-13:30)	Lunch Break (12:00-14:00)	
13h00	Lunch Break (12:00-14:00)			
13h30				
14h00	Li Q.		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		Visit RMCA (Paleogene collections and new African exhibitions)	Kynigopoulou et al.	
15h30	Maclaren J.		Jehle et al.	
15h45	Bronnert C.		Bertrand et al.	
16h00	Vallée Gillette et al.			
16h15	Yans et al.			
16h30				
16h45	Guided tour RBINS (Exhibitions and collections)		Workshop: cast exchange (Dollo Room)	
17h00				
17h15				
17h30				
17h45				
18h00	Icebreaker Party (VIP room)			
19h00			Conference Dinner (L'Horloge du Sud)	
22h00				

Sessions: Europe Africa Asia

## List of authors and abstract titles in chronological session order

Tuesday, September 10, 2019

Session Africa

Moderator: Yuan-Qing Wang

- 9h15 Keynote 01 : **Sallam H.** New vertebrate fossils from the Paleogene deposits of the Fayum Depression, Egypt.
- 9h45 **Miller E., Sallam H., Seiffert E.R., Schwartz G.T. & Gunnell G.F.** Patterns of dental emergence in early anthropoid primates from the Fayum, Egypt: implications for interpreting social behaviour.
- 10h00 **Borths M., Heritage S., Gunnell G., Friscia A. & Seiffert E.** Persistence of an ancient endemic African clade of hyaenodonts and implications for the biogeographic origins of Hyaenodonta.
- 10h15 **Gingerich P., Sameh M. Antar M. & Zalmout I.S.** New middle-to-late Eocene protocetid (Cetacea, Archaeoceti) from Wadi Al Hiton, Egypt: transition to tail-powered swimming in whales.

10h30 – 11h00 : Coffee break & posters

Session Asia

Moderator: Yuan-Qing Wang

- 11h00 **Speijer R. & Pálike H.** The Paleogene time scale 2020.
- 11h15 **Rose K., Holbrook L.T., Kumar K., Rana R.S., Ahrens H.E., Dunn R.H., Folie A., Jones K.E., Smith T.** *Cambaytherium*, most primitive known perissodactylamorph (early Eocene of India), and the origin of the mammalian order Perissodactyla.
- 11h30 **Zaher H., Folie A., Bottallo A., Rana R.S., Kumar K., Rose K.D., Fahmy M. & Smith T.** Additional vertebral material of *Thaumastophis* from the early Eocene of India provides new insights on the early diversification of colubroidean snakes.
- 11h45 **Rana R.S., Waqas M., Folie A. & Smith T.** A new basal raoellid artiodactyl (Mammalia) from the middle Eocene Subathu Group of Rajouri District, Jammu and Kashmir, northwest Himalaya, India.

12h00 : Group photo

12h15 – 14h00 : Lunch break

Session Asia

Moderator: Chris Beard

- 14h00 **Li Q.** Paleogene rodent assemblages from the Erden Obo Section, Erlian Basin (Inner Mongolia, China), and their diversification trends and biochronological implications.
- 14h15 **Wang Y.-Q., Li Q., Li C.-K., Tong Y.-S. & Ting S.-Y.** Asian Paleocene Land Mammal Ages: Age Constraint and Correlation.
- 14h30 **Bai B., Meng J., Gong Y.-X. & Wang Y.-Q.** The rise of rhinoceroses—Evidences from the new Eocene ceratomorph perissodactyls from the Erlian Basin of Inner Mongolia, China.
- 14h45 **Paepen M., Li H., Sun Y. & Smith T.** An early Eocene mammal assemblage from Bayan Ulan (Inner Mongolia, China) and reassessment of the Arshantan Land Mammal Age.

15h00 – 15h30 : Coffee break & posters

Session Europe  
Moderator: Chris Beard

- 15h30 **MacLaren J.** Functional implications of joint morphology and muscle attachments in the manus of Eurasian Paleogene equoids (Perissodactyla: Equoidea).
- 15h45 **Bronnert C.** Review of early Eocene perissodactyls (Mammalia, Laurasiatheria) from Europe.
- 16h00 **Vallée Gillette N., Smith R. & Smith T.** The micropreparation of a juvenile marine turtle from the Ypresian of Belgium.
- 16h15 **Yans J., Noiret C., Tabuce R., Marandat B., Marivaux L., Lihoreau F., Adnet S., Gheerbrant E., Billet G., Métais G., Vautrin Q., Bronnert C., Smith T. & Steurbaut E.** Application of long-term chemostratigraphy (organic carbon isotopes) in age calibration of Paleogene mammal faunas.

16h30 – 18h00 : Guided tour RBINS (Exhibitions and collections)

18h00 – 22h00 : Icebreaker Party (VIP room)

Wednesday, September 11, 2019

Session Europe

Moderator: Florence Quesnel

- 9h00 Keynote 02: **Mayr G.** Birds – the most species-rich vertebrate group in the Eocene Messel ecosystem.
- 9h30 **Rabenstein R., Engels S., Gunnell G., Simmons N.B. & Habersetzer J.** The Messel bat community and a cryptic new species.
- 9h45 **Čerňanský A. & Smith K.T.** New eolacertid material from the early-middle Eocene of the Messel Pit (Germany).
- 10h00 **Rabi M., Ring S., Wings O. & Bocherens H.** Divergent mammalian body size during the stable middle Eocene climate of Geiseltal.
- 10h15 **Solé F.** On the history of the European Paleogene carnivorous mammals.

10h30 – 11h00 : Coffee break & posters

Session Africa

Moderator: Florence Quesnel

- 11h00 **Zouhri S., Gingerich P.D., Elboudali N., Bouzarzar W., Amane A. & Saddiqi O.** Discovery of a new middle-upper Eocene vertebrate locality (Sabkha of Lebreij) in the Sahara Desert, southeastern Morocco.
- 11h15 **Gheerbrant E.** African origin of the embrithopod mammals (Paenungulata): new evidence from the early Eocene of Morocco.
- 11h30 **Elboudali N., Zouhri S., Gingerich P.D., Bouzarzar W. & Aman A.** First evidence of marine Oligocene in the Tarfaya-Lâayoune-Dakhla Basin (Moroccan Sahara).
- 11h45 **Steeman T., De Weirtd J., Smith T., De Putter T., Mees F. & Louwye S.** Dinoflagellate cyst biostratigraphical and palaeoecological analysis of the early Paleogene Landana reference section, Cabinda Province, Angola.

12h00 – 13h30 : Lunch break

13h30 – 18h00 : Visit RMCA (Paleogene collections and new African exhibitions)

Thursday, September 12, 2019  
Session Africa  
Moderator: Emmanuel Gheerbrant

- 9h00 Keynote 03: **Stevens N, Roberts E.M. & O'Connor P.M.** Evolutionary and paleoenvironmental patterns in African vertebrate faunas at the close of the Paleogene.
- 9h30 **Mayr G.** Hoatzins – a South American bird group in the Cenozoic of Africa and Europe.
- 9h45 **Jouve S., de Muizon C., Céspedes-Paz R., Sosa-Soruco V. & Knoll S.** Differential diversification and dispersal of crocodyliforms through the K-Pg boundary.
- 10h00 **Lambert O., Bianucci G., Salas-Gismondi R., Di Celma C., Steurbaut E., Urbina M. & Muizon C.** A new protocetid from the middle Eocene of Peru provides insights on the colonization of the New World by African four-legged whales.
- 10h15 **Zouhri S., Gingerich P.D., Khalloufi B., Elboudali N., Amane A., Bouzarzar W. & Saddiqui O.** The middle-upper Eocene vertebrate record from Tarfaya–Laâyoune–Dakhla Atlantic Basin (Morocco).

10h30 – 11h00: Coffee break & posters

Session Europe  
Moderator: Emmanuel Gheerbrant

- 11h00 **Tabuce R., Lopez E., Marandat B., Yans J., Noiret C. & Steurbaut E.** A new adapiform primate from the early Eocene of Fournes, Minervois Basin, Southern France.
- 11h15 **Lihoreau F., Vautrin Q., Solé F., Luccisano V., Claude J., Marandat B., Girard F., Martin J., Rémy J., Vianey-Liaud M., Sudre J., Yans J. & Tabuce R.** Revision of the fossil locality of Aumelas (Montpellier area), and the Ypresian/Lutetian Gap in Europe.
- 11h30 **Godinot M., Escarguel G., Pélissié T. & Vidalenc D.** The Primates from Cos (Eocene, Quercy), a first assessment.
- 11h45 **Quesnel F., Iakovleva A., Fléhoc C., Baele J.-M., Smith T., Roche E., Bourdillon C., Garel S., Jacob J., Schnyder J., Breillat N., Storme J.-Y., Yans J., Lerouge C. & Dupuis C.** The Paris Basin Sparnacian: Revision of the lithostratigraphic nomenclature thanks to new sedimentary, mineralogical, chemo- and bio-stratigraphic data.

12h15 – 14h00 : Lunch break

Session Europe  
Moderator: Ellen Miller

- 14h00 **Codrea V., Maridet O., Tissier J., Fărcaș C., Solomon A., Bordeianu M. & Petrișor A.D.** The vertebrate locality Morlaca, keystone for the uppermost Eocene terrestrial bio-events from Transylvania (Romania).
- 14h15 **Beard C., Métais G., Ocakoğlu F., Coster P., Licht A., Sanisidro O., Mattingly S., Wood M., Sanders W.** Splendid isolation of middle Eocene mammals on the Pontide terrane (central Anatolia): genesis of a Tethyan island paradise.
- 14h30 **Tissier J., Codrea V., Becker D. & Maridet O.** New data about the Eocene-Oligocene mammals of Western and Eastern Europe: towards a new scenario of the “Grande Coupure” in Europe.
- 14h45 **Métais G., Beard K.C., Ocakoğlu F., Coster P.M.C., Licht A., Mattingly S.G., Wood M. & Sanders W.J.** Connecting Anatolia to Asia and the end of a Tethyan island paradise.

15h00 – 15h30 : Coffee break & posters

Session Europe  
Moderator: Ellen Miller

- 15h30 **Kynigopoulou Z., Shelley S.L., Williamson T.E. & Brusatte S.L.** Postcranial morphology of taeniodonts (Mammalia: Taeniodonta) indicating fossorial adaptations in the Palaeogene.
- 15h45 **Jehle M., Godinot M., Delsate D., Phélizon A., Pellouin J.-L.** New species of micromammals from the Late Paleocene of the Paris Basin.
- 16h00 **Bertrand O.C., Brusatte S.L., Shelley S.L., Wible J.R., Williamson T.E., Holbrook L.T., Chester S.G.B., Smith T., Butler I.B. & Meng J.** First virtual endocasts of the Paleocene arctocyonids *Arctocyon* and *Chriacus*: Insight into the behavior of early placental mammals after the end-Cretaceous mass extinction.

16h15 – 17h45 : Workshop: cast exchange (Dollo Room)

19h00 – 22h00 : Conference Dinner (Restaurant *L'Horloge du Sud*)

Tuesday September 10 to Thursday September 12, 2019  
Poster Session (VIP Room)

**Ahrens H.E., Luongo R. & Cozart H.** Dental morphology and disparity in the Eocene herbivore lineage *Esthonyx* (Tillodontia).

**Ménouret B., Coster P., Balme C. & Legal S.** Vertebrate paleontology and the Cenozoic history of Luberon, southern France.

**Pérez-García A.** An enigmatic basal turtle (Stem Testudines) in the Paleogene of Europe.

**Pérez-García A. & Smith T.** The large trionychid turtles from the early Eocene record of Belgium.

**Püschel H., Shelley S., Williamson T., Wible J. & Brusatte S.** Understanding the phylogeny of Peripitychidae and “archaic” Palaeocene mammals using Bayesian analysis.

**Rabi M. & Smith T.** Eocene fossil dermochelyid provides insights into why leatherback turtles “want to become” marine mammals.

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

**Trif N. & Codrea V.** Batoid rays from the Oligocene of Suceag (Transylvanian Basin), Romania.

**Waqas M., Rana R.S., Smith T. & Folie A.** High diversity of Raoellidae (Artiodactyla, Mammalia) from the middle Eocene Subathu Group of Kalakot, Northwest Himalaya, India.

**Weppe R., Blondel C., Vianey-Liaud M., Escarguel G., Pélissié T., Antoine P.-O. & Orliac M.J.** Cainotheriidae (Mammalia, Artiodactyla) from Dams (Quercy, SW France); phylogenetic relationships and evolution around the Eocene-Oligocene transition (MP19-MP21).





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**Dental morphology and disparity in the Eocene herbivore lineage**  
***Esthonyx* (Tillodontia)**

Heather E. Ahrens<sup>1\*</sup>, Ricki Luongo<sup>1</sup>, Hannah Cozart<sup>1</sup>

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**Keywords:** geometric morphometrics, Holarctic, Wasatchian, Bighorn Basin

Tillodontia includes numerous species representing relatively common, specialized herbivores of the Holarctic Paleogene. The Eocene (Wasatchian NALMA) fossil record of the Bighorn Basin, western North America contains abundant fossils of the Euramerican tillodont lineage, *Esthonyx*. Due to the abundance of specimens and their specialized diet, *Esthonyx* provides a valuable case study in phenotypic variation during climatic change on an extended temporal scale. Our objective was to quantify morphological disparity along the tooth row and assess interspecific and temporal variation. To evaluate patterns of dental variation within *Esthonyx*, we used two-dimensional geometric morphometrics based on twelve landmarks representing prominent cusps and additional anatomical features in occlusal and lingual views of the lower fourth premolar and the three molars. Principal components analysis indicated that the majority of shape variation, though slight, occurred within the trigonid. In occlusal view, p4 and m3 possessed greater disparity than m1 and m2, whereas p4 and m1 possessed the greatest disparity in lingual view. However, differences along the tooth row based on mean pairwise dissimilarity were not significant. When dental loci were examined by species and biochron, distinct species groupings and temporal shifts were difficult to distinguish due to the well-conserved dental morphology within the lineage. These results indicate that the lower dentition of *Esthonyx* is relatively conservative both along the tooth row, as well as between species and through time. The lack of evidence for morphologic change during significant climatic events may indicate low capacity for evolution and could have ultimately led to the extinction of this lineage.

We thank High Point University for funding, Nick Pyenson and Amanda Milhouse from the National Museum of Natural History, Washington, D.C. for specimen loans, and Katrina Jones for feedback.



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**The rise of rhinoceroses—Evidences from the new Eocene ceratomorph perissodactyls from the Erlian Basin of Inner Mongolia, China**

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**Keywords:** Rhinoceroidea, Eocene, Nomogen and Arshanto formations, Hyrachyidae, Erlian Basin

Rhinoceroidea conventionally comprises Hyracodontidae, Amarynodontidae, and Rhinocerotidae; however, the paraceratheres were recently treated again as a separated family from Hyracodontidae. Rhinoceroses probably originated from some tapiroids during the middle Eocene, and their first appearance was much later than the earliest tapiroids (e.g. *Heptodon*). '*Hyrachyus*' (or Hyrachyidae) was usually considered to be a transitional form from the tapiroids to different rhinocerotoids, however, the status and classification of '*Hyrachyus*' complex still remained to be controversial. Here on the basis of diverse rhinocerotoid materials from the early Eocene to the early middle Eocene deposits of the Erlian Basin, China, we describe three genera (including a new genus) and four new species of rhinoceroses: two new species of *Yimengia* and a new species of *Triplopus* represent early members of hyracodontids, while a new genus represents a basal paraceratheriid. We further resurrected the genus *Ephyrachyus*, which has been considered to be a synonym of *Hyrachyus*, and erected a new species of *Ephyrachyus* from the Arshanto Formation. In addition, we tentatively assigned a fragmentary maxilla to a new species of *Hyrachyus* with a query from the Arshanto Formation, noting its similarities with rhinocerotid *Uintaceras*. Thus, these new rhinocerotoid materials from the Bumbanian and Arshantan ALMA fill the gap between the early Eocene ceratomorphs and Uintan/Irdinmanhan rhinoceroses, indicating divergence of different rhinocerotoid groups occurred as early as the late early Eocene, contemporary or soon after the split of rhinoceroses from the tapiroids. The result also indicates that '*Hyrachyus*' could not be ancestral to hyracodontids or paraceratheriids. The phylogeny and classification of primitive ceratomorphs need to be reconsidered on the basis of these new, diverse early rhinocerotoids by further cladistic analysis.

We thank Z.X. Qiu for the discussion, S.J. Li, Q. Li for the preparation of specimens, W. Gao for the photography, Y. Xu for the drawing, and many IVPP staffs for the fieldworks. Funding: XDB26000000.



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### **Splendid isolation of middle Eocene mammals on the Pontide terrane (central Anatolia): genesis of a Tethyan island paradise**

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**Keywords:** Endemism, Eocene, Biogeography, Phylogeny, Mammals

Ongoing field work in the Orhaniye Basin of north-central Anatolia has vastly improved our knowledge of the middle Eocene mammal fauna of the Uzunçarşidere Formation (UCF). Consistent with its location in an area of tectonic convergence between Africa and Eurasia, the fauna includes a unique combination of Gondwanan and Laurasian mammals. Taxa bearing a northern biogeographic signal include the autapomorphic herpetotheriid metatherian *Galatiadelphys minor*, an anachronistically young radiation of pleuraspidothereiid ungulates (*Hilalia* spp.), the palaeochiropterygid bat *Anatolianycteris insularis*, and an undescribed omomyid primate. Taxa bearing a southern biogeographic signal include one or more embrithopods (*Palaeoamasia* sp. and/or *Hypsamasia seni*) and an endemic radiation of anatoliadelphid metatherians (*Anatoliadelphys maasae* and *Orhaniyeia nauta*). Notably absent from the UCF are multiple Laurasian mammal clades that are otherwise ubiquitous by the middle Eocene. These include Perissodactyla, Artiodactyla, Rodentia, Carnivora and Creodonta. Available evidence indicates that the UCF mammal fauna inhabited an island situated along the northern margin of Neotethys, which explains the presence of so many insular and/or relictual taxa there and the absence of widespread and ecologically dominant clades like rodents. During the 2018 field season, two relatively complete specimens of a new higher-level taxon of mammals were recovered from the UCF. One specimen includes both dentaries (measuring ~25 cm anteroposteriorly) of an adult individual with nearly complete dentition. The other is a juvenile represented by both dentaries and the associated rostral part of a skull. The anatomy of this new mammal defies ready allocation to any previously known mammal clade. Attempts to assess the phylogenetic position of this new Anatolian mammal are ongoing, but the new taxon emphasizes the power of Simpson's "splendid isolation" as an engine of evolutionary novelty.

Funding for this research has been provided by grants from the National Science Foundation (EAR 1543684 and EAR 1923294), the David B. Jones Foundation, and a Big XII Faculty Fellowship to KCB.



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### **First virtual endocasts of the Paleocene arctocyonids *Arctocyon* and *Chriacus*: Insight into the behavior of early placental mammals after the end-Cretaceous mass extinction**

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**Keywords:** brain, inner ear, endocast, 'condylarth', locomotion

The vacant niches left by the non-avian dinosaurs and other vertebrates after the end-Cretaceous mass extinction, provided a crucial opportunity for placental mammal diversification. The general neurosensory organization exhibited by extant mammals has been maintained since the Late Triassic-Early Jurassic. Much later during the Eocene, fossils of early members of extant placentals display neurosensory innovations, such as a proportionally larger neocortex and a higher encephalization quotient (EQ), compared to their Mesozoic ancestors. However, few studies have focused on the brain of the oldest placentals that lived during the Paleocene. We analysed the neurosensory system of two species of arctocyonid 'condylarths', a likely non-monophyletic group, including some species potentially implicated in the origins of extant ungulates. 'Arctocyonids' were of small-to-medium size, omnivorous and mainly terrestrial. We obtained cranial and bony labyrinth endocasts for *Arctocyon* and two species of *Chriacus* using high-resolution computed tomography. Both species exhibit plesiomorphic features shared with other early Paleocene mammals such as a relatively small lissencephalic brain with an EQ range of 0.07-0.31 using Eisenberg's equation. The olfactory bulbs and the petrosal lobules represent 7% and less than 1% of the total endocranial volume, respectively. The neocortical height represents ~25% of the total endocranial height. Based on the cochlea, these species had hearing capabilities similar to extant wild boars. Agility scores between 2 and 3, show that these taxa were similar to the American badger and the crab-eating raccoon, suggesting that *Arctocyon* and *Chriacus* were moderately agile. These results support the growing evidence that early placentals had low EQs and less expanded neocortices compared to Eocene and later taxa, potentially indicating that complex neurosensory organization was not key to the placental radiation after the end-Cretaceous mass extinction.

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### **Persistence of an ancient endemic African clade of hyaenodonts and implications for the biogeographic origins of Hyaenodonta**

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**Keywords:** Biogeography, Phylogeny, Ancestral State Reconstruction, Carnivores

Hyaenodonta is a clade of morphologically and taxonomically diverse mammals that occupied carnivorous niches in Africa, Eurasia, and North America through the Paleogene and into the early Neogene. The oldest known hyaenodont is *Lahimia*, a small, hypercarnivorous mammal from the middle Paleocene of Morocco whose antiquity has led some to suggest an African origin for all of Hyaenodonta. Multiple studies have recovered *Lahimia* as the sister taxon of *Boualitomus*, an early Eocene, small-bodied hyaenodont from Morocco. Among other characters, *Lahimia* and *Boualitomus* are united by the loss of a lower premolar and tall trigonids. Here we present a new, tiny hyaenodont from the late early Eocene of Egypt (Locality 41, Jebel Qatrani Formation). Like *Lahimia* and *Boualitomus*, the new hyaenodont is a diminutive hypercarnivore with only three premolars. Phylogenetic analyses – including Bayesian “tip-dating” methods – demonstrate the new L-41 hyaenodont is part of the *Lahimia-Boualitomus* clade. The discovery of the L-41 taxon suggests this endemic lineage was present in Afro-Arabian ecosystems through the Eocene, but went extinct near the Eocene-Oligocene boundary. Phylogenetic analyses recover the *Lahimia* clade nested deeply within Hyaenodonta. The phylogenetic placement of the oldest hyaenodont therefore implies significant ghost lineages near the base of Hyaenodonta, and the ultimate phylogenetic and biogeographic origins of the group remain elusive. Based on known data we reconstruct the most likely biogeographic origin of Hyaenodonta using a newly developed locality-based method of Bayesian biogeographic inference. This method places the origins of Hyaenodonta in Eurasia, indicating a Paleocene dispersal of Hyaenodonta from Eurasia to Afro-Arabia. The *Lahimia* clade provides evidence that Hyaenodonta rapidly diversified in Afro-Arabia during the Paleogene, occupying the unfilled carnivorous mammal niches on the isolated continent.

We thank the collections managers and curators who made this research possible. Data collection was supported by US NSF grants DEB-1311354 and DBI-1612062.



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**Review of early Eocene perissodactyls (Mammalia, Laurasiatheria) from  
Europe**

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**Keywords:** Perissodactyla, early Eocene, Europe, phylogeny, biogeography

Perissodactyls (horses, rhinoceroses and tapirs) appeared near the Paleocene-Eocene boundary, probably in Asia, and quickly spread across the Northern Hemisphere. European fossils have been poorly studied, and the Muséum national d'Histoire naturelle in Paris, France has acquired a large number of fossil specimens from various early Eocene localities of the Paris Basin in the last decades. The review of this material allowed to identify 12 species, including two new species of basal hippomorphs. In total, 10 species are present in the Paris Basin and the South of France. These new results have been integrated in a phylogenetic analysis based mostly on dental characters and including most of basal perissodactyls known in the early and middle Eocene of the Northern Hemisphere. The obtained trees indicate that European hippomorphs are closely related to the North American equids, which form a clade included within the European hippomorphs. Moreover, the faunas related to the MP7 show taxonomic differences between Northern and Southern France. These differences could be related to a climate barrier between Northern and Southern Europe at the base of the Eocene, as suggested by floral evidence. A renewal of perissodactyls at the generic level takes place between MP7 and MP8-9, suggesting the end of this climatic barrier. A homogenization of the perissodactyl faunas between the North and the South of France is also recognized in the sites close to the MP8-9 and persists in the sites close to the MP10.



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**New eolacertid material from the early-middle Eocene of the Messel Pit  
(Germany)**

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**Keywords:** *Eolacerta*, *Stefanikia*, Palaeogene, Europe

The Messel Pit in Germany is renowned due to the exceptional preservation of its fossils, both animals and plants, which have made it into one of the most important Eocene localities in the world. Among the nearly three dozen reptile species reported from Messel thus far is the large lizard *Eolacerta robusta*. This taxon was first described from the lignite mines of Geiseltal in eastern Germany, and later recognized at Messel on the basis of nearly complete skeletons. Its spatial distribution during the Eocene includes not only Germany but also France. However, this taxon was long an enigmatic one. The most recent work concludes that *Eolacerta* is closely related to Lacertidae, the dominant group of reptiles in Europe today, but lies outside of the crown. Together with the recently described taxon *Stefanikia siderea*, it forms the clade Eolacertidae. Other undescribed species may also be related to Eolacertidae. Besides these results, we here also present the first juvenile specimen of *E. robusta*. With help of micro-CT, several new anatomical features are observed for this taxon.

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### **The vertebrate locality Morlaca, keystone for the uppermost Eocene terrestrial bio-events from Transylvania (Romania)**

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**Keywords:** Priabonian, mammals, Transylvanian Basin, Romania

The uppermost Eocene (Priabonian) terrestrial vertebrates from Transylvania are still very poorly known. On the north-western side of the Paleogene Transylvanian Basin, the vertebrate locality of Morlaca breaks this rule: teeth and bones were unearthed by systematic diggings from rocks of fluvial origin of the Valea Nadășului Formation. The vertebrate assemblage concerns reptiles (indeterminate turtles and crocodiles) and mammals as Perissodactyls (the amynodont *Amynodontopsis* aff. *bodei*, another amynodontidae indet, as well as two indeterminate brontotheres: a medium sized one, and a very large second one) and Artiodactyls (a small sized anthracothere, close to *Prominatherium*). Until now, the single locality in Romania that yielded brontothere remains was Rădaia (= Andrășháza), near Cluj-Napoca, where the mandible documenting the species *Brachydiastematherium transylvanicum* was collected over a century ago from the same Priabonian formation, together with the rhinocerotoid *Prohyracodon orientale*. However, no *Prohyracodon* remain was found in Morlaca and none of the brontotheres from this locality could be related to *B. transylvanicum*. Based on these new findings, a rather large brontothere diversity in Transylvania is identified. The Asian origin of the brontotheres from Europe is since long time accepted. As in Rădaia, the representatives from Morlaca evidence their dispersal and diversification in this region of Europe before the Eocene/Oligocene boundary. A lot of the Priabonian terrestrial vertebrates from Romania were found only as isolated fossils. Therefore, the faunal assemblage of Morlaca is a key for a better understanding of the bio-events that occurred in Transylvania in the latest Eocene.

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### First evidence of marine Oligocene in the Tarfaya-Lâayoune-Dakhla Basin (Moroccan Sahara)

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**Keywords:** Planktonic Foraminifera, Eocene, Rupelian, Ad-Dakhla, Morocco

The Alaouate outcrop southeast of Ad-Dakhla at the southern Tarfaya-Lâayoune-Ad-Dakhla Basin (TLDB) is a rhythmic complex of alternating gray cherts and marly silts that includes three important fossiliferous levels A1, B1 and B2. The levels correspond to Unit 1, Unit 2 and Unit 3 in the stratigraphic sequence. The three fossiliferous levels provided a diverse middle and late Eocene vertebrate fauna. This sequence also yielded planktonic foraminifera, which enabled dating of different levels of the sequence.

The level is limited at its base by the upper part of the bonebed B2 attributed to the Priabonian and at its summit by the *Rhizolithes* level (the summit part of the studied sequence). This level is about two meters thick and corresponds to the base of lithostratigraphic unit 3. It consists essentially of marly sand alternating with gypsum changing laterally to fine laminar levels.

This level yielded an assemblage of planktonic foraminifera composed of *Pseudohastigerina micra*, *P. nagewichiensis*, *Tenuitella gemma*, *Cassigerinella chipolensis*, *Catapsydrax unicavus*, *Globigerina officinalis praebulloides* and *G. praebulloides leroyi*. The presence of *Cassigerinella chipolensis* would correspond to the base of P18 zone in South Australia. *Globigerina praebulloides leroyi* is known from the lower Oligocene of the Lindi area section of Tanzania.

Plotting these on the range chart, *Pseudohastigerina nagewichiensis*, *Cassigerinella chipolensis* and *Tenuitella gemma* overlap in O1, so O1 [P18; early Rupelian] is our best estimate for the age of the upper assemblage.

The presence of a similar planktonic foraminifera assemblage of the O1 zone corresponding to the Rupelian (lower Oligocene) is the first undisputed characterization of the marine Oligocene in the Tarfaya-Laâyoun-Dakhla Basin.



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### **African origin of the embrithopod mammals (Paenungulata): new evidence from the early Eocene of Morocco**

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**Keywords:** Afrotheria, Tethytheria, Embrithopoda, Africa, Ypresian

The extinct order Embrithopoda was discovered with the genus *Arsinoitherium* in the early Oligocene of the Fayum (Egypt). *Arsinoitherium* was part of the old endemic African herbivorous megafauna of the Island Africa, together with proboscideans and hyracoids. It is characterized by unique specialized traits such as hyperdilambdodont molars. Since its discovery, primitive embrithopods of the family Palaeoamasiidae were discovered in the Eocene of Romania and Turkey, suggesting a possible Eurasian origin of the order. More recently, we described two species of *Stylolophus* from the early Eocene of the Ouled Abdoun Basin (Morocco) as the earliest known embrithopods. The Embrithopoda is included in the African clades Afrotheria and Paenungulata, but with uncertain inter-ordinal relationships, the best supported hypothesis being a sister group relationships to Proboscidea. The two species of *Stylolophus* are the smallest and most primitive known embrithopods. However, they share the distinctive embrithopod hyperdilambdodont molars, and are close in morphology to Palaeoamasiidae. A cladistic analysis confirms their basal relationships within embrithopods. Some MPTs recover the sister group relationships to Proboscidea, but most MPTs support they are sister group to crown tethytherians (Proboscidea and Sirenia). In this hypothesis, the Embrithopoda is an early tethytherian offshoot predating Proboscidea and Sirenia divergence. It shows its old origin, at least from Paleocene onset. Its stem tethytherian position elucidates the evolution of major dental specializations within paenungulates. It is most consistent with the evolution of the hyperdilambdodont pattern from an ancestral paenungulate dilambdodont morphotype. In specialized embrithopods, hyperdilambdodonty evolved in a pseudolophodont state, as a convergence with true lophodonty of Proboscidea and Sirenia. Early Tertiary herbivorous niches of the African island favoured convergence of the folivorous diet in several paenungulate lineages. The discovery of the oldest and basalmost embrithopods in the early Eocene of Morocco supports the African origin of the order.



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**New middle-to-late Eocene protocetid (Cetacea, Archaeoceti) from Wadi Al Hitan, Egypt: transition to tail-powered swimming in whales**

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**Keywords:** Cetacea, Protocetidae, Eocene, undulatory swimming

A new African protocetid is based on two specimens. The better of the two, 'WH-203' interpreted as male, is a partial skull with much of an associated postcranial skeleton. Both were found near the base of the Gehannam Formation of the Wadi Al Hitan World Heritage Site in Egypt. The cranium of WH-203 is distinctive in having ventrally-deflected exoccipitals. The vertebral column is complete from cervical C1 through caudal Ca9, with a vertebral formula of 7:15:4:4:9+, representing, respectively, the number of cervical, thoracic, lumbar, sacral, and caudal vertebrae. WH-203 has two more rib-bearing thoracics than other known protocetids, and two fewer lumbar. Sacral centra are unfused, and there is no defined auricular surface on the ilium. Thus there was no longer a weight-bearing sacroiliac joint. The sternum is distinctive in being exceptionally broad and flat. The body weight in life for this individual is estimated at about 890 kg. Bones of the forelimb are shorter and those of the manus and more robust than expected for a protocetid this size. The tibia is shorter and the pes is both shorter and less robust than expected. A vertebral-centrum-length profile for WH-203 parallels that of early middle Eocene *Maiacetus inuus* through the anterior and middle thorax, but more-posterior vertebrae are proportionally longer. Vertebral elongation, loss of a sacroiliac articulation, and hind limb reduction indicate an animal more fully aquatic and less specialized as a foot-powered swimmer than early protocetids. Mid-body-through-tail undulation is inferred to have provided propulsion during swimming. It is doubtful that WH-203 had a tail fluke, and it also seems doubtful that Eocene basilosaurids had a tail fluke. The transition from foot-powered swimming to tail-powered swimming in whale evolution involved an intermediate stage of mid-body-through-tail undulation.

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### The Primates from Cos (Eocene, Quercy), a first assessment

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**Keywords:** Fossil primates, Eocene, Quercy

The Quercy locality of Cos, rediscovered and excavated by one of us, has yielded a very interesting primate fauna. First, a relatively large species documented by a mandible bearing p/3-m/3, and one upper molar, shows m/1-2 very similar to those of *Cercamonius brachyrhynchus*. p/4 is close in overall shape, but differs in having a small basal paraconid, a slightly larger metaconid and a broader lingual talonid valley. Major differences are present in the anterior premolars that clearly indicate that the new species is more primitive than *C. brachyrhynchus*: instead of having a single-rooted p/2 closely appressed to the p/3, the new specimen has a small diastema between p/3 and a double-rooted p/2, and a small p/1 was present. This discovery also allows the description of teeth previously unknown in this genus, p/3, m/3. An upper molar of congruent size also appears remarkably primitive, being simple, without a cuspidate hypocone (only a small swelling on the cingulum). Second, a medium-sized species appears very similar to *Pronycticebus gaudryi*. A mandible preserves the double-rooted p/2, a tiny fragmentary p/1, a high and slender lower canine, and a small i/2. The slender canine in this specimen contrasts with the very large size of the upper canine alveoli in the skull of *P. gaudryi*. Third, a small microchoerid is identified on the basis of having smooth upper molars more transversely elongated than those of *Pseudoloris*, and with only an incipient hypocone. A transversely elongated P4/ and a similar-sized m/1,2 with cuspidate paraconid are probably associated. This species is a primitive representative of the *Pseudoloris* clade. Fourth, a paromomyid is present, and this is the first record of the family in the Quercy. This combined fauna is unique in the European fossil record. The presence of a paromomyid and the primitive evolutionary stage of two of these species lead to a first assessment of the age of the fauna between MP 9 and MP 12.



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### **New species of micromammals from the late Paleocene of the Paris Basin**

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**Keywords:** Paris Basin, Pseudorhyncocyonidae, Adapisoricidae, Adapisoriculidae, Pantolestidae

The Paris Basin has delivered important faunas of fossil mammals from the Thanetian. A rich sample of Late Paleocene mammals has recently been collected from the Marnes de Montchenot in the Montagne de Reims (Marne, France). Study of the new fauna and comparisons with collections from other localities (Cernay, Berru) result in the identification of at least four previously undescribed species of eutherian micromammals in the Late Paleocene of the Paris Basin.

A new small-sized species of the genus *Phakodon*, member of the endemic European family Pseudorhyncocyonidae (order Leptictida), is documented from Montchenot and Cernay in addition to the type species *P. levei*; a third species of large size may be present at Cernay. The genus *Adapisorex* (Adapisoricidae, Macroscelidea?) is represented at both localities not only by the type species *A. gaudryi*, but also by a new species about 25% smaller in size. A new species of the Euro-African and possibly Indian family Adapisoriculidae (Euarchonta?) is identified on the basis of new material from Montchenot, Cernay and the Lentille de Berru, including all molar positions and P<sub>4</sub>. The new taxon is not closely related to *Nosella europaea* from Tremp (Spain), to which part of the material had previously been assigned, but identified instead as a large species of *Afrodon*. Finally, a maxillary fragment from Montchenot and isolated upper molars from Cernay are evidence of the first European species of the pantolestid genus *Bessoecetor* (order Pantolesta), hitherto known only from North America. The new species is the largest known for the genus, and documents an additional case of intercontinental mammalian dispersal from North America to Europe in the Late Paleocene.

The newly identified species show that several groups were more diversified in the Late Paleocene of the Paris Basin than previously recognized, and highlight important faunal similarities between Montchenot and Cernay, supporting close correlation of those faunas in age.

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### Differential diversification and dispersal of crocodyliforms through the K-Pg boundary

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**Keywords:** Crocodyliformes, Dyrosauridae, Gavialoidea, K-Pg crisis, Palaeobiogeography

New crocodyliform material from the early Paleocene of South America and North Africa provides the opportunity to evaluate the distribution of longirostrine crocodyliforms through the K-Pg boundary. We conducted simple diversity analyses on two longirostrine groups that crossed the crisis: gavialoids and dyrosaurids. Even if they should be considered with caution because of the poor fossil record on some continents for these periods of time, the analyses highlighted a rapid radiation of these surviving crocodyliform groups in the early Paleocene. The paleogeographic distribution of longirostrine crocodyliforms demonstrates the existence of two paleogeographic bioprovinces. In the North Tethyan bioprovince the Late Cretaceous-Paleocene crocodyliform fauna is almost exclusively represented by gavialoid crocodylians, while south Tethyan fauna is mainly formed by dyrosaurids, with gavialoids being excluded from South America at the end of the Maastrichtian. Contrary to the gavialoids, the dyrosaurids are excluded from warm temperate climatic zones that are largely present in Northern Province, suggesting that gavialoids have a better temperature tolerance than dyrosaurids. The presence of a warm European oceanic current could also have precluded the presence of dyrosaurids in Europe where numerous gavialoids were recorded. Both gavialoid and dyrosaurid groups have a different history through the K-Pg boundary. While gavialoids gently diversified in North Tethyan bioprovince, the dyrosaurids, that slowly began their diversification during the Maastrichtian, strongly diversified after the K-Pg boundary in Southern province. So, if the history of the crocodyliforms on the whole is important, the evolution of each group should be considered separately, as global analyses could obscure the real evolution trends: the evolution of different crocodyliform groups is influenced by regional factors and environmental conditions, and differences in climatic preferences.



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**Postcranial morphology of taeniodonts (Mammalia: Taeniodonta)**  
**indicating fossorial adaptations in the Palaeogene**

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**Keywords:** Palaeogene, mammals, function, morphology, postcranial

Mammals originated during the Mesozoic and survived the Cretaceous-Palaeogene (K-Pg) mass extinction. Their evolution from small, opportunistic animals to more specialised animals with diverse locomotor behaviours following the extinction is still unclear. An ideal group to address this question is the Taeniodonta which are among the few eutherians that purportedly crossed the K-Pg boundary and diversified in the early Palaeogene. They are known thus far from the Palaeogene of North America and are characterised by their unique dentition adapted for an abrasive diet and their robust skeleton. There are 10 genera of taeniodonts classified into two families. The Conoryctidae are smaller with more generalised body plan, whereas the Stylinodontidae reached large body size (up to 100kg) and evolved crown hypsodonty. We focused our study on the postcranial functional morphology of the two taeniodont subgroups. We conducted linear discriminant analysis using 9 linear measurements of the humerus, comparing *Onychodectes* (a conoryctid) and *Stylinodon*, *Ectoganus*, *Psittacotherium* (stylinodonts) with extant mammals of known locomotion. We also used 29 linear tarsal measurements to evaluate the locomotor behaviour of *Onychodectes* and *Conoryctes* (conoryctids) and *Ectoganus* alongside a sample of extant mammals and other Palaeogene taxa. Our results show that *Onychodectes*, which is one of the most basal taeniodonts, might have been terrestrial/semi-fossorial, similar to the numbat. Postcranial features of *Onychodectes* show it possessed digging adaptations i.e. a long olecranon process of the ulna, enlarged manual unguals and a well-developed deltopectoral crest and broad distal end of the humerus. We find stylinodontid taeniodonts to be distinctly more fossorial, comparable to the striped skunk, gopher and the armadillo. Our study suggests that digging is an ancestral behaviour for taeniodonts implying the importance of burrowing for surviving the K-Pg extinction.

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### **A new protocetid from the middle Eocene of Peru provides insights on the colonization of the New World by African four-legged whales**

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**Keywords:** Cetacea, amphibious, Protocetidae, Lutetian, Peru

Cetaceans originated in south Asia more than 50 Ma, from a small, four-legged artiodactyl ancestor. Amphibious whales gradually dispersed westward along North Africa, eventually reaching North America before the end of the Lutetian (41.2 Ma). However, because the fossil record on both sides of the Atlantic remains relatively scarce, when, through which pathway, and under which locomotion abilities these early whales made it to the New World remains debated.

Marine deposits dated to 42.6 Ma (Lutetian) from the locality of Playa Media Luna (Pisco Basin, Peru) yielded the associated skeleton of a new protocetid cetacean, including mandibles, teeth, vertebrae, scapulae, pelvis, and many fore- and hind limb elements. The new genus and species *Peregocetus pacificus* constitutes the first indisputable four-legged whale skeleton described from the whole Pacific Ocean and Southern Hemisphere and probably the geologically oldest from the Americas.

Fused sacral vertebrae, pelvis firmly attached to sacrum, insertion fossa for the round ligament on femur, and retention of small hooves at fingers and toes indicate that *Peregocetus* was still capable of moving on land. Caudal vertebrae with bifurcated transverse processes (like those of several semiaquatic mammals) suggest a more significant contribution of the tail during swimming in *Peregocetus* than in more ancient forms. The large, webbed feet with long toes indicate that strokes from hind limbs may also have contributed to underwater locomotion, as in otters.

Sharing morphological similarities with some western African protocetids (e.g. *Pappocetus* from Nigeria and southern Morocco), this new Peruvian taxon further supports the hypothesis that early quadrupedal whales crossed the South Atlantic from the African coast to South America, and reached a nearly circum-equatorial distribution with a combination of terrestrial and aquatic locomotion abilities less than 10 million years after their origin in south Asia.





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**Paleogene rodent assemblages from the Erden Obo Section, Erlian Basin (Nei Mongol, China), and their diversification trends and biochronological implications**

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**Keywords:** Nei Mongol, Erden Obo, rodent fossil assemblages

The Erden Obo section is one of the best known Paleogene sections in central Asia and is a key to understand the stratigraphy from the Paleocene to the early Oligocene in the Erlian Basin. Numerous rodent fossils have been systematically collected from eight horizons of the strata that are distributed from the “Basal Red” to the “Upper White” beds in the Erden Obo section. These rodent fossils were included in Alagomyidae, Ctenodactyloidea, Cricetidae, Dipodidae, Ischyromyidae and Cylindrodontidae.

The rodent assemblages from the Erden Obo section varied in different intervals of the strata. On the basis of the comparison of the rodent assemblages, we propose that the age of the “Basal Red” beds is most likely the Bumbanian Asian Land Mammal Age. The age of the lower part and middle part of the “Basal White” beds correspond to the Arshantan and Irdinmanhan, respectively. The age of the “Lower Red” beds is correlative to the Sharamuronian, and the age of the “Middle Red” and “Middle White” beds is probably more similar to the age of late Eocene. The age of the “Upper Red” beds is close to the Eocene/Oligocene boundary and the age of the “Upper White” beds is early Oligocene.

Ctenodactyloids are highly diversified in the lower part of the “Basal White” but declined in the “Lower White” beds. During the late Eocene, the diversity of cricetids, dipodids and cylindrodontids in the “Middle Red”, “Middle White” and “Upper Red” beds increased. It is evident that the rodent assemblages of the Erden Obo section show a transformation from being ctenodactyloid dominant in early-middle Eocene to cricetid-dipodid-cylindrodontid dominant in late Eocene. The turnover of the rodent fauna possibly responded to the environmental and climatic change towards the end of the middle Eocene.

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### Revision of the fossil locality of Aumelas (Montpellier area), and the Ypresian/Lutetian Gap in Europe

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**Keywords:** biochronology, systematics, faunal list, southern France

Terrestrial vertebrate evolutionary history in Europe suffers from an important lack of fossil at the interval between Ypresian and Lutetian (Y/L). The Y/L boundary gap in the stratigraphy of Northern Europe has been highlighted by recent identification of deep-marine sediments from Pyrenees. This lack of knowledge for this time interval (2-3 myrs) led to misinterpret the age of many fossil localities.

The locality of Aumelas, near Montpellier, yielded numerous vertebrate taxa excavated from lacustrine sediments. Previously dated close to the end of the Lutetian (attributed to MP13-14, Mammal Paleogene reference level), most of the mammalian species from Aumelas displays doubtful position in reconstructed phylogeny whatever its order. Discoveries of new material from Aumelas led us to begin a program of faunal revision. This first synthesis proposes to double the number of recognized species. It highlights the presence of taxa known from localities of the base of the Lutetian (e.g. *Macrocranion tupaïodon* and *Aumelasia gabineaudi*) and from Ypresian localities (e.g. *Eurodexis russelli* and *Hyrachyus stehlini*). The biochronological analysis therefore suggests an older age for Aumelas than previously reported, most probably from the late Ypresian between MP10 and MP11. Moreover, this analysis implies that numerous localities from southern France might also be considered from this short interval. Detailed faunal discrimination and description of their stratigraphical position allow a refined relative dating between these localities. Further researches on sedimentology, mineralogy, stratigraphy, geochemistry and paleomagnetism began to constrain these localities in a geochronological framework. The numerous and continuous stratigraphical sequence from southern France will allow to describe the Y/L transition and to discuss mammalian evolution around the Early Eocene Climatic Optimum.



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### Functional implications of joint morphology and muscle attachments in the manus of Eurasian Paleogene equoids (Perissodactyla: Equoidea)

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**Keywords:** interosseus, locomotion, magnum, palaeothere, tridactyl

The evolutionary transition from a tetradactyl (four-toed) to tridactyl (three-toed) forelimb in perissodactyls is well documented. Two equoid clades underwent this transition: North American Equidae and Eurasian Palaeotheriidae. Here I compare specific manus morphology of palaeotheres and equids, informed by osteological and myological studies of tetradactyl tapiromorphs (tapirs). Within the manus of tetradactyl perissodactyls, the metacarpophalangeal (MCP) joint allows a modest degree of flexion, and the elongate volar processes of the magnum and unciform carpals offers broad attachment sites for the digital interossei muscles which abduct and adduct the phalanges. Through the transition from tetradactyl to tridactyl equids, the mean sagittal keel of the MCP (proxy for range of parasagittal rotation) increases from 101°–125°, whereas keel angle in palaeotheres increases from 107°–114°. Additional variation is observed in the palmar carpus. In equids, the volar processes reduced very rapidly, with the earliest tridactyl equid *Mesohippus* presenting no evidence of a prominent volar process on the magnum. However, contemporaneous tridactyl palaeotheres (*Plagiolophus* & *Palaeotherium*) exhibit prominent volar processes, indicative of a forelimb with fleshy digital interossei allowing extensive muscular control over the medial and lateral digits. Relatively increased manoeuvrability in adduction and abduction of the digits would have provided palaeotheres with greater muscular control, ideal when interacting with compliant substrates such as those in moist forest. This would not have been beneficial in drier environments with firmer substrates following the 'Grande Coupure', which would have favoured highly tendinous interossei retaining elastic energy for efficient locomotion (as present in equids). These results offer a possible locomotor feature which may have limited palaeothere adaptability in the Oligocene of Eurasia, potentially contributing to their extinction.

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**Birds – the most species-rich vertebrate group in the Eocene Messel  
ecosystem**

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**Keywords:** Messel, Germany, Eocene

The latest early/earliest middle Eocene (48 Ma) German fossil locality Messel, a UNESCO World Heritage site, yielded a particularly rich avian fossil record, and to date many hundred bird skeletons have been discovered. The Messel avifauna is characterized by a fair number of terrestrial birds, several of which were flightless, as well as a high diversity of aerial insectivores and arboreal birds. With about 70 currently known species in 40 named “genus”-level and at least 37 “family”-level taxa, it approaches extant tropical biota concerning species richness and taxonomic diversity. The talk gives an overview of some of the major avian groups found in Messel and highlights taxa of biogeographic significance. A characteristic feature of early Eocene avifaunas in Europe is the absence of passerines (Passeriformes), which constitute the majority of extant birds. Ecological niches for small arboreal birds were then occupied by representatives of various non-passeriform groups, most of which either belong to extinct clades (e.g., Zygodactylidae, Halcyornithidae) or to clades that today comprise only a few species, such as hoopoes/woodhoopoes (Upupiformes), the African mousebirds (Coliiformes), the Masdagaskan cuckoo-roller (Leptosomiformes), or the Neotropic potoos (Caprimulgiformes, Nyctibiidae).



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**Hoatzins – a South American bird group in the Cenozoic of Africa and Europe**

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**Keywords:** Opisthocomiformes, Eocene, Miocene

Hoatzins (Opisthocomiformes) include a single extant species, which occurs in riparian lowland vegetation of tropical South America. It is an obligate folivore, which processes plant matter with a ruminant-like foregut fermentation in an unusually large crop. Until recently, the evolutionary history of hoatzins was virtually unknown, but new fossils have shed some light on the biogeographic history of these unusual birds. It has been shown that *Namibiavis senutae* from the early Miocene of Namibia is a previously misclassified representative of the Opisthocomiformes, and hoatzin remains have also been reported from the middle Miocene of Maboko Island in Kenya. These African fossils suggest that the extant Neotropic distribution of hoatzins is relictual. Hoatzins have very weak flight capabilities and their occurrence on both sides of the South Atlantic is best explained by dispersal from Africa to South America, with Opisthocomiformes providing the first example for transatlantic rafting among birds. Another recently described species, *Protoazin parisiensis* from the late Eocene of France, constitutes the earliest fossil record of hoatzins and the first one from the Northern Hemisphere. The earliest New World fossils belong to *Hoazinavis lacustris* from the Oligo-Miocene of Brazil. Because Opisthocomiformes have a fossil record in sub-Saharan Africa, their extinction outside the Neotropic region was probably not primarily due to climatic factors.



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**Vertebrate Paleontology and the Cenozoic History of Luberon, southern France**

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**Keywords:** mammals, Eocene, Oligocene, Luberon

Cenozoic sediments of the Luberon area in southern France are rich in fossils that provide unique evidence of Paleogene mammal evolution in western Europe. This presentation highlights the diversity of the Paleogene fossil localities in the Apt-Forcalquier basin that range from the late Eocene to the late Oligocene. The oldest record of fossil mammals known so far from the Luberon area comes from the fossiliferous lignites of La Débruge. This locality yielded a great diversity of late Eocene mammals including 43 species representing 8 distinct orders. This site corresponds to the reference-level MP18 of the mammalian biochronological scale for the European Paleogene. The locality of Pont du Lauzon that documents the biochron MP20 has only produced limited material so far. The earliest Oligocene is primarily documented by rich ichnofaunas (MP21) that represent hundreds of footprints and trackways attributed to early rhinocerotids, lophiomerycids, entelodonts, creodonts and carnivores. The late early Oligocene lacustrine deposits of the Campagne-Calavon Formation (MP23) yielded remarkably well preserved terrestrial and aquatic vertebrates, representing Actinopterygii, Amphibia, Reptilia, Aves and Mammalia. The quality of preservation, quantity and diversity of fossils is exceptional, ranging from almost complete articulated skeletons to soft tissue structures. The mammal faunal succession in the late early-late Oligocene is documented by several localities ascribed to MP23 (Murs, Les Chapelins), MP24 (Saint-Martin-de-Castillon), MP24-25 (Sigonce), MP25 (Terrenoire, Villemus, Aubenas-les-Alpes), MP25-26 (Vachères) and MP30 (La Ferme Pavoux). This presentation underlines the importance of the Luberon fossils to refine biogeographic patterns in Europe and better understand the biotic changes in European faunas through the "Grande Coupure" and during the important Oligocene climatic events.

We thank Jean Rémy (ISEM), Marguerite Huguency and Serge Legendre (Université Claude Bernard Lyon 1), Loïc Costeur (Museum d'Histoire naturelle de Bâle) and Olivier Maridet (Jurassica Museum).



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### Connecting Anatolia to Asia and the end of a Tethyan Island Paradise

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**Keywords:** mammals, Turkey, Eocene/Oligocene

The mammalian fauna of the Uzunçarşidere Formation (Central Anatolia, middle middle Eocene) displays a high endemic cachet with a unique association of Gondwanan and Laurasian mammals, obviously related to the geographic isolation of the area during most of the Paleogene. The Oligocene faunas of Central and Eastern Anatolia display a clear Eurasian cachet suggesting paleogeographic changes related to the collision of the Anatolian Archipelago to the southern margin of Eurasia. However, the question of when the endemism of the Central Anatolian faunas ceased and what were the abiotic factors that triggered the cosmopolitanism of the Anatolian fauna during the late Eocene (i.e. prior to the Grande Coupure) remain unanswered questions. Here, we provide a review of the few late Eocene faunas of Turkey including new fossil data from the Çiçekdağı Basin. This connection of Anatolia to Eurasia, and the related mammal turnover seems to have been multiphasic, and with different patterns on the various continental blocks that collided along the southern margin of Eurasia.



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**Patterns of dental emergence in early anthropoid primates from the  
Fayum, Egypt: implications for interpreting social behavior**

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**Keywords:** Anthropeidea, Paleogene, life history, dental eruption, Egypt

Paleontological field work in the Fayum Depression of Egypt has produced an impressive array of fossil anthropoids, and decades of collaborative work has achieved some degree of consensus regarding their temporal and phylogenetic framework. Less well understood are the evolutionary mechanisms and selective factors behind the origin and early diversification of anthropoids, and this is a major omission given that understanding patterns of growth and development is essential for interpreting the paleobiology of fossil species. Here we present the dental emergence sequences for five species in four families of early anthropoid primates, 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 one species had a dental eruption sequence identical to that observed among crown catarrhine primates; 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.

We thank the Egyptian Mineral Resources Authority and the Egyptian Geological Museum for their support of field work in Egypt.





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**An early Eocene mammal assemblage from Bayan Ulan (Inner Mongolia, China) and reassessment of the Arshantan Land Mammal Age**

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**Keywords:** Perissodactyla, Bayan Ulan, Arshanto Formation

Paleogene mammal localities are particularly well represented in the area of Eriianhot, Inner Mongolia. Among them, the locality of Bayan Ulan is most famous for its late Paleocene Gashatan fauna. The Arshantan fauna of the site is not well known, since no extensive study has been done so far. Here we present a mammal assemblage based on dental and tarsal material from a new Arshantan collection resulting from excavations done by a Belgian-Chinese expedition in Inner Mongolia in 1995 – retrieved from the red beds of the late early to early middle Eocene Arshanto Formation at Bayan Ulan. It consists of at least six different taxa: the primitive lagomorph *Dawsonolagus antiquus*, the large pantodont *Pantolambdodon* sp., the lophialetid tapiroid *Schlosseria magister*, the rhinocerotoid *Hyrachyus crista*, and a new smaller rhinocerotoid. The latter is closely related to the genera *Yimengia* and *Rhodopagus*. The species exhibits transverse Hunter-Schreger bands, no reduction of the lower premolars, m3 has no hypoconulid, and P4 bears a continuous “V”-shaped protoloph-metaloph loop. The Arshantan assemblage at Bayan Ulan is dominated by small perissodactyls, represented by extensive lower and upper dentition as well as foot bones. Also, for the first time, p4-m1 of *Dawsonolagus antiquus*, tarsal material from *Pantolambdodon*, and lower dentition of *Hyrachyus crista* are illustrated. Unlike other described Arshantan faunas, the Bayan Ulan Arshantan mammal assemblage has been collected exclusively from a single locality, which allows it to be used in the reassessment of the Arshantan Land Mammal Age.

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**An enigmatic basal turtle (Stem Testudines) in the Paleogene of Europe**

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**Keywords:** Testudinata, Paleocene, Western Europe

Two lineages of basal turtles (i.e. members of Testudinata not attributable to the crown group Testudines) are identified in the Cretaceous record of Europe. One of them is known from the uppermost Jurassic to the uppermost Cretaceous. It is Helochelydridae, represented by several European species, but also known in the North American Cretaceous record. The other is represented by a single valid species, *Kallokibotion bajazidi*. This form is currently recognized as exclusive to the Maastrichtian (Late Cretaceous) record of the Hațeg Basin, in Transylvania (Romania). The basal turtles are very scarce in the Cenozoic record and, until now, they have not been described in the Northern Hemisphere. Although the survival of *Kallokibotion* beyond the Cretaceous was proposed from the preliminary observation of scarce material from the Paleocene area of Berru, in France, this hypothesis had not been demonstrated, having been subsequently considered as doubtful. The detailed study of this Paleocene turtle from Western Europe is presented here. Abundant material is identified, allowing its detailed characterization. Its attribution to a basal turtle (Stem Testudines) is confirmed. However, it is not referred to *Kallokibotion*, but it represents a still undiagnosed taxon.



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### The large trionychid turtles from the early Eocene record of Belgium

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**Keywords:** Cryptodira, Trionychidae, Paleogene

Remains of trionychid turtles are abundant in the early Eocene fossil record of Belgium where several species are recognized. In this context, the remains of several large-bodied individuals, with a shell length of about one meter, stand out both for their size and good preservation. The Royal Belgian Institute of Natural Sciences houses several unpublished large-size specimens, but also others with a high historical value (e.g., those from Erquelinnes and Leval), which had not been, until now, studied in detail. Recent studies proposed that all large trionychids from the Eocene of Western Europe could belong to a single species, attributable to the North American genus *Axestemys*. However, a valid diagnosis for this putative European single species is not currently available, since the characters that allow its differentiation with each of the North American species have not been well established. Several of the best preserved Belgian specimens have been recently restored, which allows us to perform their detailed study. Thus, the description of several anatomical elements hitherto poorly known or not described for the large-bodied trionychids of the Eocene of Europe can be performed for the first time. The study of the Belgian specimens, which correspond to the most complete and best preserved in Europe, allows us to evaluate the hypothesis on whether they belong to the same species as the other large-bodied trionychids found in the Paleogene record of this continent. Thus, this study significantly increases the information on the relatively poorly known Paleogene large trionychids of Europe.

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**Understanding the phylogeny of Periptychidae and “archaic”  
Palaeocene mammals using Bayesian analysis**

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**Keywords:** Palaeocene, “condylarths”, Periptychidae, Bayesian analysis, phylogeny

The end-Cretaceous mass extinction was a major event, with enormous repercussions for life on the planet. Following this extinction, mammals had a unique opportunity to radiate during the Palaeocene, occupying new and diverse ecological niches. The phylogenetic position of these so-called “archaic” Palaeocene mammals within Placentalia and the phylogenetic relationship between them has yet to be fully resolved. An important clade that emerged after this catastrophic event are the Periptychidae, composed of ~17 distinctive genera of small to large bodied terrestrial ungulates, distinctive for their bunodont dentition adapted towards an herbivorous diet. Historically, the Periptychidae have been considered a definitive “condylarth” subgroup, even though their higher-level phylogenetic relationships have been seldom tested. Here, we present an inclusive Bayesian analysis to determine the phylogenetic affinities of Periptychidae and other relevant Paleocene taxa within Placentalia. We scored 140 taxa for 503 dental, cranial and postcranial characters, incorporating new morphological and taxonomic data. The data was then subject to Bayesian tree searching protocols, using a Mk +  $\Gamma$  model of morphological evolution, running 5000000 generations with samples every 200 generations and discarding 25% of the samples as burn-in. Stationarity was achieved and a 50 percent majority rule consensus tree from the sampled trees was obtained, recovering a monophyletic Periptychidae with the exception of a few problematic early Puercan taxa. Our results support the phylogenetic placement of Periptychidae within a group of “condylarths” closely related to Artiodactyla and positioned at the base of Laurasiatheria. The three major subfamilial divisions within Periptychidae were also supported. These results improve our understanding of the evolution of placental mammals after the end-Cretaceous extinction.

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**The Paris Basin Sparnacian: Revision of the lithostratigraphic nomenclature thanks to new sedimentary, mineralogical, chemo- and bio-stratigraphic data**

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**Keywords:** Paris Basin, Sparnacian, stratigraphy, PETM

In the Paris Basin, marine deposits of the Vesles and Montagne de Laon Groups bracket terrestrial to littoral litho-units of the Mont Bernon Group. Since 2007, we study those Sparnacian facies, as they record the effects of a climate crisis linked to a massive release of greenhouse gases into the atmosphere. This hyperthermal event, the Paleocene Eocene Thermal Maximum (PETM), occurred 55.8 Ma ago, was brief (170 ka) and intense (+ 5 to 8°C vs. baseline). Studied as an analogue to the current global warming, it is marked by a negative isotopic excursion of 2 to 6 ‰ of the  $\delta^{13}\text{C}$  and coincides with environmental perturbations.

About thirty reference successions have been studied, to which well-described information is incorporated, providing a comprehensive and detailed set of geological data. The aim is to 1) revise the lithostratigraphic nomenclature by integrating new  $\delta^{13}\text{C}_{\text{org}}$  and biostratigraphic data, 2) establish well-calibrated correlations in these series prone to hiatuses and lateral facies changes, 3) build a robust framework to reconstitute and discuss the evolution of landscapes, flora and fauna.

We show a prominent record of the PETM over 15-25 m, marked by a strong increase in the sedimentation rate. Steps identified in the  $\delta^{13}\text{C}_{\text{org}}$  curves enable fine correlation, 1) especially at the beginning of the event in



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fluvial and more rarely lagoonal to lacustrine environments, 2) then in alluvial plains, with development of calcretes and variegated paleosols, 3) and in swamps, lakes and lagoons, formed in a context of rising water level. We further observe faunal and floral turnovers, eutrophication of aquatic environments, extreme acme of *Apectodinium* and few other dinoflagellate cyst groups as well as the occurrence of new dinoflagellate species. Lateral facies variations are anchored and paleogeographic maps drawn. It appears that some litho-units previously considered as unique in the Paris Basin (e.g. lignite, plastic clay, fluvial sand, lacustrine limestone and lagoonal sediments) are not synchronous and cannot be regarded as stratigraphic markers for a unique event.

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### The Messel bat community and a cryptic new species

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**Keywords:** Chiroptera, Messel, Eocene, palaeobiology, species richness

In 1917 Pierre Revilliod described three fossil bat species from the open cast mine “Messel Pit” as the first and oldest bat fossils from Germany (Eocene, MP11). During the last 100 years, knowledge of the Messel bat fauna has increased considerably due to intense excavation activities as well as new examination and preparation methods. The Messel bat fauna currently comprises seven species in four families (Archaeonycteridae †, Hassianycteridae †, Palaeochiropterygidae †, Emballonuridae). As such it is tied with a fauna from the Eocene of Vastan (India) in ranking earliest worldwide for overall fossil bat biodiversity.

In addition to documenting faunal diversity, the Messel bats provide unique palaeobiological information due to their outstanding preservation (articulated skeletons, often with soft-body outlines and preserved gut content). Investigations with 2D Xray, Micro-CT and SEM have revealed that Messel bats were active echolocating insect hunters, likely catching their prey at different altitudes and thus already ecologically differentiated as in extant bat communities. Fossil remains of pregnant females, juveniles, and subadults have been recovered, allowing ontogenetic studies. Tooth replacement has also been investigated using stereo micro-radiographies. In 2015 an international team of researchers even provided the first evidence of color in fossil mammals using specimens of two Messel bat species.

Here we present detailed comparative data from examinations of Messel bats housed in different museum collections that indicate previously unrecognized diversity in the fauna including a new bat species, of which the holotype and paratypes will be housed in Senckenberg Research Institute. This will be the eighth Messel bat species after the description of *Tachypteron franzeni* in 2002.

We thank the Senckenberg Messel excavation team and curators of the Messel collections from Hessisches Landesmuseum Darmstadt and Senckenberg Tübingen for the loan of Messel bats under their care.



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### **Divergent mammalian body size during the stable middle Eocene climate of Geiseltal**

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**Keywords:** *Lophiodon*, *Propalaeotherium*, Geiseltal

The negative correlation between body-size and the latitudinal temperature gradient is well established for extant terrestrial endotherms but less so in the fossil record. Paleogene hyperthermals have been shown to result in dwarfing among mammals but the impact of past global cooling remains poorly understood. Here we analyze the middle Eocene site of Geiseltal (Germany), whose record is considered to span ca. 5 Myrs of gradual global cooling, and generate one of the most extensive mammalian Paleogene body-size datasets outside North America.  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  isotopic analysis of bioapatite reveals signatures indicative of a humid subtropical forest with no apparent climatic change across Geiseltal. Yet, body mass of propalaeotherid horses and the tapiromorph *Lophiodon* diverges rapidly from an initial mean body size gap of 110kg to 220kg at the end of the record. We attribute the divergent body mass evolution to a disparity in lifestyle. The fast-slow life history concept predicts that small-sized early horses had high reproduction / biomass-production rates whereas tapiromorphs, the largest herbivores of the European Eocene, lived and reproduced more “slowly” due to the lack of comparably-sized predators. These discrepant life histories likely resulted in an opposing body-size evolution in which both taxa maximized their body size-related selective advantages. Our results therefore support the view that intrinsic biotic processes are an important driver of body mass outside of abrupt climate events. Moreover, the propalaeotherid taxonomy previously used to infer the duration of the Geiseltal biota is not reproducible which precludes chronological correlation with the global Eocene temperature curve. Furthermore, this highlights the need for a reexamination of the current biostratigraphic correlation of Geiseltal as well as the Geiseltalian European Land Mammal mega-zone with the European terrestrial mammal chronology.

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### **Eocene fossil dermochelyid provides insights into why leatherback turtles “want to become” marine mammals**

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**Keywords:** *Dermochelyidae*, *Dermochelys*, Eocene, macroevolution

Leatherbacks constitute a bizarre clade of marine turtles today represented by a single species, *Dermochelys coriacea*. A series of peculiar physiological adaptations and behaviors make this species particularly reminiscent to some marine mammals. These include particularly advanced skeleton adaptations for swimming, the largest body size among living reptiles, highly elevated growth and metabolic rates, and cold-water tolerance, which enable *D. coriacea* to lead a truly pelagic, highly migratory, cosmopolitan lifestyle. It is one of the deepest diving animal today, which aids searching for its almost exclusive prey of jellyfishes. Due to their pelagic lifestyle and reduced skeleton, however, the fossil record of leatherbacks is very poor. Here we evaluate the skeletal anatomy of *Eosphargis gigas* from the Ypresian of Belgium, represented by one of the earliest and most completely preserved fossil dermochelyid. *E. gigas* already shows several of the anatomical specializations of the extant leatherback but it is primitive in retaining a more ossified shell. The autapomorphic rugose surface decoration of the dermal skull indicates high degree of vascularization, which in turn likely aided regulation of acid–base balance relating to hypercapnia (excess blood carbon dioxide) and/or lactate acidosis based on modern and fossil analogies. Both type of acidosis typically occurs during diving and thus *E. gigas* likely had deep diving capabilities, which is consistent with its postcranial skeleton. The jaw apparatus also shares many specializations with *D. coriacea* that may represent adaptation for preying on jellyfish. The emerging hypothesis is that the skeletal and physiological adaptations of leatherbacks are all related to feeding specializations and associated deep diving. Many of these evolved early in the lineage under greenhouse climatic conditions with the likely associated deeper placement of the gelatinous plankton zone compared to icehouse conditions.

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

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**Keywords:** Raoellidae, Artiodactyla, Eocene, Subathu Formation, India

A new artiodactyl of moderate size is described on the basis of several dentaries and maxillae from the middle Eocene Subathu Group of the Kalakot area, Rajouri District, Jammu and Kashmir, India. Despite its general resemblance with the family Dichobunidae this taxon shares with Raoellidae two unambiguous characters: the presence of a hypoconulid on p4, and an asymmetrical P4. The position of the new taxon within the Cetacea / Raoellidae clade is strongly supported by eight non ambiguous synapomorphies, among which a cristid obliqua on lower molars anteriorly pointing towards the postectoprotocristid, and a P3 with only two roots.

The new taxon is characterised by the following characters: a long symphysis; p3 and p4 with small parastylid and metastylid but no metaconid; lower molars with metaconid as the highest cusp, voluminous hypoconid, and absence of 'hypolophid'; m1 and m2 with small paraconid, basally fused with metaconid, and small bifid tubercle-like hypoconulid; m3 with a crestiform paraconid; P3 and P4 with small protocone and shelf-like cingulae; upper molars with small paraconule and large metaconule (pseudohypocone); M1 and M2 with conical brachydont cusps; M3 with bunodont bulbous cusps; cristae and cingulae distinct and thick, presence of an ectoloph. The presence of a new primitive raoellid in the middle Eocene Subathu Group sheds new light on the phylogeny and paleobiogeography of basal raoellid artiodactyls.

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***Cambaytherium*, most primitive known perissodactylamorph (early Eocene of India), and the origin of the mammalian order Perissodactyla**

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**Keywords:** perissodactyls, Early Eocene, India, anatomy, Anthracobunia

*Cambaytherium* is a primitive, perissodactyl-like mammal from the early Eocene Cambay Shale Formation of Gujarat, India, discovered 15 years ago. There are now more than 350 specimens of *Cambaytherium*, representing almost the entire dentition and skeleton. Its unique combination of plesiomorphic anatomical traits typical of archaic ungulates like phenacodontids, and derived traits that characterize early perissodactyls, offers important new insight into the expected anatomy of the common ancestor of Perissodactyla as well as the geographic center of origin of the order. *Cambaytherium* was a subcursorial animal better adapted for running than phenacodontids but less specialized than basal perissodactyls. Its cheek teeth are bunodont with large upper molar conules, not lophodont as in early perissodactyls; but as in perissodactyls, 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, and at the bases of the canines, suggests an abrasive herbivorous diet. We recognize three species of *Cambaytherium*: *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 indicate an age of c. 54.5 Ma for the Cambay Shale vertebrate fauna (the oldest 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, composing the clade Anthracobunia, which is the sister group of Perissodactyla. They comprise a new higher taxon, Perissodactylamorpha. Occurrence of its most primitive known member, *Cambaytherium*, in India suggests that Perissodactyla evolved during the Paleocene either in India or in peripheral areas of southern or southwestern Asia. Where *Cambaytherium* evolved, and how and when it reached India, remain unresolved.

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### **New vertebrate fossils from the Paleogene deposits of the Fayum Depression, Egypt**

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**Keywords:** Fayum, archaeocete whale, percomorph fish, phiomorph rodent, coprolites

Paleontological work in Egypt started 140 years ago when the first vertebrate fossils were collected in 1879 from the Fayum area by German botanist and explorer Georg Schweinfurth. Numerous fossil sites in the Fayum badlands have since produced abundant and diverse mammalian assemblages of late Eocene and early Oligocene age, which are very well known for documenting the evolution of terrestrial and marine vertebrates in the later Paleogene of Africa. Our recent paleontological work in the Fayum Depression has resulted in the discovery of numerous new vertebrate fossil materials from the middle-upper Eocene Medawara, Gehannam and Birket Qarun formations, the upper Eocene Qasr el Sagha Formation, and the upper Eocene and lower Oligocene Jebel Qatrani Formation. Fossil remains recovered from the Medawara Formation provide the oldest record of basilosaurid whales from Egypt and indeed the oldest from the whole of Africa. The remains include a nearly complete skull, isolated auditory bullae, both left and right sides of the mandible with associated teeth and the first cervical vertebra (the atlas). New material from the middle Eocene Gehannam Formation include cranial, dental, and postcranial elements of an associated protocetid whale skeleton. From sediments of the type section of the late Eocene Qasr el Sagha Formation, we have collected a well preserved percomorph fish skull; the new specimen can be clearly distinguished from all previously reported percomorph crania from the African Cenozoic. In addition to the new findings, we provide morphological descriptions of dental and cranial remains of a new phiomorph rodent from the late Eocene (~34 Ma) Locality 41, the oldest and most productive quarry in the Fayum exposures of the Jebel Qatrani Formation. The new remains preserve the entire lower and upper dentition. Finally, we provide the first study of coprolites of carnivorous fishes from the late Eocene Fayum site Birket Qarun Locality 2 (BQ-2), the oldest terrestrial mammal bearing locality in the Paleogene of Egypt. This new material augments the already rich vertebrate assemblage from the Fayum deposits and helps shed light on the evolution and paleoenvironment of both marine and terrestrial vertebrates during the Paleogene of Africa.

I would like to thank students of Mansoura University Vertebrate Paleontology Center (MUVP), Dr. Mohamed S. Antar from EEAA of Egypt and Prof. Erik Seiffert from SCU, USA.



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### On the history of the European Paleogene carnivorous mammals

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**Keywords:** Hyaenodonta, Carnivora, Europe, Africa, Asia

This study documents the evolution of carnivorous mammals that lived in Europe during the Paleogene (66–23 Ma). The study was undertaken to understand the competition between the Carnivora (the present-day lions, dogs, bears, and seals among others) and three other groups of extinct placental mammals: Hyaenodonta, Mesonychia, Oxyaenidae. These groups each have carnassial teeth and are considered specialized meat-eaters. It has thus been posited that the Carnivora, Hyaenodonta, Oxyaenidae, and Mesonychia competed against one another.

Analysis of the taxonomic and morphological diversification of these groups in the North American fossil record clearly demonstrated that carnivoraforms outcompeted hyaenodonts and oxyaenids during the Eocene, specifically from around 50 Ma onwards.

The results of this study suggest that this competition trend differed between North America and Europe. Carnivoraforms did not diversify in Europe during the Eocene and thus were not as taxonomically successful in Europe as they were in North America. The situation dramatically changed during the 'Grande Coupure' (around Eocene–Oligocene boundary; ca. 33.9 Ma). This transition corresponds to a major faunal turnover in Europe.

This analysis is moreover the opportunity to scrutinize the dispersal events that modified the composition of the European carnivorous fauna during the Paleogene – and to identify periods of general endemism. Two periods of endemism can be identified: from 51 to 41 Ma and from 30 to 26 Ma. Remaining time intervals (between 57–51 Ma, 40–31 Ma, and 25–23 Ma) are characterized by dispersals of new taxa from North America, Asia, and Africa. The European carnivorous fauna of the Paleogene thus appears to have been almost constantly in a dynamic state strongly influenced by dispersals. For instance, during the 'Grande Coupure', the Eocene endemic carnivorous fauna was replaced by immigrant taxa (hyaenodonts and carnivorans), mainly from Asia.

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

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**Keywords:** Hyaenodonta, Prémontré, Europe, Ypresian, radiation

The fossiliferous locality of Prémontré (Aisne, France) is considered to be close in age to the localities from the “*Sables à Unios et Térédines*” *sensu stricto*, such as Grauves (Ypresian, MP10 reference-level; Marne, France). According to previous authors, the fossiliferous sediments of Prémontré and Grauves deposited around 50-51 Ma. Recent study of the microfossil assemblages from the Prémontré Sands allowed estimating that the deposition of the Prémontré mammal fauna postdates the onset of both NP13 biozone and Chron C22r, which are nearly coincident, by about 200 to 300 kyr, so around 50.4 Ma.

We identified three new hyaenodonts from the locality of Prémontré based on almost 150 isolated molars and premolars, as well as four fragments of maxillary. Three new species are recognized: they represent the oldest occurrences of the European endemic genera *Cynohyaenodon*, *Lesmesodon*, and *Eurotherium*. The new species referred to *Cynohyaenodon* and *Lesmesodon* are also identified in the mammal faunas of Cuis and Mancy (Marne, France; MP10) based on isolated molars. They support the presence of small hyaenodonts (300-400 g) in the late Ypresian of the Paris Basin. Estimation of dental indices indicate that these taxa had a carnivorous/non-vertebrate diet. The third species – referred to *Eurotherium* – might have weighted around 4-5 kg. These discoveries are interesting because only mostly large hyaenodonts (10-14 kg) (*i.e.*, *Matthodon* and *Oxyaenoides*) were reported from MP10 localities until now.

This moreover implies that *Cynohyaenodon*, *Lesmesodon*, and *Eurotherium* appeared in Europe earlier than previously known (*i.e.*, Lutetian). This reinforces the hypothesis – previously supported by the large hyaenodonts – that these carnivorous mammals have radiated in Europe at the end of the Ypresian.

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### The Paleogene time scale 2020

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**Keywords:** Time scale, Paleogene, stratigraphy, zonations, GTS2020 (max. 5)

It's nearly forty years ago that 'A Geologic Time Scale 1982' appeared (Harland et al. 1982); it was succeeded by major updates in 1989 (Harland et al. 1990), 2004 and 2012 (Gradstein et al. 2004, 2012 – known as GTS2004 and GTS2012, respectively). The primary rationale was “to show as clearly as we can how such a scale has been constructed” (Harland et al. 1982). Each update was about twice the length of the previous version. Consistently aiming to achieve a common language with respect to chronostratigraphic units and geological time, these books have served as state-of-the-art summaries for the entire geological community, both in academia and industry. The last two time scale books contained a discrete and extensive chapter devoted entirely to the stratigraphy of the Paleogene, summarizing information on all stages, established GSSPs, various biozonations and the creation of the time scale (Luterbacher et al. 2004; Vandenberghe et al. 2012). We are currently in the process of revising and updating the 2012 version for the next synthesis to be published as GTS2020. The main modifications of the Paleogene chapter include: 1) summaries of the GSSP proposals for the Priabonian and Chattian stages now submitted to IUGS – only the Bartonian is still in need of a GSSP proposal; 2) integration of a new standard calcareous nannofossil zonation scheme; 3) major updates of land mammal stratigraphy, particularly for those regions where research has strongly intensified over the last decade, such as South America and Central and East Asia; 4) minor to moderate revisions of the zonations based on planktic foraminifera, larger benthic foraminifera, organic dinoflagellate cysts and radiolarians; 5) an update of the main paleoclimatic developments of the Paleogene; 6) a revised geochronology and astronomical calibration of the Paleogene time scale. In this presentation, the major updates will be highlighted.



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**Dinoflagellate cyst biostratigraphical and palaeoecological analysis of  
the early Paleogene Landana reference section, Cabinda Province,  
Angola**

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**Keywords:** dinoflagellate cysts, biostratigraphy, palaeoecology, Paleocene, Eocene

Systematic palynological analysis of the Landana section has revealed 90 distinct dinoflagellate cyst taxa and has resulted in the establishment of a novel preliminary dinoflagellate cyst zonation. The zonation comprises three distinct dinoflagellate cyst zones and five unzoned, yet otherwise distinct intervals, spanning the ?Danian/early Selandian to Eocene/early Oligocene. The Landana record, which represents the first extensive sub-equatorial African Paleogene dinoflagellate cyst record, was extensively 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. The ?Danian–Selandian segment of the record is characterized by the presence of taxa such as *Alterbidinium? pentaradiatum*, *Isabelidinium? viborgense*, *Isabelidinium cingulatum* and *Spinidinium densispinatum*. The Thanetian through Ypresian succession is far more fragmentary and is devoid of any significant marker taxa. The few dinoflagellate cyst-bearing samples in the uppermost part of the record point to an Eocene to early Oligocene age. The dinoflagellate cyst assemblages are very variable, with several dinoflagellate cyst taxa and ecological groups and complexes rising to dominance successively. Overall high TOC values, significant enhancements in %TP and intervals dominated by presumably heterotrophic dinoflagellate cysts, suggest periods of significant palaeoproductivity and nutrient availability resulting from either heightened terrestrial influence or enhanced upwelling. The overall dinoflagellate cyst assemblages concur with the recorded marine vertebrate faunas and the available sedimentological data that point to a coastal/shallow marine setting for the ?Danian–Ypresian succession.

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### **Evolutionary and Paleoenvironmental Patterns in African Vertebrate Faunas at the Close of the Paleogene**

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**Keywords:** vertebrates, Africa, Oligocene/Miocene

The Paleogene records a remarkable period in Earth's history, as ecosystems restructured following the extinction of nonavian dinosaurs to herald the age of mammals. Paleontological research documents the rise and decline of key mammalian clades like adapoids and omomyoids. Such groups flourished on northern continents throughout the Eocene, then underwent sharp declines in species richness during the Oligocene as tectonic events and climate shifts profoundly influenced the composition of mammalian terrestrial communities. Primate extinctions across Europe and North America were paralleled by dramatic diversifications on the Afro-Arabian landmass, as the Oligocene witnessed the eventual emergence of major clades still common today.

Following relatively well-sampled early Oligocene records derived largely from locales in Egypt and Oman, relatively few primate fossils are known until the early Miocene when faunas appear distinct. Documenting the sequence and timing of transitions in Paleogene-Neogene vertebrate communities has long been hampered by missing temporal and geographic data, obscuring how global climate patterns and landmass configuration influenced Africa's faunal composition through time. We now know that it was very near the Oligo-Miocene boundary that African terrestrial communities underwent a dramatic restructuring, with environmental alterations associated with collision between the Eurasian and Afro-Arabian landmasses resulting in large-scale faunal changes. These changes are reflected in dietary shifts and alterations in competition and predation dynamics among Africa's resident biota. Recent work has documented a shift in vertebrate communities in some detail. Here we provide a review of African late Paleogene faunas including new data from the Rukwa Rift Basin that document a number of key first and last appearances in the Cenozoic vertebrate fossil record including the earliest evidence for the cercopithecoid-hominoid divergence.

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### **A new adapiform primate from the early Eocene of Fournes, Minervois Basin, Southern France**

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**Keywords:** Primates, Adapiformes, *Cantius*, biogeography, phylogeny

The mammal fauna from Fournes is one of the very few early Eocene mammal records in Southern Europe. Our recent bio-chemostratigraphic study indicated that the Fournes mammal bed is mid-NP11 in age (around 53.5 Ma), slightly postdating the Eocene Thermal Maximum 2, and equivalent with the North American mammalian biozone Wa-5. Until recently, *Donrussellia* cf. *gallica* was the only known primate species from Fournes. Here, we describe another adapiform, documented by a well-preserved mandible bearing p3-m3 and p1-p2 alveoli. Several characters (e.g., biradicular p2, molar bunodonty, size and relative position of the paraconid relative to the metaconid from m1 to m3) support an attribution to the notharctid *Cantius*. In Europe, this genus is documented by *C. eppsi* (Blackheath Formation of Abbey Wood, MP8+9), *C. savagei* (Avenay, Mutigny and Grauves, MP8+9 to MP10) and by three species undescribed or left in open nomenclature from Le Quesnoy (MP7), Rians (MP7?) and Meudon (MP7?). The new species from Fournes differs from *C. eppsi* and *C. savagei* by being smaller in size, and having a more compressed trigonid on m2-3, a reduced metaconid on m2, and a cristid obliqua that reaches the top of the metaconid on m1. In addition, the species from Fournes differs from *C. eppsi* and *C. savagei* in having shorter and lower p3-4 and smooth enamel, respectively. Comparisons with North American *Cantius* species indicate that, despite the age correlation to Wa-5, the new species from Fournes shows similarities with *C. torresi* (Wa-0) (small size and labially rounded molars) but differs from this taxon in preserving an oblique p2. This dental trait, which is certainly primitive, also characterizes *C. ralstoni* (Wa-1/2) and *Donrussellia*, the basal-most adapiform known. In conclusion, the new primate from Fournes complicates our understanding of the biogeographic history of the genus *Cantius*, but is of major importance for deciphering the Euramerican radiation of the first adapiform primates.



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### **New data about the Eocene-Oligocene mammals of Western and Eastern Europe: towards a new scenario of the “*Grande Coupure*” in Europe**

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**Keywords:** palaeobiogeography, Grande Coupure, Germany, Romania, mammals

About a century ago, in 1909, the paleontologist Hans Georg Stehlin described, based on the European mammalian fossil record, “the greatest and most sudden change known so far during the tertiary times”. He underlined the correlation of this terrestrial event to the Eocene/Oligocene boundary and named it “*Grande Coupure*”.

Recently, a biochronologic revision of some localities of Southern Germany and new comparisons between western and eastern European mammals have been conducted. The revised ages (now late Eocene instead of Oligocene) of some south German localities show that the faunal assemblages and taxa occurrences differ from those of western Europe and indicate two significant turnovers: one at the end of the Eocene (including immigrant taxa generally considered to be post-“*Grande Coupure*”) and another at the beginning of the Oligocene.

New excavations were also conducted in the latest Eocene of Romania and led to the identification of several taxa with Asian affinities (*Amyndontopsis*, *Brachydiastematherium*, *Prominatherium*, *Eocricetodon*). This is clearly contrasting with the latest Eocene mammals of southern Germany, which are much closer to the taxa found later in the Oligocene of western Europe (Rhinocerotidae, ruminants, *Anthracotherium*, *Eomys*, *Eucricetodon*). At the beginning of the Oligocene, the fossil record of Germany is almost identical to that of western Europe, whereas eastern European localities still present a few taxa absent in western Europe (*Sellamynodon*, Paraceratheriidae, Diatomyidae) but also mostly taxa commonly found in all of Europe (e.g. *Paracricetodon*, *Anthracotherium*, *Bachitherium*).

These observations suggest that the “*Grande Coupure*” *sensu* Stehlin, might be an exception restricted to the westernmost border of Europe (Spain, France, Belgium and England), isolated from the rest of Europe by the Rhine graben and the Molasse Sea, whereas in the rest of Europe the transition might have been more complex, involving several migrations.

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**Batoid rays from the Oligocene of Suceag (Transylvanian Basin),  
Romania**

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**Keywords:** Rupelian, Dâncu Formation, Dasyatidae

Recent survey of upper Rupelian deposits of the Suceag locality revealed a relatively rich occurrence of batoid teeth in the Dâncu Formation. This locality is situated on the north-western side of the Paleogene Transylvanian Basin (Gilău sedimentary area), in the central part of Romania, about seven kilometers north-west from the city of Cluj-Napoca. The Dâncu Formation is already known for its bony fish fauna that is based on a rather large number of otoliths. The stratigraphy and the molluscs, especially the presence of the genus *Nucula*, inferred a brackish water environment, probably in an estuarine environment. Here we add three batoid species belonging to the family Dasyatidae to the previously described fish fauna. These batoids (*Dasyatis* cf. *rugosa*, *Dasyatis* aff. *strangulata* and *Taeniurops cavernosus*) are well known from numerous sites of western Europe, where their chronostratigraphic range is restricted from the late Oligocene to the middle Miocene. The present occurrence now extends the chronostratigraphic range of these species to the early Oligocene.

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### The micropreparation of a juvenile marine turtle from the Ypresian of Belgium

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**Keywords:** micropreparation, Ypresian, marine turtle

Several years ago, amateur palaeontologist Michel Girardo collected a block of clay (25x20x18cm) encasing a partially visible small turtle shell, at the Durieux brickyard of Ghlin (Mons Basin). The Clay of Ghlin is stratigraphically important because it belongs to the early Ypresian Mont-Heribu Member of the Kortrijk Clay Formation, representing one of the earliest marine, mid-neritic, depositional environments of the Ypresian in the Mons Basin.

The fossil itself is 15x9cm and consists of a full carapace with all plates in connection, half of the marginal plates, and a crushed part of the head. The preservation is very good and the bones suffered almost no displacement during or after burial. Unfortunately, after excavation and during decades of storage, the block of clay had dried and shrunk, leading to stress deformation of the fragile thin bones and to pyrite oxidation. Thin coats of Paraloid B-72 glue were applied before any work. The block was carefully reduced using chisels and hammer. The separated chunks of clay were then disaggregated in water and sieved, resulting in the recovery of shark teeth and fish bones. The preparation of the specimen was done almost exclusively under stereomicroscope. Air scribes could not be used, only small carbide needles. Well-preserved long bones from the shoulder girdle were found during the work. The clay's shrinkage permitted to separate completely the carapace from the substrate. A well-preserved plastron was in this way discovered and almost all vertebrae were found to be still attached to the vertebral plates. All this precise and slow work produced a very fine and well-preserved marine juvenile specimen, presenting a maximum of details, much more than could be guessed when the specimen was received. This will be quite helpful for the identification of this specimen and for comparison with typical Belgian Thanetian-Ypresian turtles such as *Erquelinnesia*, *Eochelone* and other Pancheloniidae.

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### Asian Paleocene Land Mammal Ages: Age constraint and correlation

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**Keywords:** Asia, Paleocene, Land Mammal Ages, correlation

Asian Paleocene Land Mammal Ages, the Shanghuan, Nongshanian and Gashatan, have been widely used, but their age constraint and correlation remain controversial. The Shanghuan and Nongshanian were respectively defined based on the fossil mammals of the Shanghu and Nongshan formations of Nanxiong Basin, China and their correlatives. The Shanghuan is characterized by *Bemalambda*, *Hypsilolambda*, *Carnilestes*, *Wania*, *Astigale*, *Linnania*, *Zhujegale*, *Stenanagale*, *Wanogale*, *Diacronus*, *Anictops*, *Paranictops*, *Cartictops*, *Anchilestes*, *Pappictidops*, *Hukoutherium*, *Benaius*, *Meiostylodon*, *Plethorodon*, *Lofochaius*, and *Prosarcodon*, etc. The Nongshanian is characterized by *Asiostylops*, *Sinostylops*, *Allostylops*, *Eosigale*, *Qipania*, *Haltictops*, *Allictops*, *Mina*, *Heomys*, *Interogale*, *Simplodon*, *Altilambda*, *Wanolestes*, *Ernanodon*, *Petroleumur*, *Minchenella*, *Yuelophus*, *Radinskya*, *Pseudanisonchus*, *Jiangxia*, *Ganolophus*, *Ganungulatum*, *Yuesthonyx*, etc. The Gashatan was defined for the fossil mammals of the Gashato Fm. of southern Mongolia and its equivalents, and characterized by *Lambdopsalis*, *Prionessus*, *Sphenopsalis*, *Palaeostylops*, *Wanostylops*, *Bayanulanius*, *Sarcodon*, *Pseudictops*, *Prolimnocyon*, *Eomylyus*, *Tribosphenomys*, *Subengius*, *Pastoralodon*, *Prodinoceras*, *Tienshanilophus* and *Sinonyx*, etc. The recent paleomagnetic studies related to these LMAs provided evidence for the age constraint and correlation with the geological time scale and the North American Land Mammal Ages (NALMA). The Shanghuan spans from chron C27n to middle-upper chron C29r, lasting from 66 to 62.22 Ma, and corresponds to most part of the Danian and the Puercan NALMA. The Nongshanian covers the whole chron C26r, from 62.22 to 59.2 Ma, and corresponds to the uppermost Danian to Selandian and the Torrejonian to Tiffanian-4 of NALMA. The Gashatan covers chron C26n through the lower part of C24r, from 59.2 to 56 Ma, and corresponds to the Thanetian and to the Tiffanian-5 to Clarkforkian NALMA.

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**High diversity of Raoellidae (Artiodactyla, Mammalia) from the middle Eocene Subathu Group of Kalakot, Northwest Himalaya, India**

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**Keywords:** Raoellidae, Artiodactyla, Subathu Group, Himalaya, India.

The middle Eocene Subathu Group of Kalakot area (northwest Himalaya, India) is well known for its diverse mammalian fauna, especially of raoellid artiodactyls, which are presently represented by four genera: *Indohyus*, *Khirtharia*, *Kunmunella*, and *Metkatius*. Our recent work on artiodactyls from the Kalakot area recovered several new taxa in addition to earlier known raoellids. The first new taxon is characterized by its small size, higher and more conical lower molar cusps than in *Khirtharia* and *Metkatius*; protoconid and metaconid closely appressed; crista obliqua meets at trigonid notch, presence of an hypolophid and a well-developed labial cingulid; bunodont upper molars, subrectangular M1-M2, and subtriangular M3, large metaconule (pseudohypocone) and small well distinct paraconule; cristae well distinct, small metastyle on M3 (absent in the four other raoellid genera), slightly inflated anterior and posterior cingulae. The second new taxon is the smallest of all known Raoellidae; it has bunodont lower molars with tiny paraconid in m1-2 (paraconid is absent in all other raoellids) and crista obliqua meeting the labial base of protoconid; m3 with an hypolophid and well-individualized hypoconulid centrally placed and higher than entoconid; M2 subrectangular, protocone higher than metacone, para and metastyle less distinct than in *Indohyus* and *Kunmunella*, ectoloph distinct. Besides these two new taxa, *Khirtharia dayi* known from Pakistan is reported for the first time from India on the basis of its morphology and size of m3. A new species of *Metkatius* is characterized on the basis of m1-2, which differ from those of *M. kashmirensis* by the metaconid higher than the protoconid and by being more than 20% larger. Outside the Indian sub-continent, raoellid artiodactyls are also known from the middle Eocene Pondaung Formation of Myanmar and Shanghuang fissure filling of Jiangsu, China. The predominance of the family Raoellidae in Kalakot provides new information about their phylogenetic position and allow to discuss their origin, evolution, and dispersals.

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**Cainotheriidae (Mammalia, Artiodactyla) from Dams (Quercy, SW France); phylogenetic relationships and evolution around the Eocene-Oligocene transition (MP19-MP21).**

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**Keywords:** Grande Coupure, Quercy, Western Europe, phylogeny, faunal turnover.

Cainotheriids are a family of small artiodactyls, known in the fossil record from the late Eocene to the middle Miocene in Western Europe. Contrary to several European endemic ungulate groups that became extinct at the end of the Eocene or close to the Eocene-Oligocene transition (*Grande Coupure*), cainotheriids crossed this boundary and diversified during the Oligocene. The evolutionary history of cainotheriids around the Grande Coupure remains poorly documented and only a few works deal with the modalities of their evolution, notably because of the scarcity of available Eocene remains. A new fossiliferous karstic network named Dams was discovered during field prospections in the Quercy area (Tarn-et-Garonne, France). It notably displays two infillings that yielded a great abundance of cainotheriid remains, namely DAM1 (MP19, late Eocene) and DAM3 (MP22, early Oligocene), bracketing the Eocene–Oligocene transition. A detailed study of cainotheriid mandibular and dental remains from these infillings reveals that only *Paroxacron valdense* occurs at DAM1, while five species are found in DAM3. The karstic network at Dams seemingly records a local taxonomic diversification of cainotheriids after the Grande Coupure, with Cainotheriinae being particularly successful. Our phylogenetic analysis, including cainotheriids from Dams, constitutes the first formal phylogeny of Cainotheriidae. Our results, based on mandibular and dental characters, allow for (i) clarifying relationships within Cainotheriidae (ii) erecting a new family Robiacinidae, as being the sister taxon to Cainotheriidae among Cainotherioidea and, more broadly, (iii) discussing the controversial position of Cainotheriidae within Artiodactyla.





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**Application of long-term chemostratigraphy (organic carbon isotopes)**  
**in age calibration of Paleogene mammal faunas**

Johan Yans<sup>1\*</sup>, Corentin Noiret<sup>1</sup>, Rodolphe Tabuce<sup>2</sup>, Bernard Marandat<sup>2</sup>, Laurent Marivaux<sup>2</sup>, Fabrice Lihoreau<sup>2</sup>, Sylvain Adnet<sup>2</sup>, Emmanuel Gheerbrant<sup>3</sup>, Guillaume Billet<sup>3</sup>, Grégoire Métais<sup>3</sup>, Quentin Vautrin<sup>2</sup>, Constance Bronnert<sup>3</sup>, Thierry Smith<sup>4</sup>, Etienne Steurbaut<sup>4,5</sup>

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**Keywords:** chemostratigraphy, long term, carbon isotopes, mammals, Paleogene

Rapid, 'short-term' (10 kyr to several 10<sup>2</sup> kyr)  $\delta^{13}\text{C}$  -  $\delta^{18}\text{O}$  excursions on various materials (bulk, pedogenetic nodules, specific foraminiferal taxa, secondary layer of brachiopods, dispersed organic matter, wood fragments) have been used for decades as reliable stratigraphic tools during the Paleogene (*Late Danian Event*, PETM or ETM-1, ETM-2, ETM-3, MECO, Oi-1, ...). 'Long-term'  $\delta^{13}\text{C}$  isotope trends (10<sup>2</sup> kyr to several myr) may also provide new stratigraphic insights, particularly in sections without any detailed stratigraphic information. Here we show and discuss the potential uses, biases, limits, and perspectives of long-term  $\delta^{13}\text{C}$  isotope trends on organics, from vertebrate-bearing sections in Morocco, Southern France (Corbières, Minervois, Montpellier area, Provence), Angola and Belgium. Using long-term carbon isotopes on organic matter, terrestrial sections can be correlated with the marine stratigraphic international record. Inter- and intra-regional correlations are proposed on the basis of bio- and chemostratigraphic calibration of the various records, particularly with the well-known and continuous sections of the Bighorn Basin, Wyoming (USA). These correlations may contribute to the age calibration of the Paleogene mammal faunas (including endemic faunas) and may shed new light on their evolution in different parts of the world.

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**Additional vertebral material of *Thaumastophis* from the early Eocene of India provides new insights on the early diversification of colubroidean snakes**

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**Keywords:** Systematics, vertebral morphology, Squamata, Serpentes, Caenophidia

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 colubroid-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, mid-, and posterior trunk vertebrae, as well as caudal vertebrae. This species presents several characters shared with *Renenutet enmerwer* from the late Eocene of Egypt, suggesting exchange with North Africa probably along the southern margin of the Neotethys. Among these are the presence of parazygosphenal foramina (although not in all vertebrae), deep blade-like prezygapophyseal processes, and thick and tall neural spine. The available vertebral evidence is hardly sufficient to distinguish both taxa from each other, suggesting that these might be even congeneric taxa. However, more material is needed to test more appropriately this hypothesis. Both taxa are considered to be close to the root of the Colubroidean tree. We also revise the Eocene colubroidean fossil record in light of these new findings.

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**Discovery of a new middle-upper Eocene vertebrate locality (Sabkha of Lebreij) in the Sahara Desert, southeastern Morocco**

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**Keywords:** Eocene, Vertebrata, Lebreij, Sahara, Morocco

The Sahara Desert in southwestern Morocco is rapidly developing into an important region for documentation of archaeocete whale evolution complementing the Indo-Pakistan sub-continent and the Fayum Depression of Egypt. We first described a Priabonian archaeocete fauna from coastal sites in the Samlat Formation near Ad-Dakhla. This included five archaeocete species, all basilosaurids, and a diversity of associated vertebrate taxa. Later we provided preliminary documentation of a Bartonian archaeocete fauna in the Aridal Formation of the Sabkha of Gueran that included both protocetids and basilosaurids, making it one of the most diversified localities with archaeocete remains known anywhere. Ad-Dakhla and Gueran both include diverse non-cetacean faunas.

Here we report the discovery of new middle-upper Eocene localities in the Aridal Formation of the Sabkha of Lebreij, located one hundred and fifty kilometers southeast of the coastal city of Boujdour and sixty kilometers north-east of the Sabkha of Gueran. At Lebreij the vertebrate remains come from many localities on three distinct levels along a transect of several kilometers. The lower level yields fossil remains of two protocetids, one the very large *Pappocetus lugardi* and the other a smaller medium-sized protocetid. Teeth of selachians are abundant. Remains of bony fish, turtles, crocodyliformes, and a palaeophiid snake are rare. The genus *Pappocetus* is now known from a rostrum, and for the first time associated vertebrae and limb bones, confirming that the genus was a georgiacetine and semiaquatic. Some ten meters above the protocetid level, two closely-spaced fossiliferous levels have yielded partial skeletons of three archaeocete taxa: *Chrysocetus*, *Platyosphys*, and *Basilosaurus*. These are associated with abundant chondrichthyans, and with remains of bony fish, turtles, crocodyliformes, and birds.

Fieldwork research was supported by the National Geographic Society, by the Museum of Paleontology, University of Michigan, Ann Arbor, and by Hassan II University of Casablanca, Morocco.



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**The middle-upper Eocene Vertebrate Record from Tarfaya–Laâyoune–  
Dakhla Atlantic Basin (Morocco)**

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**Keywords:** Eocene, Vertebrata, Sahara, Morocco

Several palaeontological field campaigns in Ad-Dakhla and Boujdour area have resulted in the discovery of rich Eocene marine vertebrate assemblages. All this material comes from two areas in the Moroccan Sahara desert: the Aridal Formation at Gueran, ca. 150 km southeast of the city of Boujdour, and the Samlat Formation in the Ad-Dakhla area.

At Gueran, all fossils come from a single meter-thick sandstone unit. Archeocete whales are referred to at least eight species of Protocetidae and Basilosauridae. Fauna from Gueran also includes abundant selachian teeth, a few remains of bony fishes, rare fragments of turtle shells, fragments of jaws, vertebrae and osteoderms of crocodiles, palaeophiid snake vertebrae, as well as seabird remains and fragments of proboscidian teeth. The presence of both protocetid and basilosaurid whales indicates a probable Bartonian age consistent with the Bartonian age suggested by the selachian assemblage.

In the Ad-Dakhla area, fossils are known from stratigraphic sections along 30 km of Atlantic Ocean coastline. At Garitas, vertebrate remains come from three levels called A1, B1 and B2. The layer A1 of lithostratigraphic Unit 1 has provided selachian teeth, palaeophiid snake vertebrae, sternebra of a small protocetid and several cheek teeth of the large protocetid *Pappocetus lugardi*. Unit 1 strata are overlaid by 1–1.5 m of vertebrate-bearing conglomeratic sandstone (B1), another 4–8 m of rhythmically-bedded siltstone and marl, and a second 3–6 m unit of vertebrate-bearing muddy sandstone (B2) which constitutes lithostratigraphic Unit 2. Bonebed B1 has yielded abundant and diversified selachians and archaeocetes, remains of sirenians, proboscideans, actinopterygians, turtles, palaeophiid snakes, crocodiles and pelagornithid seabirds. The only identifiable cetacean found in Bonebed B2 is *Basilosaurus* sp.. Dugongid sirenians identified as cf. *Eosiren* sp. are the most common mammals in bed B2. At Porto Rico, Bonebed B2 includes a well-preserved dentary of a new protosirenid sirenian similar in molar size to *Protosiren smithae*, but with a distinctive symphyseal conformation.

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