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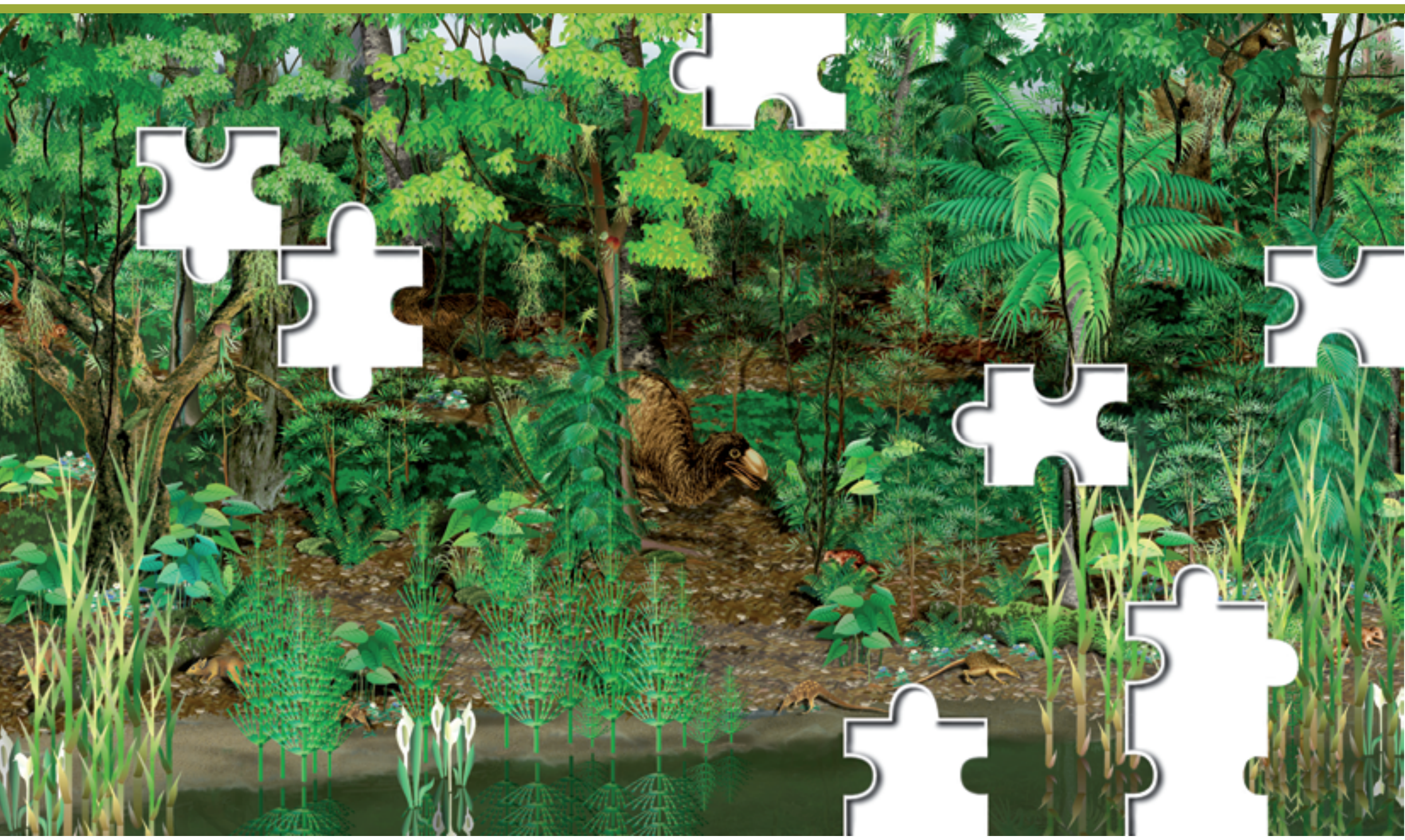

T. Lehmann & S.F.K. Schaal (eds)

The World at the Time of Messel:

Puzzles in Palaeobiology, Palaeoenvironment and the History of Early Primates

22nd International Senckenberg Conference
Frankfurt am Main, 15th - 19th November 2011

Conference Volume

SENCKENBERG Gesellschaft für Naturforschung

THOMAS LEHMANN & STEPHAN F.K. SCHAAL (eds)

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Puzzles in Palaeobiology, Palaeoenvironment, and the History of early Primates

22nd International Senckenberg Conference

Frankfurt am Main, 15th – 19th November 2011
Senckenberg Gesellschaft für Naturforschung

CONVENERS

T. LEHMANN, V. MOSBRUGGER, S.F.K. SCHAAL
(Senckenberg Gesellschaft für Naturforschung (SGN))

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PREFACE

Once or twice a year, the Senckenberg Gesellschaft für Naturforschung (SGN) supports a conference as part of its official series. For the year 2011, the conference proposed by the Department of Palaeoanthropology and Messel Research in Frankfurt was selected as the 22nd International Senckenberg Conference. Its topic: “The world at the time of Messel: Puzzles in palaeobiology, palaeoenvironment, and the history of early primates”.

The formation of the Messel maar and the subsequent deposition of the Messel oil shale in the maar lake took place during the Eocene. This period, which lasted some 22 million years, was characterized by a warm and worldwide little differentiated climate, punctuated by thermal maxima. The global climate was in fact the most equable of the whole Cenozoic. At the beginning of this epoch, right at the Paleocene-Eocene boundary, mammals experienced a major turnover. By then, modern orders, like chiropterans and primates, had become firmly established in all principal land ecosystems. The Eocene was a time of elevated sea level and, by the upper Eocene land bridges between North America and Europe as well as between South America and Antarctica had been severed. Finally, the end of the Eocene is marked by a major climatic deterioration in combination with the Grande Coupure, a large-scale mammalian extinction event and a general floral and faunal turnover. The Eocene is thus a fascinating and eventful period, suitable as a focal point for international palaeobiological discussions. It is even more so, as the site of Messel represents one of the best documented fossil sites worldwide.

The Messel Pit (Fig. 1), the first UNESCO World Natural Heritage Site in Germany, and its beautifully preserved fossil fauna and flora have been a highlight in palaeontology since the first notice of a crocodile from there in 1876. The quality of preservation, quantity and diversity of fossils is exceptional. Not only are a majority of the specimens fully articulated skeletons, they also preserve remains of soft tissue structures like feathers, hairs, and stomach contents. As such, Messel is a peerless window through which we can study life on earth during the Eocene. Over the years, teams of palaeobiologists from all around the world have described a large number of new plant and animal species. For instance, an outstanding vertebrate fauna of more than 130 species, including at least 44 species of mammals in 31 genera has been identified from Messel so far. Likewise, plants are represented by 75 families and 203 species. All these efforts contributed to make Messel one of the emblematic sites of the Eocene.

All the more, the fossils from the Messel Pit are internationally regarded as a reference fauna and flora, used for comparison in studies dealing with terrestrial Eocene organisms. For instance, fossil mammals from the Green River Formation, the Bridger Formation, and the Willwood Formation in Wyoming yield close relatives of Messel species. Some relationships even existed between Europe and Asia, as close relatives to the Messel animals have been discovered lately in India. Moreover, for many Eocene mammals the Messel fossils provide the best or only view of the complete skeleton. Both "old" and "modern" reptile and amphibian groups coexisted during the Eocene and quite a few genera from Europe are represented by well-preserved, articulated specimens from the Messel Pit. These specimens are of great interest for precise phylogenetic studies and, given the biology of reptiles and amphibians, can provide important complementary information about environmental conditions. The insects from Messel document an impressively high biodiversity in and around former Lake Messel, perhaps comparable to today’s rainforests. In comparison, they would represent a mix from different modern biogeographic regions, ranging from the Neotropical to the Australian and Oriental region. Mixed geographic affinities are also observed in the plant taphocoenosis, which is one of the richest and most diverse of the Paleogene worldwide. Finally, the Research Core Messel 2001 not only clarified the genesis of the Messel fossil site as a maar lake, but also provided a unique pre-Quarternary lacustrine climate archive. Accordingly, Messel offers unique and timely insight into the greenhouse world of the middle Eocene.

In this context, the aim of the 22nd International Senckenberg Conference is to gather prominent international specialists from different disciplines and, through their respective field of interest, to develop a synthetic perspective on continental life on earth during the Eocene, crystallised around the emblematic site of Messel. During this conference, and through 52 oral presentations and 28 posters, we hope to tackle several timely questions: What impact did the discoveries of the last decades have on our understanding of the world of the Eocene and in particular, of the evolutionary history of early primates? How did shifting climatic conditions affect Eocene ecosystems? What are the questions and challenges for the future?

The present Conference Volume conveys the results of studies carried out by international researchers, which were presented as oral communications and posters during the conference. Multiple aspects of the life on earth during the Eocene are considered, from the color of fossil insects, the ecology of fungi trapped in amber, and the diversity of northern polar forest vegetation, to the relationships of worm-lizards to lizards, mammalian dispersal routes in the northern hemisphere, and the phylogeny of early primates. In the melting pot of the conference discussions, these valuable peer-reviewed abstracts complement each other and fill in the gaps in our understanding of a crucial period in earth history for terrestrial fauna and flora.

We wish to express our gratitude to the Volkswagen Stiftung for its patronage, which helped make the 22nd International Senckenberg Conference a reality. The Senckenberg Gesellschaft für Naturforschung (SGN) hosted this conference at the Senckenberg Natural History Museum Frankfurt and provided additional financial support. We would particularly like to acknowledge the personal sponsorship of the President of the SGN, Dietmar Schmid, and the Vice President of the SGN, Emmerich Müller. The conference has also benefited from the aid of the Alexander von Humboldt Foundation, the Biodiversity and Climate Research Centre Frankfurt (BiK-F), and the Goethe University, Frankfurt am Main. We also wish to thank the Association Paléontologique française (APF) for its contribution. We are indebted to the international scientific committee and reviewers, which guaranteed the scientific quality of the contributions. Finally, this conference could not have been organised without the help of the members of the organising committee as well as the teams of the Department Paleoanthropology and Messel Research, the Messel Research Station, and the Sektion Palaeobotanik of the Senckenberg Research Institute and Natural History Museum Frankfurt.

Thomas Lehmann, Stephan F.K. Schaal
Conveners of the 22nd Intl. Senckenberg Conference
and editors of the Conference Volume

Figure 1. View of the Messel Pit in the year 2002, from Northeast to Southwest. © Senckenberg Forschungsinstitut und Naturmuseum Frankfurt.

PROGRAMME

of the

22nd International Senckenberg Conference

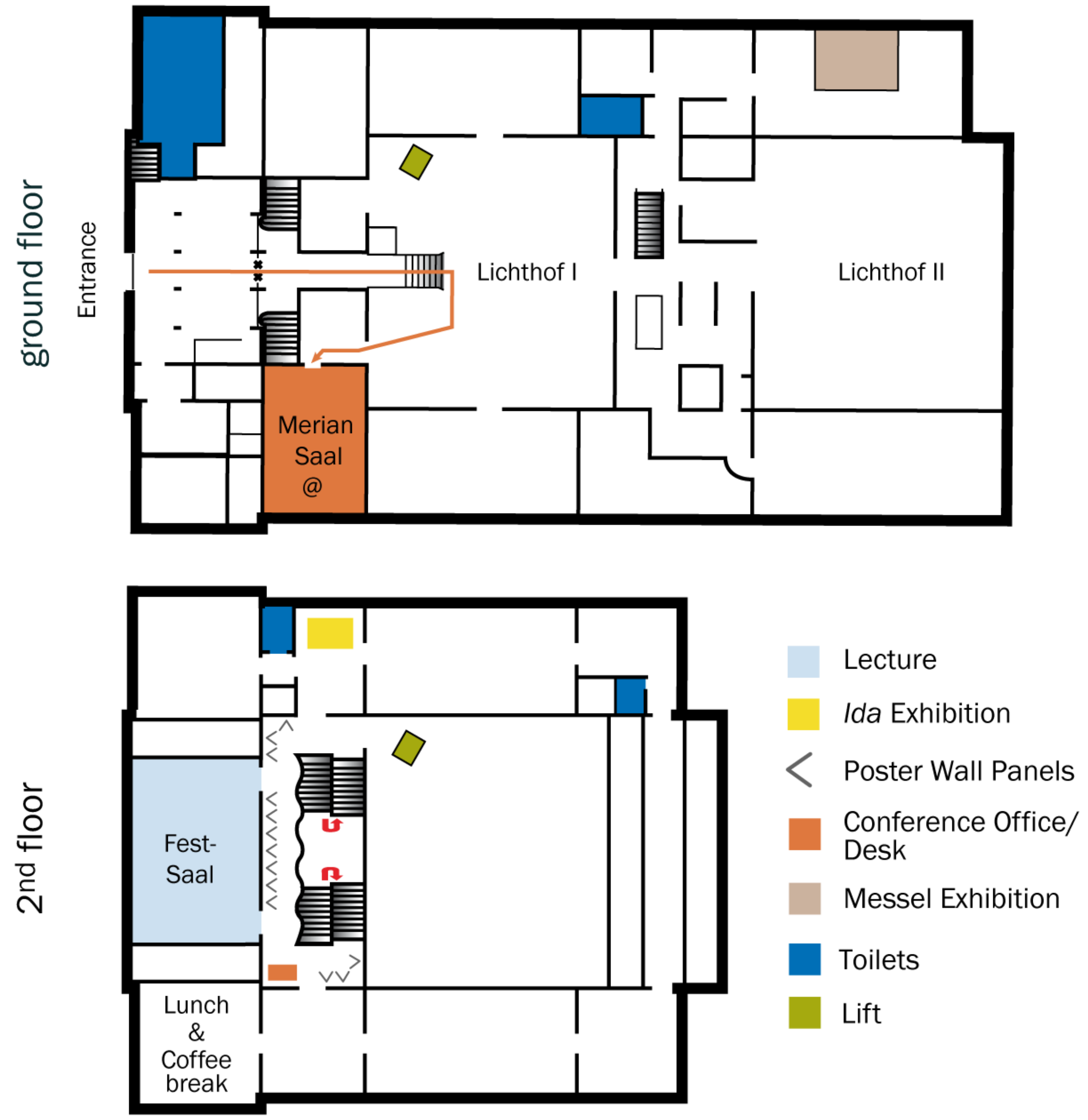
The World at the Time of Messel

PROGRAMME AT A GLANCE

	Tuesday 15th November	**Wednesday** 16th November	**Thursday** 17th November	**Friday** 18th November	**Saturday** 19th November
08:00		Presentation loading & poster installation	Presentation loading	Presentation loading	
09:00		Welcome address S1: Insect – **C.C. Labandeira** KL T. Wappler M.E. McNamara	S3: Lower Vertebrates – **J.-C. Rage** KL M. Augé J. Müller N. Micklich	S4: Mammals - General – G. Métais C. Stefen M. Morlo T. Tütken Speaker Panel	Departure by bus Field Trip to the Messel Pit
10:00		*Coffee Break*	*Coffee Break*	*Coffee Break*	Guided tour of the Messel Pit and visit of the Visitor Information Centre
11:00		S1: Insect – S. Wedmann S.B. Archibald Speaker Panel	S3: Lower Vertebrates – A. Folie M. Böhme M.R. Stocker Speaker Panel	S4: Mammals - Primates – **P.D. Gingerich** KL F. Génin X-J. Ni A.L. Rosenberger	
12:00		Special Presentation: V. Lorenz *Lunch*	*Lunch*		*Lunch*
13:00		📷 - Group Photo - 📷		*Lunch*	
14:00		S2: Plants & Climate – **J.F. Basinger** KL M.E. Collinson O.K. Lenz H. Lutz W. Riegel	S4: Mammals - Bats – **K.D. Rose** KL ~ K.T.J. Davies G.F. Gunnell	S4: Mammals - Primates – J.L. Franzen J.H. Hurum M. Godinot W. von Koenigswald J. White	*Return to Frankfurt*
15:00		*Coffee Break*	*Coffee Break* S4: Mammals - Bats – S.J. Hand A. Ravel T. Smith Speaker Panel	*Coffee Break*	
16:00	Arrival and registration	S2: Plants & Climate – J.W. Westgate R.W. Mathewes N. Boonchai A.R. Schmidt Speaker Panel	*Coffee Break* S4: Mammals - General – Y-Q. Wang M. Pickford R. Tabuce S. Engels	S4: Mammals - Primates – R. Lebrun S. Couette J. Marigó B. Senut K.C. Beard Speaker Panel	*Ida* Workshop
17:00		Poster Session: Short Oral presentations			
18:00	Special Presentation: A. Muellner			*Press Conference*	
19:00	*Ice-Breaker*	*Conference Dinner* with an address of welcome by the Director–General, SGN: V. Mosbrugger	10th G.H.R. von Koenigswald Lecture by E. Delson	Round Table moderated by E. Delson	
OpenEnd					

CONFERENCE VENUE

Oral presentation, Poster session, Conference Office:
Senckenberg Research Institute and Natural History Museum Frankfurt ~
Senckenberganlage 25, 60325 Frankfurt am Main



10th G.H.R. von Koenigswald Lecture:
Goethe-Universität Frankfurt – Aula
Mertonstraße 17–21, Jügelhaus, 2nd Floor, 60325 Frankfurt am Main

ORAL PRESENTATIONS

Tuesday, 15th November 2011

14:00 – 18:00	**Senckenberg Natural History Museum**	Arrival and registration	

18:00 – 19:00	**Senckenberg Festsaal**	Special presentation	
	A. Muellner	*Climate, plant (and animal) diversification at the time of Messel and beyond: A phylogeneticist's perspective*	p. 122

19:00	**Lichthof I**	Ice-Breaker	

Wednesday, 16th November 2011

08:00 – 09:00	**Senckenberg Festsaal & Galerie**	Loading of the oral presentations on to the Festsaal computers and installation of the posters (at the designated spot, in the Galerie)	

09:00 – 09:20	**Senckenberg Festsaal**	Opening	
	S.F.K. Schaal	Welcome address by the Head of the Department of Palaeoanthropology and Messel Research, Senckenberg Frankfurt	
	T. Lehmann	Opening by the Conveners of the 22nd International Senckenberg Conference 2011	

	Senckenberg Festsaal	Session 1: Insects **Chairperson: J. Rust**	
09:20 – 09:55	C.C. Labandeira	Keynote Lecture: *The Messel food web*	p. 95
09:55 – 10:15	T. Wappler	*Testing for the effects and consequences of mid-Paleogene climate change on insect herbivory*	p. 168
10:15 – 10:35	M.E. McNamara	*The original colours of 47 million-year-old fossil moths from Grube Messel revealed by fossilised biophotonic nanostructures*	p. 115

10:35 – 10:50	**Sonderausstellungsraum**	Coffee Break	

	Senckenberg Festsaal	Session 1: Insects (continued) **Chairperson: J. Rust**	
10:50 – 11:10	S. Wedmann	*Insects from the Eocene of Messel and their biogeographical implications*	p. 170
11:10 – 11:30	S.B. Archibald	*Climate, global patterns of Cenozoic biodiversity, and Eocene insects*	p. 23
11:30 – 11:45	Speaker Panel		

11:45 – 12:10	**Senckenberg Festsaal**	Special presentation	
	V. Lorenz presented by P. Suhr	*Maar-diatreme volcanism and its relevance for the Messel volcano*	p. 104

12:10 – 13:10	**Sonderausstellungsraum**	Lunch	

13:10 – 13:30		***– GROUP PHOTO –***	

	Senckenberg Festsaal	**Session 2: Plants and Climate** **Chairperson: M.E. Collinson**	
13:30 – 14:05	J.F. Basinger	Keynote Lecture: *The fossil forests of Axel Heiberg Island: A window onto polar climate and environments during Eocene global warmth*	p. 29
14:05 – 14:25	M.E. Collinson	*The value of X-ray approaches in the study of the Messel fruit and seed flora*	p. 38
14:25 – 14:45	O.K. Lenz	*Lake Messel, an extraordinary archive for the middle Eocene greenhouse climate*	p. 102
14:45 – 15:05	H. Lutz	*The Eocene Eckfeld Maar in the Tertiary Hocheifel Volcanic Field, Germany: 25 years of research - an overview*	p. 106
15:05 – 15:25	W. Riegel	*The edge of the sea at the time of Messe: Mangroves and related coastal wetlands in the Eocene of the Helmstedt mining district*	p. 141

15:25 – 15:40	**Sonderausstellungsraum**	Coffee Break

	Senckenberg Festsaal	**Session 2: Plants and Climate** (continued) **Chairperson: M.E. Collinson**	
15:40 – 16:00	J.W. Westgate	*Paleoecology of a primate-friendly, late middle Eocene (late Uintan), tropical rain forest/mangrove swamp community from Laredo, Texas, USA*	p. 172
16:00 – 16:20	R.W. Mathewes	*Paleoclimate of early Eocene highland floras of British Columbia, Canada, with focus on Falkland and Quilchena*	p. 112
16:20 – 16:40	N. Boonchai	*Petrified woods from the Big Sandy Reservoir, southwestern Wyoming: More evidence for warm climate in the early Eocene*	p. 34
16:40 – 17:00	A.R. Schmidt presented by H. Dörfelt	*New Ascomycota from Eocene forests and their interactions with plants and arthropods*	p. 149
17:00 – 17:15	Speaker Panel		

17:15 – 17:45	**Senckenberg Festsaal**	**Poster Session: Short oral presentations** **Chairperson: V. Volpato**	
		(for more information, see List of posters)	p. 19

19:00	**Lichthof I**	Conference Dinner
with an address of welcome by the Director—General, Senckenberg Gesellschaft für Naturforschung: V. Mosbrugger		

Thursday, 17th November 2011

08:00 – 09:00	**Senckenberg Festsaal**	Loading of the oral presentations onto the Festsaal computers

	Senckenberg Festsaal	**Session 3: Lower Vertebrates** **Chairperson: C.J. Bell**	
09:00 – 09:35	J.-C. Rage	Keynote Lecture: *Amphibians and squamates in the Eocene of Europe: What do they tell us?*	p. 135
09:35 – 09:55	M. Augé	*Fossil amphisbaenians from the European Eocene*	p. 25
09:55 – 10:15	J. Müller	*A new Eocene squamate from Messel and the origin of Amphisbaenia*	p. 124
10:15 – 10:35	N. Micklich	*Palaeoichthyology versus Geology? An interdisciplinary palaeoecological approach*	p. 118

10:35 – 10:50	**Sonderausstellungsraum**	Coffee Break	

	Senckenberg Festsaal	Session 3: Lower Vertebrates (continued) **Chairperson: C.J. Bell**	
10:50 – 11:10	A. Folie	*New data on the early Eocene frogs from Vastan, Gujarat, India*	p. 57
11:10 – 11:30	M. Böhme	*Newly discovered Eocene vertebrate and invertebrate faunas from Na Duong (northern Vietnam)*	p. 33
11:30 – 11:50	M.R. Stocker	*The herpetofauna from the late Uintan of West Texas*	p. 159
11:50 – 12:05	Speaker Panel		

12:05 – 13:30	**Sonderausstellungsraum**	Lunch	

	Senckenberg Festsaal	Session 4: Mammals	
13:30 – 14:05	K.D. Rose AvH Preisträger	Keynote Lecture: *Importance of Messel for interpreting Eocene Holarctic mammalian faunas*	p. 143

	Senckenberg Festsaal	Session 4: Mammals – Bats **Chairperson: G.F. Gunnell**	
14:05 – 14:25	K.T.J. Davies	*Echolocation, flight and inner-ear adaptation in bats*	p. 50
14:25 – 14:45	G.F. Gunnell	*Primitive chiropteran teeth - The complete dentition of the Messel bat* Archaeonycteris trigonodon	p. 73

14:45 – 14:55	**Sonderausstellungsraum**	Coffee Break	

	Senckenberg Festsaal	Session 4: Mammals – Bats (continued) **Chairperson: G.F. Gunnell**	
14:55 – 15:15	S.J. Hand	*Eocene biogeography of eastern Gondwanan bats*	p. 79
15:15 – 15:35	A. Ravel	*Eocene Chiroptera from Tunisia and Algeria: New insight into the early evolution of bats in North Africa*	p. 139
15:35 – 15:55	T. Smith	*Diversity and biogeography of early bats*	p. 156
15:55 – 16:10	Speaker Panel		

16:10 – 16:20	**Sonderausstellungsraum**	Coffee Break	

	Senckenberg Festsaal	Session 4: Mammals – General **Chairperson: M.R. Dawson**	
16:20 – 16:40	Y.Q. Wang	*Eocene mammal record in the Erlian Basin, Inner Mongolia, China*	p. 166
16:40 – 17:00	M. Pickford	*Geochronology and palaeontology of the Palaeogene deposits in the Sperrgebiet, Namibia*	p. 129
17:00 – 17:20	R. Tabuce	*The early Eocene radiation of Hyracoidea (Mammalia, Afrotheria): New fieldwork evidence from northwestern Africa*	p. 161
17:20 – 17:40	S. Engels	*Origins of early Eocene Hippomorpha of Europe and North America*	p. 56

19:30	**Goethe Universität Frankfurt - Aula**	10th G.H.R. von Koenigswald Lecture	
	E. Delson	*Paleoanthropology in 3D: A review of analysis and visualization of primate (especially human) evolution*	p. 52

Friday, 18th November 2011

08:00 – 09:00	**Senckenberg Festsaal**	Loading of the oral presentations onto the Festsaal computers	

	Senckenberg Festsaal	**Session 4: Mammals – General** (continued) **Chairperson: M.R. Dawson**	
09:00 – 09:20	G. Métais	*Re-interpretation of the genus* Parabunodon *(Ypresian, Turkey): Implications for the evolution and distribution of pleuraspidotheriid mammals*	p. 116
09:20 – 09:40	C. Stefen	*On new material of* Kopidodon macrognathus *(Mammalia, Paroxyclaenidae) from Messel*	p. 157
09:40 – 10:00	M. Morlo	*Mammalian carnivores from Messel and a comparison of non-volant predator guilds from the middle Eocene of Europe and North America*	p. 120
10:00 – 10:20	T. Tütken	*Exceptional geochemical preservation of vertebrate remains from the Eocene Messel Pit, Germany – Paleo-environmental and paleoecological implications of the stable isotope signatures*	p. 164
10:20 – 10:35	Speaker Panel		

10:35 – 10:50	**Sonderausstellungsraum**	Coffee Break	

	Senckenberg Festsaal	**Session 4: Mammals – Primates** **Chairperson: J.H. Hurum**	
10:50 – 11:25	P.D. Gingerich AvH Preisträger	Keynote Lecture: *Primates in the Eocene*	p. 67
11:25 – 11:45	F. Génin presented by J.C. Masters	*Mouse lemurs as model primate ancestors: The evolution of body size in Cheirogaleidae*	p. 65
11:45 – 12:05	X-J. Ni	*Phylogeny of the primates and their relatives: An analysis based on a large data matrix*	p. 125
12:05 – 12:25	A.L. Rosenberger	*Functional morphology, fossils and the origins of the tarsier and anthropoid lineages*	p. 147

12:25 – 13:50	**Sonderausstellungsraum**	Lunch	

	Senckenberg Festsaal	**Session 4: Mammals – Primates** (continued) **Chairperson: J.H. Hurum**	
13:50 – 14:10	J.L. Franzen	*Palaeopathology of* Darwinius masillae *(Mammalia, Primates)*	p. 61
14:00 – 14:30	J.H. Hurum	*Cranial morphology of the Eocene primate* Darwinius masillae	p. 84
14:30 – 14:50	M. Godinot	*Tarsals of European Cercamoniinae (Primates, Adapiformes) and their phylogenetic implications*	p. 69
14:50 – 15:10	W. von Koenigswald	*Morphology and evolution of the distal phalanges in primates*	p. 91
15:10 – 15:30	J. White	*Morphometric analysis of Eocene adapiform lower molar shape variation: Inferring function and ecological adaptation from the fossil record*	p. 174

15:30 – 15:45	**Sonderausstellungsraum**	Coffee Break	

	Senckenberg Festsaal	**Session 4: Mammals – Primates** (continued) **Chairperson: J.H. Hurum**	
15:45 – 16:05	R. Lebrun	*The labyrinthine morphology of* Pronycticebus gaudryi *(Primates, Adapiformes)*	p. 98
16:05 – 16:25	S. Couette	*The haplorhine/strepsirhine position of* Darwinius masillae*: New insights based on the CT analysis of* Pronycticebus gaudryi *middle ear morphology*	p. 44
16:25 – 16:45	J. Marigó	*Paleogene primates from the Iberian Peninsula: Past, present and future*	p. 108
16:45 – 17:05	B. Senut	*Palaeogene primates from the Sperrgebiet, Namibia*	p. 153
17:05 – 17:25	K.C. Beard	*Iterative dispersal of early Cenozoic primates across Beringia: Phylogenetic, paleoclimatic, and paleobiogeographic implications*	p. 31
17:25 – 17:40	Speaker Panel		

17:45 – 18:45	**Merian-Saal**	Press Conference

18:45 – 20:45	**Lichthof II**	**Round Table**	
	moderated by E. Delson	*Evolutionary history of early primates and the origin of modern clades*	
with	K.C. Beard	J.L. Franzen	P.D. Gingerich (AvH Preisträger)
	M. Godinot	W. von Koenigswald	A.L. Rosenberger
	E.R. Seiffert	E.L. Simons (AvH Preisträger)	X-J. Ni

Saturday, 19th November 2011

		Excursion to the Messel Pit Fossil Site **Field guides: K.T. Smith, T. Lehmann, S. Wedmann, V. Wilde**
09:00	**Senckenberg Natural History Museum**	*Departure by bus*
10:00 – 13:00	**Messel Pit & Visitor Information Centre**	*Guided tour of the pit and visit of the exhibition (in alternating groups)*
12:00 – 14:00	**Visitor Information Centre**	*Lunch at the "Bistro"*
14:00	**Visitor Information Centre**	*Departure by bus*
15:00	**Senckenberg Natural History Museum**	*Arrival in Frankfurt*

		Ida Workshop (for prearranged participants only) J.L. Franzen, J. Habersetzer, J.H. Hurum
14:00 – 18:00	**Visitor Information Centre**	*Workshop*
18:00	**Restaurant**	*Dinner at a nearby restaurant*
21:00		*Departure by bus*
22:00	**Senckenberg Natural History Museum**	*Arrival in Frankfurt*

LIST OF POSTERS

Galerie

Poster Session
Chairperson: V. VOLPATO

Numbers in bold indicate posters, which will be introduced in the *Short oral presentations* session between 17:15 – 17:45 on Wednesday, 16th November.

A1	S.B. ARCHIBALD	*Messel to Wyoming: Eocene giant ants, Arctic bridges and gates*	p. 24
A2	M. KOCH	*Fossil bugs (Insecta: Heteroptera) of Messel and the Green River Formation (USA) – Are there any connections?*	p. 89
B1	M. GRUDINSKI	*Shedding new light on the phylogeny and historical biogeography of* Hoya *(Apocynaceae)*	p. 71
B2	D.E. LEE presented by H. LUTZ	*Eocene vegetation of New Zealand and Australia: High latitude "tropics" in the Southern Hemisphere*	p. 100
B3	S. MATUSZAK	*Up to the top – Plant diversification on the Tibetan Plateau*	p. 114
C1	J. GAUDANT	*A short account on the Eocene fish fauna from Huadian, Jilin Province, China*	p. 63
C2	W.G. JOYCE	*The taphonomic settings of the Eocene Messel pit, Germany: Insights from the turtle fauna*	p. 87
D1	J. HABERSETZER	*Morphological specializations of the shoulder joints in extant and fossil bats*	p. 77
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ABSTRACTS

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The World at the Time of Messel

Climate, global patterns of Cenozoic biodiversity, and Eocene insects

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Eocene fossil sites such as the famous locality of Messel, Germany, are noted for their communities of unfamiliar assemblages that apparently reflect different climates from today, allowing taxa associated with the tropics in the modern world to range well into higher latitudes and mix with those now associated with cool climates. This suggests the possibility of employing these ancient communities and climates as comparative foils with which to examine modern tropical/temperate community differences and understand the change in those patterns through time.

The effects of individual climatic factors on global patterns of diversity are difficult to evaluate in the modern world because of their broad covariance with latitude. This was not, however, true in the Eocene (Greenwood and Wing, 1995). We take advantage of globally low seasonality of the Eocene to separate these factors, examining Eocene insect alpha diversity (diversity at a location) and beta diversity (change in diversity between localities), and compare them with modern global diversity patterns relative to climate.

We separated the effects of insolation (light and associated heat) and thermal seasonality on alpha diversity by mass sampling insects at cool, low seasonality Eocene McAbee, British Columbia, Canada, comparing its diversity with samples from cool, high seasonality temperate zone Harvard Forest, Massachusetts, USA, and hot, low seasonality tropical La Selva, Costa Rica. We found high diversity at McAbee, comparable with the modern tropical sample. This implies a key role of seasonality in driving the modern latitudinal gradient of species diversity (Archibald *et al.*, 2010).

We further examine insect beta diversity among fossil sites across a thousand kilometer transect of the Okanagan Highlands, a series of Eocene montane localities (including McAbee) in southern British Columbia, Canada, and northern Washington, USA. We used mass samples from these localities to test Janzen's (1967) *Mountain passes are higher in the tropics* hypothesis. He proposed a modern world relationship between dispersal, topography, climate, and latitude: warm valleys and cool mountain passes in temperate regions with wide seasonality overlap in temperature between parts of the year, thus facilitating dispersal of organisms adapted to valley climates across passes; the same elevation difference in the equable tropics share no common temperatures, and so should constitute a physiological dispersal barrier resulting in higher overturn of species across the landscape, *i.e.*, increased beta diversity.

Montane regions in the globally less seasonal Eocene should then show such high beta diversity even in higher latitudes. We evaluated similarities of Okanagan Highlands insect communities in a variety of taxa, including herbivores, active predators, parasitoids, and detritivores. We find that beta diversity was indeed high, as Janzen predicted for modern low-seasonality tropical uplands.

Our findings of high mid-latitude alpha and montane beta diversities support the idea that overall global diversity was higher in the Eocene relative to today. Consistent with this, Eocene plant diversity was high into mid-latitudes. Published data repeatedly show a low or absent gradient of diversity across early Paleogene latitudes examined. The Cenozoic appears "pear-shaped" with regard to diversity, *i.e.*, with high global diversity in equable early Cenozoic climates, and lowered global diversity in modern times, associated with the development of highly seasonal extra-tropical climates.

Archibald, S.B., Bossert, W.H., Greenwood, D.R., Farrell, B.D. (2010). Seasonality, the latitudinal gradient of diversity, and Eocene insects. Paleobiology 36: 374–398.

Greenwood, D.R., Wing, S.L. (1995). Eocene continental climates and latitudinal temperature gradients. Geology 23: 1044–1048.

Janzen, D.H. (1967). Why mountain passes are higher in the tropics. American Naturalist 101: 233–249.

Messel to Wyoming: Eocene giant ants, Arctic bridges and gates

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The extinct, giant formiciine ants (Lutz, 1986, 1990; Wappler, 2003), best known from numerous exquisitely preserved specimens from Messel, Germany, are sharp reminders that even though the Eocene was in many ways a familiar world with numerous modern elements, it also contained distinctly strange aspects. This was a time when the modern world was emerging, not only of modern lineages and their community arrangements, but also of their global distributions.

One such major early Eocene change in taxa distribution was the intercontinental migration of plants and animals that established major aspects of modern Holarctic biogeography. Land bridges across the Arctic were established from the late Palaeocene into the Eocene that allowed numerous plant and animal species to cross between Europe and North America. While many species that were suited to prevailing cool Arctic climates would have been able to cross throughout much of this period, others would have found dispersal opportunities only during limited intervals when their requirements for higher temperatures were met.

A new giant (> 5-cm-long) formiciine ant from the early Eocene (~49.5 Ma) Green River Formation of Wyoming, USA, shows new information on the operation of the climate gate controlling taxon access through this intercontinental dispersal corridor.

We show that the ant subfamily Formiciinae is known only from localities with estimated mean annual temperature of about 20 °C or greater, consistent with the tropical ranges of almost all of the largest living ant species. This is the first known formiciine of gigantic size in the Western Hemisphere and the first reported case of cross-Arctic dispersal by a thermophilic insect group. This implies dispersal across the Arctic during high temperature episodes (hyperthermals), representing brief, episodic openings of a climate-controlled physiological gate during the interval between the late Palaeocene establishment of intercontinental land bridge connections and the presence of giant formiciines in Europe and North America by the early middle Eocene.

Lutz, H. (1986). Eine neue Unterfamilie der Formicidae (Insecta: Hymenoptera) aus dem mittel-eozänen Ölschiefer der “Grube Messel” bei Darmstadt (Deutschland, S-Hessen). Senckenbergiana Lethaea 67: 177–218.

Lutz, H. (1990). Systematische und palökologische Untersuchungen an Insekten aus dem Mittel-Eozän der Grube Messel bei Darmstadt. Courier Forschungsinstitut Senckenberg 124: 1–165.

Wappler, T. (2003). Die Insekten aus dem Mittel-Eozän des Eckfelder Maars, Vulkaneifel. Mainzer Naturwissenschaftliches Archiv, Beiheft 27: 1–234.

Fossil amphisbaenians from the European Eocene

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Amphisbaenians are small, fossorial reptiles that inhabit tropical or semitropical regions of the world. Among the six families of Amphisbaenia, all taxa are limbless except the Bipedidae, which have no hind limbs but do have well-developed forelimbs. Aside from the monophyly of Amphisbaenia, the relationships among its members are still disputed and there is substantial disagreement between morphological and molecular data about the taxonomy of amphisbaenians. Here I only consider "crown" amphisbaenians (Rhineuridae, Bipedidae, Blanidae, Trogonophidae, Amphisbaenidae) and purported stem taxa like *Cryptolacerta* Müller *et al.*, 2011 are not discussed.

The majority of fossil amphisbaenians are known from North America (Estes, 1983). Thus, the fossil record outside North America is often ignored or underestimated, and this may cause some difficulty in interpreting the relationships within amphisbaenians as well as their historical biogeography (Kearney, 2003). Europe has yielded a diversity of remains of amphisbaenians. The oldest fossil records of European amphisbaenians (several fossil vertebrates) may be of Late Cretaceous age (Late Campanian–Maastrichtian). However, Blain *et al.* (2010) questioned the relationships of these fossils and attributed them to an indeterminate anguid. A Late Cretaceous fossil from Mongolia (*Sineoamphisbaena*) was identified as a primitive amphisbaenian. However, as recognized by Kearney (2003), *Sineoamphisbaena* is not related to amphisbaenians. Thus, the presence of amphisbaenian lizards in the Late Cretaceous is not demonstrable. This is in accord with the ideas advanced by Vidal and Hedges (2009); three molecular studies show that the major intrafamilial divergences among the amphisbaenians took place in the Cenozoic, less than 66 Myr ago (with the exception of the basal clade Rhineuridae). These authors estimated the split between African and South American amphisbaenids at 40 Myr ago.

Numerous amphisbaenian fossils have been collected throughout the Cenozoic in Europe. The fossil record has been tabulated by Rage and Augé (1993), Delfino (1997), and Augé (2005) and their lists, although incomplete, provide a good starting point for the understanding of the fossil history of amphisbaenians. Amphisbaenians are present in Europe in the early Paleogene (Paleocene, earliest Eocene), and this material is currently under study by A-L Folie in Brussels. More than twenty localities in the European Eocene have yielded amphisbaenian remains. Here, I briefly report two new taxa from the French Eocene. Interestingly, the middle Eocene epoch (Lutetian, Bartonian) is a "dark age" for the amphisbaenians in Europe. In particular, crown amphisbaenian fossils are absent from the Messel pit. The burrowing lifestyle of the amphisbaenians might explain their absence. However, in the localities of Lissieu (France, middle Eocene, MP 14) and St. Maximin (MP 12-13, France), fossils are recovered from fissure fillings, and amphisbaenians have thus far not been found. The herpetofauna from Lissieu is approximately as diverse as is that from Messel, as the latter is published today (Rage and Augé, 2010). Thus, apparently, the lack of amphisbaenian remains could reflect a true absence rather than a taphonomic bias.

The study of the Paleogene amphisbaenians from Europe has been hampered by our limited understanding of the relationships of those fossils within the amphisbaenians. Some specimens have been referred to the extant genus *Blanus* (Milner *et al.*, 1982); or, for instance, Hecht and Hoffstetter (1962) noted similarities to the genus *Blanus* in the material from Dormaal (MP7, Belgium). The confusion clearly results from the limited available material (vertebrae, premaxillae and dentaries). As recognized by Smith (2009), these fossils (at least the dentaries) show four synapomorphies of the "higher" amphisbaenians (*Bipes*, *Blanus*, Amphisbaenidae, Trogonophidae; see Kearney and Stuart, 2004): loss of the anterolateral process of the coronoid; posterior extension of the intramandibular septum; development of a facet for the splenial on the ventral side of the intramandibular septum; increased height of the dentary posteriorly.

NEW TAXA A

Locality: Mutigny (Bassin de Paris, France).
Age: early Eocene, MP 8-9
Description: The right dentary (MNHN, Mu 7912) is nearly complete. The tooth row is complete and includes nine teeth.

This dentary shows all the characters (synapomorphies?) common to *Blanus*, *Bipes* and Amphisbaenidae (see above). It also possesses the diagnostic feature of the genus *Anniealexandria* Smith (2009); it differs from all living amphisbaenian taxa in having nine dentary teeth. It also differs from most Amphisbaenidae in having a deep Meckelian groove, even anteriorly. The material from Mutigny is provisionally referred to the genus *Anniealexandria*, pending a thorough description of those fossils.

Anniealexandria gansi is a fossil lizard from the earliest Eocene of Wyoming, USA. If the European fossils are correctly referred, *Anniealexandria* is distributed on both sides of the Atlantic. Oceanic dispersal has already been proposed as an explanation for the distribution of Amphisbaenidae (Africa and South

America; Vidal and Hedges, 2009). The same dispersal may explain the distribution of *Anniealexandria*. However, during the early Eocene, North America and Western Europe were to a greater or lesser extent connected via terrestrial routes (through southern Greenland). Given the warm climate of the early Paleogene, this land bridge linking North America to Europe would have allowed lizard taxa, particularly *Anniealexandria*, to exchange freely.

New taxa B

Locality: Escamps, Phosphorites du Quercy, France
Age: late Eocene (MP 19)
Description: The material from Escamps consists of dentaries, premaxillae, vertebrae and one maxilla. The dentary bears eight pleurodont teeth and shows the synapomorphies of higher amphisbaenians. Hence, these fossils could be referred to higher amphisbaenians, except Trogonophidae (*Blanus*, Amphisbaenidae, *Bipes*).

The complete left maxilla (USTL, ECC 2508) has a row of three foramina on the lateral side. A large anterior concavity (dimple, according to Smith, 2009) is situated just behind the premaxillary process. This process is not forked and it projects dorsally. The nasal process of the maxilla is moderately high; posteriorly its drops steeply and then levels out somewhat. The posterior end of the maxilla is rather long and tapers posteriorly. Its posterior end is forked. The maxilla bears five pleurodont teeth. The low tooth count and tooth morphology are sufficient to refer this maxilla to Amphisbaenia. This maxilla is very similar to *Blanus*: the labial foramina form a row; the premaxillary process projects dorsally; the posterior end of the maxilla tapers posteriorly and its posterior margin is forked. This fossil differs from the maxilla of Amphisbaenidae, based on description in Montero and Gans (1999). Hence, this maxilla is tentatively referred to the extant European family Blanidae.

Geographical distribution of Eocene amphisbaenians supports the hypothesis that dispersal had had an important influence on their current distribution. The maxilla described here bears significant taxonomic features. It may be considered the first evidence in favor of the presence of Blanidae in the European Eocene.

Augé, M. (2005). Evolution des lézards du Paléogène en Europe. Mémoires du Muséum National d'Histoire Naturelle, Paris 192, 369pp.

Blain, H-A, Canudo, J-I, Cuenca-Bescos, G., Lopez-Martinez, N. (2010). Amphibians and squamate reptiles from the latest Maastrichtian (Upper Cretaceous) of Blasi 2 (Huesca, Spain). Cretaceous Research 31: 433-446.

Delfino, M. (1997). *Blanus* from the Early Pleistocene of Southern Italy, another small tessera from a big mosaic. In: Böhme, W., Bischoff, W., Ziegler, T. (eds) Herpetologia Bonnensis, pp 89-97.

Estes, R. (1983). Sauria terrestria, Amphisbaenia. In: Kuhn, O., Wellnhofer, P. (eds) Handbuch der Paläoherpetologie, Teil 10A, G. Fischer Verlag, 249pp.

Hecht, M.K., Hoffstetter, R. (1962). Note préliminaire sur les Amphibiens et les Squamates du Landenien supérieur et du Tongrien de Belgique. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 39: 1-30.

Kearney, M. (2003). Systematics of the Amphisbaenia (Lepidosauria: Squamata) based on morphological evidence from recent and fossil forms. Herpetological Monographs 17: 1-74.

Kearney, M., Stuart B.L. (2004). Repeated evolution of limblessness and digging heads in worm lizards revealed by DNA from old bones. Proceedings of the Royal Society of London B, 271: 1677-1683.

Milner, A.C., Milner, A.R., Estes, R. (1982). Amphibians and Squamates from the Upper Eocene of Hordle Cliff, Hampshire, a preliminary report. Tertiary Research 4(4): 149-154.

Montero, R., Gans C. (1999). The head skeleton of *Amphisbaena alba* Linneaus. Annals of Carnegie Museum 68: 15-80.

Müller, J., Hipsley, C.A., Head, J.J., Kardjilov, N., Hilger, A., Wuttke, M., Reisz, R.R. (2011). Eocene lizard from Germany reveals amphisbaenian origins. Nature 473: 364–367

Rage, J.C., Augé, M. (1993). Squamates from the Cainozoic of the western part of Europe. A review. Revue de Paléobiologie, volume spécial 7: 199-216.

Rage, J.C., Augé, M. (2010). Squamate reptiles from the middle Eocene of Lissieu (France): A landmark in the middle Eocene of Europe. Geobios 43: 253-268.

Smith, K.T. (2009). A new lizard assemblage from the earliest Eocene (zone WAO) of the Bighorn Basin, Wyoming, USA/ Biogeography during the warmest interval of the Cenozoic. Journal of Systematic Palaeontology 7(3): 299-358.

Vidal, N., Hedges, B. (2009). The molecular evolutionary tree of lizards, snakes, and amphisbaenians. Comptes Rendus Biologies 332: 129-139.

Eocene mammalian fossil record and biodiversity from Iberia: New primate and sirenian discoveries and palaeobiogeographic implications

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New finds of mammals from the Eocene of the Iberian Peninsula, including rodents, primates, artiodactyls, perissodactyls, and sirenians, are crucial to investigating the evolutionary and palaeobiogeographic history of the Eocene mammalian faunas across Europe. The fossils come from the Pyrenean Realm and from adjacent Cenozoic basins of the Basque-Cantabrian region and central Iberia (Fig. 1). Many of the remains are already published (Astibia *et al.*, 2010; Badiola *et al.*, 2009 and references therein; Cuesta and Badiola, 2009; Marigó *et al.*, 2010, 2011*a*; Minwer-Barakat *et al.*, 2010; Quer and Agustí, 2010), whereas others are unpublished or their study is still ongoing.

Middle and late Eocene perissodactyl faunas of the western and central Iberian basins (Duero, Almazán, Oviedo and Miranda-Trebiño basins) are clearly different from those of the southern Pyrenean basins (Fig. 1). In contrast, the Eocene mammalian faunas of the southern Pyrenees are similar to those of the southern part of the Central European Island (southern France, Switzerland), where the typical western Iberian endemic taxa are absent. On the basis of this faunal differentiation the existence of the Western Iberian Bioprovince is hypothesized (Badiola *et al.*, 2009). Five genera and 16 species of equoids and five taxa of lophiodonts, which are unknown elsewhere in Europe, have been identified so far in this bioprovince. In the context of Iberian biochronology, rodent, primate and artiodactyl fossils have been less well known than perissodactyls. However, various middle and late Eocene taxa of artiodactyls, rodents and primates found in this bioprovince may also support the endemism of these faunas (Badiola *et al.*, 2009). The endemic nature of the primates is supported mainly by adapoid taxa, such as the new genus and species *Mazateronodon endemicus* found in the Almazán Basin (Marigó *et al.*, 2010). The study of the first fossil record of microchoerine omomyids from the Western Iberian Bioprovince is in progress in collaboration with the aforementioned authors from the Institut Catalá de Paleontologia (ICP) of Barcelona. These fossils will extend what is known in this matter. Further and more detailed information about Eocene primate fossils from Iberia can be found in Marigó *et al.* (2011*b*).

Recent discoveries and investigations of new sirenian material from the Pyrenean Realm illustrate the high palaeontological potential of the Iberian Peninsula for marine mammals too. The best-known sirenian fossils, consisting of various cranial and postcranial remains, come from the Bartonian deposits of the eastern margin of the Pyrenean Realm. The fossils were initially described as *Prototherium*

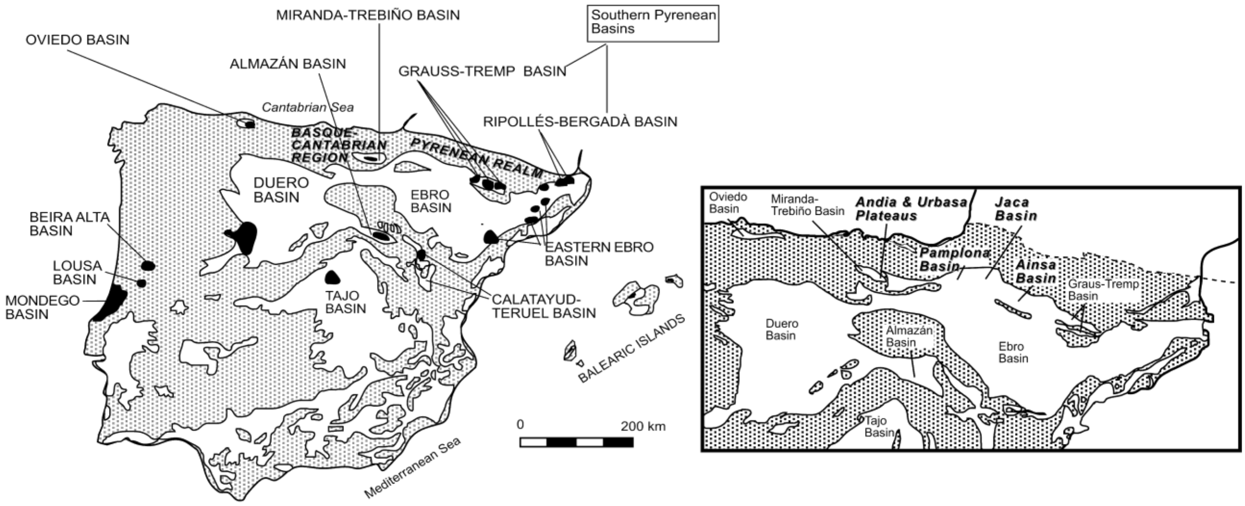

Figure 1. Map showing Cenozoic basins of the Iberian Peninsula and the Balearic Islands. The areas with Eocene terrestrial mammalian fossils are indicated by black (Further details in Badiola *et al.*, 2009). Inset: the enlarged area of the Pyrenean Realm and adjacent regions showing the areas in which sirenian fossils have been recovered in bold type.

solei and *P. montserratense* (Pilleri *et al.*, 1989), but were later assigned to *P. intermedium*, which is also found in the late Eocene of northern Italy (Bizzotto, 2005). Much more scarcely documented is the sirenian fossil record of the western Pyrenees. The fossils consist of vertebrae and ribs found in the Bartonian beds of the Pamplona and Jaca basins (Fig. 1). The caudal vertebrae from the Jaca Basin are described as Dugongidae indet. (Pilleri *et al.*, 1989; Astibia *et al.*, 1999). A large number of disarticulated vertebrae and ribs are described from the Uztarrotz and Ardanatz sites in the Pamplona Basin. According to their morphology as well as the biogeographical and stratigraphic data, they seem to be closely related to a basal dugongid such as *Prototherium* (Astibia *et al.*, 2005). Our recent field and research activities have extended the distribution of the sirenian fossil record to most of the western Pyrenees. The earliest sirenian fossils from Western Europe have been found in the Urbasa and Andia Mountains (Navarre), and in the Ainsa Basin (Huesca) (Fig. 1). Two partial atlases, one humerus fragment, and several dorsal ribs found in two beds in Navarre are dated as late Lutetian and referred to ?Dugongidae indet. (Astibia *et al.*, 2010). More complete and diverse fossil remains have been found in the Ainsa Basin, consisting of a skull with teeth, numerous vertebrae and ribs, scapula, humerus, ulna, and a possible pelvic bone, possibly belonging to the same individual. The fossil-bearing bed is located in the deltaic deposits of the Sobrarbe Formation, which is dated as late Lutetian (De Federico, 1981; Bentham, 1992). The morphology of the fossils is consistent with referral to basal forms of Dugongidae, the only sirenian clade known so far in the middle Eocene of Europe, sharing some cranial morphological features with *Prototherium* and *Eotheroides*. These fossils, as well as those found at other Lutetian sites of the Sobrarbe Fm., the study of which is in progress, will be essential in investigating the palaeobiogeography and evolution of the first clades that appeared in the Tethys Seaway during the rapid early middle Eocene diversification of the group.

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Astibia, H., Bardet, N., Pereda-Suberbiola, X., Payros, A., V. De Buffrénil, Elorza, J., Tosquella, J. Berreteaga, A., Badiola, A. (2010). New fossils of Sirenia from the Middle Eocene of Navarre (Western Pyrenees): The oldest West European sea cow record. Geological Magazine 147: 665-673.

Astibia, H., Murelaga, X., Payros, A., Pereda Suberbiola, X., Tosquella, J. (1999). Tortugas y sirenios fósiles en el Eoceno marino de Navarra y Cuenca de Jaca. Geogaceta 25: 15-18.

Astibia, H., Payros, A., Pereda-Suberbiola, X., Elorza, J., Berreteaga, A., Etxebarria, N., Badiola, A., Tosquella, J. (2005). Sedimentology and taphonomy of sirenian remains from the Middle Eocene of the Pamplona Basin (Navarre, western Pyrenees). Facies 50: 463–75.

Badiola, A., Checa, Ll., Cuesta, M. A., Quer, R., Hooker, J.J., Astibia, H. (2009). The role of new Iberian finds in understanding European Eocene mammalian paleobiogeography. Geologica Acta 7(1-2): 243-258.

Bentham, P.A. (1992). The tectonostratigraphic development of the western oblique ramp of the South-Central Pyrenean thrust system, Northern Spain. Doctoral Thesis. University of Southern California, 252p.

Bizzotto, B. (2005). La struttura cranica di *Prototherium intermedium* (Mammalia: Sirenia) del l'Eocene superiore veneto. Nuovi contributi alla sua anatomia e sistematica. Lavori della Società Veneziana di Scienze Naturali 30: 107-125.

Cuesta, M.A., Badiola, A. (2009). *Duerotherium sudrei* gen. et sp. nov., a new anoplotheriine artiodactyl from the Middle Eocene of the Iberian Peninsula. Journal of Vertebrate Paleontology 29(1): 303-308.

De Federico, A. (1981). La sedimentación de talud en el sector occidental de la Cuenca paleógena de Ainsa. Publicaciones de Geología, Universidad de Barcelona 13, 271 pp.

Marigó, J., Minwer-Barakat, R., Moyà-Solà, S. (2010). New Anchomomyini (Adapoidea, Primates) from the Mazaterón Middle Eocene locality (Almazán Basin, Soria, Spain). Journal of Human Evolution 58: 353–361.

Marigó, J., Minwer-Barakat, R., Moyà-Solà, S. (2011*a*). New *Anchomomys* (Adapoidea, Primates) from the Robiacian (Middle Eocene) of northeastern Spain. Taxonomic and evolutionary implications. Journal of Human Evolution 60: 665–672.

Marigó, J., Minwer-Barakat, R., Moyà-Solà, S. (2011*b*). Paleogene primates from the Iberian Peninsula: past, present and future. In: Lehmann, T., Schaal, S.F.K. (eds) The World at the Time of Messel: Puzzles in Palaeobiology, Palaeoenvironment, and the History of Early Primates. 22nd International Senckenberg Conference. 15th – 19th November 2011, Frankfurt am Main. Conference Volume. Senckenberg Gesellschaft für Naturforschung, Frankfurt am Main. pp. 108-109.

Minwer-Barakat, R., Marigó, J., Moyà-Solà, S. (2010). A new species of *Pseudoloris* (Omomyidae, Primates) from the middle Eocene of Sant Jaume de Frontanyà (Eastern Pyrenees, Spain). American Journal of Physical Anthropology 143: 92–99.

Pilleri, G., Biosca, J., Via, L. (1989). The Tertiary Sirenia of Catalonia. Ostermundigen: Brain Anatomy Institute, University of Berne, 98pp.

Quer, R., Agustí, J. (2010). A new genus of rodents (Remyidae, Mammalia) from the Iberian Eocene. Palaeontology 53: 53-58.

The fossil forests of Axel Heiberg Island: A window onto polar climate and environments during Eocene global warmth

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Scientific exploration of the northern polar regions during the 19th century brought to light evidence of forest vegetation in regions now far beyond treeline. Oswald Heer wrote extensively of polar fossil floras in his 7-part *Flora Fossilis Arctica*, published between 1868 and 1883. In describing fossils from Arctic Canada, Heer (1868) recognized their implication for the interpretation of polar climate in the geological past. Prior to widespread acceptance of the theory of plate tectonics almost a century later, however, such evidence for polar warmth was difficult to place into a model for global climate change over geological time scales. It is now understood that global climate has swung between great warmth and glaciation, and that the polar regions are most sensitive to global change. An understanding of mechanisms for global change, and its consequence for the biosphere, has gained urgency in light of the need to comprehend the growing anthropogenic impact on Earth's climate engine. Nowhere is the impact of climate change so apparent as in the Paleogene fossil record of the Far North.

Fossil plants are abundant within Paleogene deposits of the coal-bearing Eureka Sound Group of the Canadian Arctic Archipelago (Fig. 1). In addition to compression fossils, permineralized logs and stumps including *in situ* fossil forests reveal not just composition of the floras but also stature of the forests. Among the earliest documented is that of Brainard's forest, described within the report of the ill-fated Greeley Expedition of 1881–84 to the northeast margin of Ellesmere Island. A more recent description of fossil forests from central Ellesmere by Jane Francis (1988) reveals densely spaced stumps of ~1 m diameter, and in southern Ellesmere there exist stumps of greater than 3 m diameter (*pers. obs.*). Large fossil trees, amidst the remains of a primarily deciduous coniferous–broadleaved vegetation, indicate that a rich forest once covered Ellesmere. Tectonic reconstructions reveal only minor displacement since the Paleogene, and thus also the extent to which climate change has influenced the Far North. An overview of the Paleogene record of fossil plants of this region has been presented by McIver and Basinger (1999). Discovery of vertebrate remains in the Eocene of central Ellesmere has contributed to a broader understanding of polar ecosystems and Eocene polar climate (see Eberle and McKenna, 2002; Eberle *et al.*, 2010).

Figure 1. Arrow points to Ellesmere Island, with Axel Heiberg Island adjacent to the west.

Among the most important sources of insight into the Eocene environments of the Far North are the well-preserved remains of plants in the middle Eocene Buchanan Lake Formation of Axel Heiberg Island at 80°N, or about 78°N paleolatitude. The Axel Heiberg Island deposits consist of interbedded silt, sand, and coal that represent episodic drowning of the landscape as a consequence of subsidence of a narrow foreland basin. Shallow burial of the deposits and limited consolidation has resulted in exquisite preservation, including mummification of woody remains and forest-floor litters (Fig. 2). Three broad categories of sedimentary units are recognized, representing different components of the regional vegetational mosaic: peat/coal representing lowland swamps; siltstones, floodplain forests; and fluvial sands, "uplands" vegetation.

Peat deposits may be largely unaltered such that leaf litter is easily disaggregated, and are typically thin, rarely exceeding 1 m in thickness. In some cases, a single peat layer appears to preserve a single forest generation. Peat typically sits upon paleosol, and represents onset of drowning of the landscape, with stumps occasionally protruding into overlying lacustrine deposits. Peats appear to represent *in situ* remains of forests which were commonly dominated by taxodiaceous Cupressaceae, most conspicuously *Metasequoia* and *Glyptostrobus*, frequently to the exclusion of all else. Other conifers (e.g. *Chamaecyparis*, *Larix*, *Pseudolarix*, *Picea*, *Pinus*) and angiosperms including Betulaceae, Fagaceae, and Trochodendraceae were also present in the low

Figure 2. Above, a fossil forest of Middle Eocene age on Axel Heiberg Island. The stump in the foreground is about 1 m diameter. Below are cones of *Metasequoia* recovered from leaf litter.

lands. Floodplains supported a rich, largely deciduous dicot flora (e.g. Betulaceae, Fagaceae, Juglandaceae, Platanaceae, and Cornaceae), commonly with *Ginkgo* and *Metasequoia*. Fluvial sands preserve remains resistant to transport, including woody debris, conifer cones, and rare nuts. The term "upland" is used only to describe the source as a better-drained and floristically distinct part of the landscape. While the distance these fossils were transported is unknown, their remains may represent forests of the nearby uplands of central Axel Heiberg Island, within sight of the place of deposition.

The Axel Heiberg Island site allows for an appreciation of the vegetational mosaic of this region during the middle Eocene. With the exception of a few, possibly ecologically restricted evergreen conifers such as *Chamaecyparis*, *Picea* and *Pinus*, the flora was deciduous. Deciduousness is part of a dormancy response now commonly associated with a strategy to cope with drought or winter frost. While modern representatives of all plant groups preserved in the Axel Heiberg flora are at least moderately frost hardy, the vertebrate fauna preserved within the roughly contemporaneous deposits of Ellesmere Island include frost-sensitive reptiles such as alligators, which are considered valid proxies for largely frost-free conditions year-round (Eberle *et al.*, 2010). In the absence of severe frost, deciduousness appears to have been a strategy associated with dormancy during the polar winter night, which is approximately 4 months long at 80ºN. If an environment can become extinct, the Eocene polar winter would be an example.

The use of plants as proxies for paleoclimate parameters has a long history, and has evolved as two parallel inquiries: climatic tolerance of extant members of lineages (e.g. Utescher and Mosbrugger, 2007), and correlation between plant form and climate (see Peppe *et al.*, 2011 for a recent review). Accuracy continues to remain somewhat elusive on a global scale, and is inherently problematic for an environment that no longer exists on Earth. Furthermore, floristic consistency throughout a vast region of the northern hemisphere, from almost 50ºN to as far northward as land existed during the Eocene, would seem to point to an exceptionally low latitudinal temperature gradient, at least for the growing season, or a very broad climatic tolerance of the boreal taxa, or both. Key limiting factors for survival in the modern world such as cold month mean and minimum temperature and mean annual temperature may have had less meaning in the Eocene high latitudes.

The defining feature of the Eocene high latitudes – the absence of winter frost during a long, dark polar winter – is difficult to comprehend on the modern Earth, and does not appear to be achievable within realistic manipulation of general circulation models for global climate. The fossil record for Eocene polar climate may argue for an alternative model for atmospheric circulation, one which may represent a distinctly different stability beyond a tipping point. As humankind is expected to enhance the atmospheric greenhouse to a level not seen since the Paleogene, a deeper understanding of climate systems of the geological past and the response of the Earth's terrestrial biosphere, as evidenced by the plant fossil record, becomes imperative.

Eberle, J.J., Fricke, H.C., Humphrey, J.D., Hackett, L., Newbrey, M.G., Hutchison, J.H. (2010). Seasonal variability in Arctic temperatures during early Eocene time. Earth and Planetary Science Letters 296: 481-486.

Eberle, J.J., McKenna, M.C. (2002). Early Eocene Leptictida, Pantolesta, Creodonta, Carnivora, and Mesonychidae (Mammalia) from the Eureka Sound Group, Ellesmere Island, Nunavut. Canadian Journal of Earth Sciences 39: 899-910.

Francis, J.E. (1988). A 50-million-year-old fossil forest from Strathcona Fiord, Ellesmere Island, Arctic Canada: evidence for a warm polar climate. Arctic 41: 314-318.

Heer, O. (1868). Die fossile Flora der Polarländer, enthaltend die in Nord Grönland, auf der Melville-Insel, im Banksland am Mackenzie, in Island und in Spitzbergen entdeckten fossilen Pflanzen. Flora Fossilis Arctica, Vol 1, pp. 1-192. Zurich.

McIver, E.E., Basinger, J.F. (1999). Early Tertiary floral evolution in the Canadian High Arctic. Annals of the Missouri Botanical Garden 86: 523-545.

Peppe, D.J. and 26 others. (2011). Sensitivity of leaf size and shape to climate: Global patterns and paleoclimatic applications. New Phytologist (published on-line), 16 pp; doi: 10.1111/j.1469-8137.2010.03615.x.

Utescher, T., Mosbrugger, V. (2007). Eocene vegetation patterns reconstructed from plant diversity – A global perspective. Palaeogeography, Palaeoclimatology, Palaeoecology 247: 243-271.

Iterative dispersal of early Cenozoic primates across Beringia: Phylogenetic, paleoclimatic, and paleobiogeographic implications

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Living primates are ecologically specialized mammals, enabling early Cenozoic primates to function as paleoecological proxies. With the partial exception of a few large-bodied catarrhines (such as *Homo*, *Macaca* and *Papio*), all living primates show tropical and/or subtropical geographic distributions and all living primates require ready access to trees. Eocene primates were small to medium-sized taxa, especially in comparison to modern catarrhines. It is therefore reasonable to assume that Eocene primates were even more thermophilic and further constrained by arboreality than their living descendants. Accordingly, despite the fact that the range of Eocene primates is known to have extended to much higher latitudes than their modern counterparts, the value of Eocene primates as paleoecological proxies is substantial, although this aspect of primate paleobiology has frequently been overlooked or discounted. Their presence, and sometimes even their inferred presence, in ancient settings indicates warm, relatively wet, and at least partially forested conditions.

Northeastern Asia and northwestern North America were connected by the subaerial Beringian region from at least the Cretaceous until the terminal Miocene (Gladenkov *et al*., 2002). This land bridge functioned as a longstanding “filter” corridor, allowing the dispersal of terrestrial organisms from Asia to North America and vice versa throughout the early Cenozoic. Furthermore, no alternative pathway for direct dispersal between Asia and North America is known. Given the high-latitude position of Beringia and the paleoecological requirements of early Cenozoic primates posited earlier, ancient episodes of primate dispersal across Beringia must have corresponded to intervals of extraordinary global warmth.

The earliest evidence of primate dispersal across Beringia corresponds to the initial colonization of North America by primates, which took place during the Paleocene-Eocene Thermal Maximum (PETM; ~55.8 Ma). The omomyid *Teilhardina magnoliana* from the uppermost Tuscahoma Formation on the Gulf Coastal Plain of Mississippi is the oldest primate currently known outside of Asia (Beard, 2008; Beard and Dawson, 2009). Phylogenetically, *T. magnoliana* is also the most basal species of *Teilhardina* currently known outside of Asia, being more basal than either *T. belgica* from Dormaal, Belgium, or *T. brandti* from the Wa-0 faunal zone in the Bighorn Basin, Wyoming (Beard, 2008). *Teilhardina asiatica* from the Bumbanian Lingcha local fauna of Hunan Province, China (Ni *et al*., 2004) is the only omomyid described to date that is phylogenetically more basal than *T. magnoliana*. These data indicate that paleoenvironmental conditions in the Beringian region during the PETM were adequate to support at least a transient habitation of that region by primates.

An alternative reconstruction of the dispersal history of early Eocene *Teilhardina* supporting an Asia to Europe to North America route has been proposed (Smith *et al*., 2006), but this hypothesis is inherently less parsimonious than the trans-Beringian route supported here. Progressively westward dispersal of *Teilhardina* from Asia to Europe to North America requires at least two synchronous causal mechanisms (global warming during the PETM and either marine regression or overwater dispersal of *Teilhardina* across the Turgai Straits), whereas progressively eastward dispersal from Asia to North America to Europe hinges on a single causal mechanism (global warming during the PETM) (Beard *et al*., 2010).

Convincing evidence for primate dispersal across Beringia next occurs in the middle Eocene (early Uintan; ~45 Ma). At least three omomyid primate clades are known to have existed on both sides of the North Pacific at this time. These clades are as follows: (1) *Stockia powayensis* (known from southern California) + *Asiomomys changbaicus* (known from Jilin Province, China) (Beard and Wang, 1991); (2) various species of *Macrotarsius* (known from Jiangsu Province, China, and multiple sites in western North America) (Beard *et al*., 1994); and (3) Tarkadectinae (known from Nei Mongol, China, and Wyoming and Montana, USA) (Ni *et al*., 2010). In contrast to the example of primate dispersal across Beringia at the base of the PETM, the directionality of dispersal (North America to Asia or vice versa) remains unclear for these middle Eocene omomyid clades. However, the number of examples of trans-Beringian dispersal of primates at this time suggests that primate dispersal occurred in both directions, and that the true picture of primate dispersal across Beringia during the middle Eocene will be more complicated than we currently realize.

Following the final inundation of the North Atlantic land bridge linking northeastern North America with northwestern Europe in the early Eocene, potential source areas for new primate clades appearing suddenly in the North American fossil record are virtually restricted to Asia. Hence, we can predict that sister groups for such enigmatic North American primates as *Mahgarita stevensi* and *Rooneyia viejaensis* will ultimately be discovered in Asia. Using episodes of primate dispersal across Beringia as a paleoecological proxy for inferring paleoenvironmental conditions in Beringia makes primate paleobiogeography compelling to earth scientists and climate modelers who would otherwise have little incentive to follow developments in this field.

Beard, K.C. (2008). The oldest North American primate and mammalian biogeography during the Paleocene-Eocene Thermal Maximum. Proceedings of the National Academy of Sciences 105: 3815-3818.

Beard, K.C., Dawson, M.R. (2009). Early Wasatchian mammals of the Red Hot local fauna, uppermost Tuscahoma Formation, Lauderdale County, Mississippi. Annals of Carnegie Museum 78: 193-243.

Beard, K.C., Qi, T., Dawson, M.R., Wang, B.-Y., Li, C.-K. (1994). A diverse new primate fauna from middle Eocene fissure-fillings in southeastern China. Nature 368: 604-609.

Beard, K.C., Wang, B.-Y. (1991). Phylogenetic and biogeographic significance of the tarsiiform primate *Asiomomys changbaicus* from the Eocene of Jilin Province, People's Republic of China. American Journal of Physical Anthropology 85: 159-166.

Beard, K.C., Wang, y.-q, Meng, J., Ni, X.-J., Gebo, D.L., Li, C.-K. (2010). Paleocene *Hapalodectes* (Mammalia: Mesonychia) from Subeng, Nei Mongol: Further evidence of "East of Eden" dispersal at the Paleocene-Eocene boundary. Vertebrata PalAsiatica 48: 375-389.

Gladenkov, A.Y., Oleinik, A.E., Marincovich, L., Jr., Barinov, K.B. (2002). A refined age for the earliest opening of Bering Strait. Palaeogeography, Palaeoclimatology, Palaeoecology 183: 321-328.

Ni, X.-J., Meng, J., Beard, K.C., Gebo, D.L., Wang, Y.-Q., Li, C.-K. (2010). A new tarkadectine primate from the Eocene of Inner Mongolia, China: Phylogenetic and biogeographic implications. Proceedings of the Royal Society B 277: 247-256.

Ni, X.-J., Wang, Y.-Q., Hu, Y.-M., Li, C.-K. (2004). A euprimate skull from the early Eocene of China. Nature 427: 65-68.

Smith, T., Rose, K.D., Gingerich, P.D. (2006). Rapid Asia-Europe-North America geographic dispersal of earliest Eocene primate *Teilhardina* during the Paleocene-Eocene Thermal Maximum. Proceedings of the National Academy of Sciences 103: 11223-11227.

Newly discovered Eocene vertebrate and invertebrate faunas from Na Duong (northern Vietnam)

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Since 2008, several joint German-Vietnamese palaeontological expeditions to the Cenozoic basins of northern Vietnam have been carried out. Three field campaigns revealed a rich, diverse, and largely well-preserved plant, invertebrate, and vertebrate fossil record (Böhme *et al.*, 2010). With regard to palaeontology, some of the most spectacular and scientifically interesting results are derived from the Na Duong Basin.

Tectonically, northern Vietnam is positioned at the boundary between the Indochina and Southern China microplates. The Indian-Asian collision during the Eocene caused the southeastward extrusion of Indochina along a continental transform plate boundary, creating the more than 1,000-km stretching, NW-SE trending, left-lateral shearing Red River Fault Zone (RRFZ). Resulting from these tectonic movements, several deep strike-slip basins evolved within this fault system. One of the major faults of the zone, the Cao Bang–Tien Yen fault, is 230 km long and parallels the RRFZ in the north for 160 km. The Na Duong Basin is one of the largest strike-slip basins that occur along this fault (Böhme *et al.*, 2010).

The Cenozoic sediments filling the Na Duong Basin are up to 570 m thick and belong to the Na Duong and Rinh Chua formations. The coal-bearing Na Duong Formation represents an alternation of thickly bedded lignites, lignitic clays, marls, siltstones, and fine- to middle-grained sandstones, indicating swampy to lacustrine-deltaic environments. The overlying, deep-lacustrine Rinh Chua Formation lacks lignite seams and is dominated by rhythmically alternating claystones.

The sedimentary succession exposed in the Na Duong coal mine reveals rich and diverse plant, mollusc, and vertebrate associations. The mollusc assemblage found in the marls and silts comprises four species of unionid bivalves, abundant large viviparid gastropods and rare thiarids and pachychilids. Eleven species of fishes, mostly belonging to the Cyprinidae (carps), are recorded from the same sediments.

The most productive tetrapod-bearing horizons, however, are located at the base of the main coal seam and in the underlying lignitic clays. In these layers, vertebrate remains are exceptionally well preserved, and many specimens occur as partial to complete skeletons.

During three excavation campaigns, more than 70 shells of freshwater turtles, 15 crocodiles, and seven mammal specimens were found. The turtles belong to at least six taxa from the families Trionychidae, Geoemydidae and Ptychogastridae, whereas crocodiles are documented by a large longirostrine taxon and a small brevirostrine species. The majority of mammals belong to the Anthracotheriidae, whereas primitive Ruminantia and Perissodactyla are rare. Biostratigraphically most important are a medium-sized anthracotheriid and the small bothriodontine *Elomeryx*, the latter probably conspecific with *Elomeryx* cf. *crispus* from the Naduo and Gongkang formations of the Bose Basin in Southern China (Ducrocq and Lihoreau, 2006). Based on biostratigraphic evidence, both Chinese formations are considered to be either late Eocene to early Oligocene (Zhai *et al.*, 2003) or late middle Eocene (Ducrocq and Lihoreau 2006, Wang *et al.*, 2007; Naduan Asian Land Mammal Age of Tong *et al.*, 1995).

In summary, the Na Duong Basin offers great potential for taxonomic, palaeoenvironmental, and palaeobiogeographic studies owing to its diverse and exceptionally well-preserved fossil assemblages. Furthermore, it represents the only Paleogene basin of Southeast Asia that contains complete vertebrate skeletons, and will thus provide new insights into the phylogeny and palaeobiology of Asian vertebrates during "The Time of Messel".

BÖHME, M., PRIETO, J., SCHNEIDER, S., HUNG, N.V., QUANG, D.D., TRAN, D.N. (2010). The Cenozoic on-shore basins of Northern Vietnam. Biostratigraphy, vertebrate and invertebrate faunas. Journal of Asian Earth Sciences 40: 672-687.

DUCROCQ, S., LIHOREAU, F. (2006). The occurrence of borthriodontines (Artiodactyla, Mammalia) in the Paleogene of Asia with special reference to *Elomeryx*. Palaeobiogeographical implications. Journal of Asian Earth Sciences 27: 885-891.

TONG, Y., ZHENG, S., QIU, Z. (1995). Cenozoic mammal ages of China. Vertebrata PalAsiatica 33: 290-314.

WANG Y, MENG J, NI X, LI C (2007). Major events of Paleogene mammal radiation in China. Geological Journal 42: 415-430.

ZHAI, R., CIOCHON, R.L., TONG, Y., SAVAGE, D.E., MORLO, M., HOLROYD, P.A., GUNNELL, G.F. (2003). An aberrant amphicyonid mammal from the latest Eocene of the Bose Basin, Guangxi, China. Acta Palaeontologica Polonica 48: 293-300.

Petrified woods from the Big Sandy Reservoir, southwestern Wyoming: More evidence for warm climate in the early Eocene

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Southwestern Wyoming is one of the world's famous places for Eocene fauna and flora. Many localities in the Eden Valley area, e.g., Big Sandy Reservoir (Fig. 1), Blue Forest, and Parnell Draw, have been popular sites for petrified wood collecting for almost a century, but the floristic composition and tree diversity are poorly known. From an expedition in June 2010 to these localities, about fifty petrified stems from the Early Eocene Bridger Formation, east of Big Sandy Reservoir, were studied anatomically.

The stems we identified include *Edenoxylon parviareolatum* (Fig. 2A) (Anacardiaceae) (Kruse, 1954); *Laurinoxylon* sp. (Fig. 2B) (Lauraceae) (Ritcher, 1981; Dupéron-Laudoupeneix and Dupéron, 2005); a representative of Canellaceae, and a species of undetermined dicotyledonous wood; and *Palmoxylon* (Fig. 2C) (Palmae) (Tidwell *et al.*, 1971). *Edenoxylon* and *Palmoxylon* appear to have been dominant in the local vegetation at the time of deposition. Besides wood, fossil leaves, fish (Fig. 2D), coiled shells of small snails were also found in the same sediments. Additional specimens of petrified woods and leaves from other localities are under study. The paleoflora from this study is consistent with other evidence that the late early Eocene climate of this region was subtropical, contrasting with the present sagebrush-steppe vegetation and arid, temperate conditions. However, the diversity at this site appears to have been relatively low. The ancient forest in that time was probably an early successional forest habitat, as estimated from the diameter of petrified wood stems we found, which range from approximately 8 cm to 30 cm. The largest specimen, *Laurinoxylon*, is about 60 cm in diameter. The information from these woods augments data from leaf impressions from other sites in the Bridger and Green River Formations to give a more complete understanding of the vegetation characterising this region during this part of the early Eocene.

Figure 1. Eocene petrified wood fragments and the present sagebrush-steppe vegetation near Big Sandy Reservoir, southwestern Wyoming.

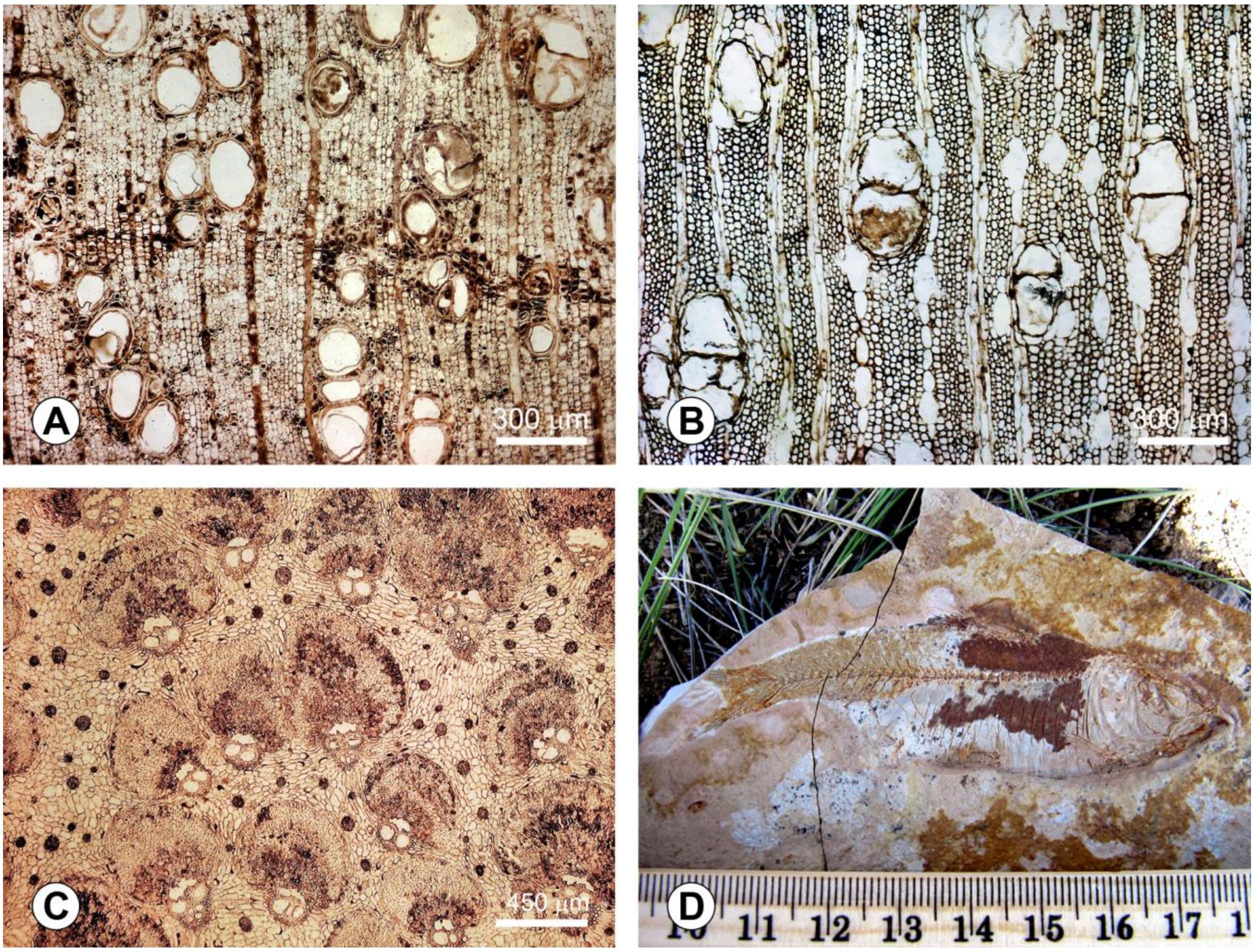

Figure 2. (A-C: Microscopic photos of petrified woods in cross-sections) **A.** *Edenoxylon parviareolatum* Kruse **B.** *Laurinoxylon* sp. **C.** *Palmoxylon* sp. **D.** Example of fish fossil found in associated shale at Big Sandy Reservoir.

Dupéron-Laudoupeneix, M., Dupéron, J. (2005). Bois fossiles de Lauraceae: Nouvelle découverte au Cameroun, inventaire et discussion. Annales de Paléontologie 91: 127-151.

Kruse, H.O. (1954). Some Eocene dicotyledonous woods from Eden Valley, Wyoming. The Ohio Journal of Science 54 (4): 243-268.

Richter, H.G. (1981). Anatomie des sekundarien Xylems und der Rinde der Lauraceae. Sonderbände des Naturwissenschaftlichen Vereins in Hamburg 5: 1-148.

Tidwell, W.D., Simper, A.D., Medlyn, D.A. (1971). A *Palmoxylon* from the Green River Formation (Eocene) of Eden Valley, Wyoming. The Botanique (Nagpur) 2 (2): 93-102.

Paleoclimatic implications and stratigraphic position of the first Uinta C micro-mammal community from the Uinta Formation, Uintah County, Utah

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Mammal fossils from the Uinta Formation comprise the topotype fauna for the Uintan NALMA (North American Land Mammal Age). The Uintan age succeeded the Bridgerian NALMA, with which the German Messel fauna is a correlate. The Uinta Formation is divided into members A, which is composed mostly of poorly fossiliferous sandstones, and B & C, which yield large numbers of vertebrate specimens. Uinta B beds tend to be dark gray and green mudstones with local channel sandstones. Uinta C is characterized by much more oxidized claystones and sandstones, with common red and maroon paleosols (Fig. 1). Townsend (2004) interpreted these lithologic differences as indicating that forest and woodland habitats existed during deposition of Uinta B, while more open habitats of restricted woodlands existed during deposition of Uinta C. A lack of fossil botanical evidence leaves us to use vertebrate fossils to attempt to reconstruct the paleoecologic and paleoclimatologic factors which existed as the Uinta Formation sediments were accumulating.

The WU-26 fossil locality lies in the Uinta C (Myton) Member of the Uinta Formation. WU-26 micro-fossils were discovered in 2007 through collection and processing of a one ton test sample and include *Amia* sp. vertebrae and teeth in association with *Lepsisosteus* sp.; *Apalone*, carettochelyid and emydid turtles; the crocodilian cf. *Allognathosuchus*; the lizard *Glyptosaurus* sp.; and a diverse suite of mammals. The lower vertebrates indicate that a frost-free, subtropical or tropical climate existed at the time they inhabited the region.

The WU-26 fauna is the first late Uintan fauna to yield large numbers of micro-mammal remains along with macro-mammals. This provides the first opportunity to compare the species diversity of both early and late Uintan micro- and macro-mammal faunas in hopes of determining whether climate change affected species diversity. Recently collected mammalian taxa are based on more than 50 micro-mammal teeth from insectivores, the omomyine primates *Mytonius* and cf. *Omomys*, the rabbit *Mytonolagus petersoni*, and the rodents *Microparamys, Pareumys, Janimus* and sciuravid rodents. Medium-sized to large mammals represented include pantolestids, the tapiroid *Colodon*, carnivorans, brontotheres, small cetartiodactyls such as *Protoreodon parvus*, and ischyromyid rodents (Westgate *et al.*, 2008; Harsh *et al.*, 2009). Additional bulk samples were taken at WU-26 in 2008 and 2009, and a 4800-kg sample collected in 2010 is being processed for micro-mammals. These samples are expected to double the current micro-mammal sample size.

The WU-26 fauna increases the known diversity of Uinta C omomyine primates to at least three genera, as a third undescribed primate has been found at another Uinta C locality. This brings into question the recent suggestion of Dunn (2009) that decreasing primate diversity from Uinta B to Uinta C is an indicator of deteriorating climate conditions. Dunn (2009) stated that *Mytonius* is the only omomyine primate known from Uinta Basin Uinta C localities. Low diversity in primate species diversity appears to be more a result of sampling methods than of climate change.

Townsend *et al.* (2006) measured 366 meters of Uinta Formation section from WU-11, their lowest vertebrate-yielding locality in Uinta B, up to the Uinta/Duchesne River Formation contact. We measured two detailed stratigraphic sections in 2009 with a brunton compass and meter tape, and using trigonometric formulas to compensate for local structural dip, we determined the position of WU-26 relative to the top of the Uinta C strata exposed along the west end of Deadman Bench and also relative to the stratigraphic position of Uinta B and C faunas shown in Townsend *et al*. (2006).

Our measurements indicate that WU-26 lies 138 meters below the uppermost Uinta C stratum, exposed interfingering with Duchesne River Formation channel sands on the west end of Deadman Bench. Using the measured section faunal table of Townsend *et al.* (2006) suggests that WU-26 is approximately 336 meters above the WU-11 locality in Uinta B. This indicates that the WU-26 fauna is one of the stratigraphically higher and chronologically younger faunas in the Uinta C Member of the Uinta Formation.

In summary, the WU-26 fauna provides both micro- and macro-mammal species diversity information to compare with older Uintan faunas. Preliminary analysis of primate species diversity suggests that it did not change significantly from early to late Uintan time. Therefore, although climatic conditions in the Central Rocky Mountains may have changed during the Uintan time interval, it appears that those changes were not sufficient to cause a significant decrease in primate species diversity there.

Dunn, R. (2009). Mammalian postcranial evolution and primate extinction in the middle Eocene of North America. Ph.D. dissertation, Washington University, St. Louis, Missouri, 384pp.

Harsh, S., Mika, J., Burnes, J., Knapp, J. (2009). Field and lab techniques for recovering micro-mammal remains from low yielding Uinta Formation facies. 9th North American Paleontologic Convention, Cincinnati Museum Center for Scientific Contributions 3:55.

Figure 1. Mika and Burnes use a brunton compass and 50-meter tape to measure a Duchesne River Formation channel sand below the uppermost Uinta C outcrop on the west end of Deadman Bench.

Townsend, K.E. (2004). Stratigraphy, paleoecology, and habitat change in the middle Eocene of North America. Ph.D. Dissertation, Washington University, Saint Louis, Missouri, 353pp.

Townsend, K.E., Rasmussen, D.T., Friscia, A. (2006). Stratigraphic distribution of upper middle Eocene fossil vertebrate localities in the eastern Uinta Basin, Utah, with comments on Uintan biostratigraphy. The Mountain Geologist 42(2):115-134.

Westgate, J., Townsend, B., Cope, D.,Friscia, A. (2008). Snapshot from the past: A Uintan vertebrate assemblage preserving community structure. Journal of Vertebrate Paleontology 28(3): sup.159A.

The value of X-ray approaches in the study of the Messel fruit and seed flora

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Following the initial overview of the Messel fruit and seed flora by Collinson (1988), the collections have been greatly expanded through continuing field work, and Collinson, Manchester and Wilde have prepared a monograph that is due to be submitted in mid-May 2011. More than 65 species in 34 families of flowering plants are identified along with 60 distinctive morphotypes of unknown familial affinity. Identification of Messel fruits and seeds frequently requires knowledge of internal organisation and tissue and cell anatomy that is not evident externally. Traditional wax- or resin-embedding and sectioning methods proved unsuccessful for Messel specimens because embedding media did not penetrate into the oil shale; in addition, such destructive techniques are discouraged for rare or unique morphotypes. X-ray visualization offers an alternative method for gathering data on internal structures. Smith *et al.* (2009a) first successfully applied Synchrotron Radiation X-Ray Tomographic Microscopy (SRXTM) to Messel specimens in their study of fruiting heads of *Volkeria* (Cyperaceae, sedge family), one of the more common small-fruited species in the flora. To evaluate the general suitability for study of Messel fruits and seeds, SRXTM has now been used to examine about twenty species. Micro-computed tomography (microCT) imaging has been applied to four larger specimens (> 1 cm diam), and one of these will be used to provide direct comparison with SRXTM images of the same specimen. For methods, see final paragraph.

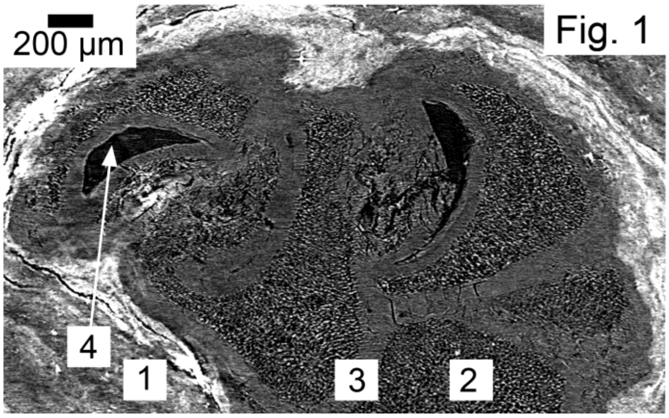
In all cases the part of the specimen hidden from view within the oil-shale block has been successfully visualised. This has proven useful in identifying specimens (e.g., *Tapiscia*, Tapisciaceae) where key features of their morphology were buried in the oil shales. In some examples, such as the single Messel taxon with spiny fruits, the understanding of the revealed symmetry was crucial in enabling comparative investigation of superficially similar extant fruits of various familial affinities. Furthermore, examination of the spine tips buried in the oil shale confirmed our opinion, based on exposed tips, that the spines were not hooked. Therefore, there is no evidence for epizoochory in the Messel fruit and seed flora.

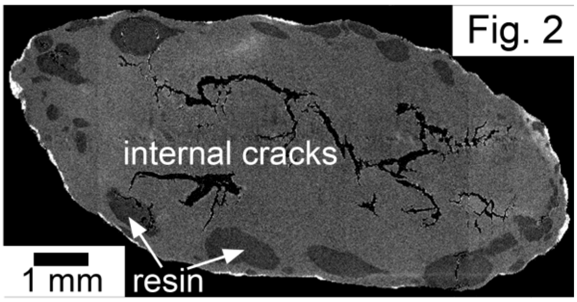
SRXTM has proven crucial in the identification of several taxa. The single specimen of *Pleiogynium* (Anacardiaceae, cashew nut family) was identified on the basis of locule and fibre-bundle number and position revealed by SRXTM. Taxa within the Icacinaceae were also identified through features of the locule and wall visualised by SRXTM. This method has revealed cellular detail in some cases but not in others. For example, cellular details of all layers of the fruit and seed walls are visualised in fine detail in a single-seeded fruit of Vitaceae (grape family). In a many-seeded *Decodon*-like fruit (Lythraceae, loosestrife family) cellular detail is visualised in one tissue layer of the seeds but not in others (Fig. 1). In several cases, such as the *Eomastixia* fruit stone (Cornaceae, dogwood family), neither cellular detail nor internal organisation is visualised. However, the resin secretions, characteristic of the genus *Eomastixia*, are distinguished by SRXTM (Fig. 2).

In addition to sometimes providing crucial tissue and anatomical information, SRXTM enables the digital removal of selected tissues and/or the visualization of internal spaces—virtual taphonomy—to facilitate comparisons between fossils in different states of preservation and with related extant fruits and seeds (Smith *et al.,* 2009*b*). This includes the preparation of digital locule casts, of considerable value for comparison with fossil floras in other preservation states, such as London Clay and Clarno (Smith *et al.,* 2009*b*). Whilst compression has obscured the locule shape in most Messel specimens, digital locule casts of fruit stones from living relatives can be used to compare exceptionally preserved fruits from Messel with fossilised locule casts from other sites. The Menispermaceae (moonseed family, ten types at Messel) are among the families particularly well suited for this approach.

As noted above, at least 60 morphotypes are as yet unidentified as to family. Ongoing work (led by Smith) is focussing on possible affinities of some of these with the gingers (order Zingiberales). The digital sections showing seed coat structure and virtual extraction of the operculum from SRXTM data has enabled the bananas and cannas to be eliminated as possible affinities. The seed present in gut contents of the rodent *Masillamys* (Collinson, 1988) still defies our attempts at identification, in spite of additional information gained from SRXTM.

Nevertheless, our study of Messel fruits and seeds has revealed that, in terms of mammalian frugivorous diet, many fruits and seeds contain substantial thicknesses of tough and hard materials whilst soft material is common. In contrast, abrasive material is rare, phytoliths are absent in *Volkeria* (Smith *et al.*, 2009*a*) and there are only very rare examples of other taxa with possible indication of presence of crystal cells in their tissues.





1 = enclosing oil shale; 2 = thin-walled cells;
3 = thickened tissue, (not cell detail); 4 = embryo cavity.

SRXTM of Messel fruits: **Figure 1.** Tissue organisation of seeds in *Decodon*-like fruit; **Figure 2.** Fruit stone of *Eomastixia* showing resin pockets (darker) but no other information.

The use of X-ray techniques remains constrained by the proprietary software required to analyse the 3D data, the high demand on the few available facilities, and potential cost of machine use. Both SRXTM and microCT are non-destructive and are therefore particularly important in studying specimens that are unique or are rare examples that curators do not wish to damage. External features hidden within the oil shale could perhaps be physically exposed by removing all of the shale. However, this is time consuming and total removal from shale can result in breakage, especially of delicate surface features such as spines and trichomes. Hence we favour the current practice of partial exposure, leaving most specimens partially buried in the oil shale. While there is a trade-off in resolution and suitable specimen size between SRXTM and microCT, both are useful tools for studying fossil fruits and seeds and have revealed significant information about the plants of Messel.

Methods

SRXTM imaging was undertaken at the TOMCAT beamline (Stampanoni *et al.,* 2006), Swiss Light Source, Paul Scherrer Institute, Villigen, Switzerland. Oil-shale blocks with specimens were trimmed to a suitable size, rinsed, and briefly soaked in water to remove the glycerol in which they are stored. Specimens were imaged with the small blocks of oil shale either (i) immobilized at the base (and sometimes also at the sides and top) with foam (Plastazote™) in a plastic tube, or (ii) held in a metal clamp. Specimens free from oil shale were completely enclosed and immobilized in Plastazote. Data were acquired using the 1.25x, 2x or 4x objectives on an X-ray microscope, with an exposure time of 70-350 ms at 20 keV. A total of 1501–2048 projections were acquired over 180°. Projection data were processed, and corrected sinograms were then used for reconstruction. MicroCT imaging was undertaken at the Natural History Museum, London, UK, on a Metris X-Tek HMX ST 225 scanner using a tungsten reflectance target, a voltage of either 105 or 180 kV, a current of either 71 or 190 mA, and an exposure time of 250 ms. Because of the longer scan time (~1 hour for microCT vs. ~10 min for SRXTM), specimens were wrapped in cling film to reduce risk of damage by drying. Wrapped oil-shale blocks or loose specimens were carefully inserted into small blocks of Oasis™ (foam used in flower arranging) to hold and support them. Reconstructed images from SRXTM and microCT were processed using Avizo 6.0 (Mercury Computer Systems, France). Images were captured in Avizo itself and then processed in Adobe Photoshop CS for Mac OS X.

Collinson, M.E. (1988). The special significance of the Middle Eocene fruit and seed flora from Messel, West Germany. Courier Forschungsinstitut Senckenberg 107: 187–197.

Collinson, M.E., Manchester, S.R., Wilde, V. (in progress). Fossil fruits and seeds of the Middle Eocene Messel biota, Germany. Abhandlungen der Senckenberg Gesellschaft für Naturforschung.

Smith, S.Y., Collinson, M.E., Rudall, P.J., Simpson, D.A., Marone, F., Stampanoni, M. (2009*b*). Virtual taphonomy using synchrotron tomographic microscopy reveals cryptic features and internal structure of modern and fossil plants. Proceedings of the National Academy of Sciences 106: 12013-12018.

Smith, S.Y., Collinson, M.E., Simpson, D.A., Rudall, P.J., Marone, F., Stampanoni, M. (2009*a*). Elucidating the affinities and habitat of ancient, widespread Cyperaceae: *Volkeria messelensis* gen. et sp. nov., a fossil mapanioid sedge from the Eocene of Europe. American Journal of Botany 96: 1506–1518.

Stampanoni, M., Groso, A., Isenegger, A., Mikuljan, G., Chen, Q., Bertrand, A., Henein, S., Betemps. R., Frommherz, U., Böhler, P., Lange, M., Abela, R. (2006). Trends in synchrotron-based tomographic imaging: The SLS experience. In: Bonse, U. (ed) Proceedings of SPIE Developments in X-ray Tomography V. 6318: 6318M-1—6318M-14.

A new skull of *Tapirulus* from the late Eocene of France

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Tapirulus Gervais, 1850 is an enigmatic small artiodactyl from the late Eocene and early Oligocene of Europe (Erfurt and Métais, 2007). The genus contains five species all characterised by a tapiroid bilophodont dentition, which makes them quite different from other European artiodactyls. The genus is endemic to Western Europe and is known from a relatively small amount of material (but with a rather good geographic distribution), though a very nice skull (Fig. 1) has been recovered from the Quercy Phosphorites. It is one of the few genera to cross the famous Eocene-Oligocene "Grande Coupure". The fossil we describe here is an almost complete skull with most of the dentition from a late Eocene site in Central-Eastern France.

The site "Les Plantées" is situated in the vicinity of the city of Saint-Etienne, not far from the shores of the Loire River. Geologically the sediments are fluvial in origin, and the skull presented here was found in greenish coarse and not strongly consolidated sands that are correlative to biochronological levels MP18–20 (Hugueney, 1997), thus of late Eocene age. The site yielded few fossils, and a preliminary faunal list was published in Hugueney (1997).

The new skull is ascribed to *Tapirulus* cf. *hyracinus* Stehlin, 1910. Preliminary comparisons to Eocene *Tapirulus* from the middle to late Eocene were carried out, especially with skull NMB Q.B.185 (Fig. 1), one of the best-preserved specimens from the Quercy Phosphorites and ascribed by Stehlin (1910) to *Tapirulus hyracinus*. Based on size alone, the four other species – *T. majori*, Stehlin, 1910, *T. depereti* Stehlin, 1910, *T. schlosseri* Stehlin, 1910, and *T. perrierensis* Sudre, 1978 – can be excluded, as they are much smaller. Skull MHNL 20164554 is well preserved except in its basal part; the left tooth row with I^3-M^3 and the right tooth row with P^1-M^3 are preserved. It is slightly smaller than that from Quercy, but overall proportions are similar. It is flat and has an elongated snout and thus a facial part longer than the posterior. There seems to be two lacrimal orifices, or maybe a split orifice inside the orbit, while the skull from Quercy clearly shows two separated orifices on its virtually uncrushed right orbit: one inside the orbit above a second one situated on the rim, both orifices separated by a small projection of the lacrimal bone. A strong infraorbital foramen lies above the anterior part of the P^3, just like on skull NMB Q.B.185. Teeth are worn such that few characteristics can be described in detail. However, on the upper molars, paraconules are absent and parastyles are rather strong; pre- and post-cinguli are strong especially on M^3, much like on skull NMB Q.B.185 from Quercy. The M^1 and M^3, although being larger than longer, do not reach the antero-posterior compression of the M^2. P^4 is triangular, with strong labial styles and pre- and

Figure 1. Left, skull MHNL 20164554 and right, skull NMB Q.B.185 from the Quercy Phosphorites in dorsal, palatal and lateral view from top to bottom. Scale bar 10 mm.

post-cinguli. Sudre (1978) mentions smaller-sized *Tapirulus* (smaller than *T. hyracinus*) from the early Oligocene of Belgium and France and proposes to investigate this material in more detail since he suggests that another early Oligocene species might exist. Comparisons to this material will be necessary to see whether an intermediate-sized species between the small *Tapirulus* and *T. hyracinus* did indeed exist. The locality “Les Plantées” is tentatively dated to MP18–20 (Hugueney, 1997), and a late Eocene age would fit well with *T. hyracinus*, as this species is known only from the late Eocene and early Oligocene, the other species described so far being found in older localities.

ERFURT, J., MÉTAIS, G. (2007). Endemic European Paleogene artiodactyls – Cebochoeridae, Choeropotamidae, Mixtotheriidae, Cainotheriidae, Anoplotheriidae, Xiphodontidae, and Amphimerycidae. In: Prothero D.R., Foss, S. (eds) The Evolution of Artiodactyls. The John Hopkins University Press, Baltimore, pp 59-84.

HUGUENEY, M. (1997). Biochronologie mammalienne dans le Paléogène et le Miocène inférieur du centre de la France : Synthèse réactualisée. In: Aguilar, J.-P, Legendre S., Michaux J. (eds) Actes du Congrès BiochroM’97. Mémoires et Travaux de l’E.P.H.E, Institut de Montpellier 21, pp. 417-430.

STEHLIN, H.G. (1910). Die Säugetiere des Schweizerischen Eocaens. Critischer Catalog der Materialien. Abhandlungen der schweizerischen paläontologischen Gesellschaft 36: 855-1164.

SUDRE, J. (1978). Les artiodactyles de l’Eocène Moyen et Supérieur d’Europe occidentale (systématique et évolution). Mémoires et Travaux de l’E.P.H.E, Institut de Montpellier, 229 pp.

Eocene mammals at the Natural History Museum Basel – Focus on reference levels and type material

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Since 1855 and the time of its first "curator" for vertebrates, Ludwig Rütimeyer, the Natural History Museum Basel (NMB) has a long tradition of collecting and studying the European continental Eocene. Both Rütimeyer (1862, 1891) and later Stehlin (1912, 1915–1916) enriched the Eocene collection and produced seminal works on the Swiss mammal faunas of this time period. Many fossils were then elected to types and are still currently valid type specimens for several important components of the European Eocene faunas. An example of a locality hosted at the NMB and very rich in holotypes is the Swiss fauna of Egerkingen (old collections and Egerkingen α + β, reference locality for MP level 14), where about 40 species of various mammal groups were described. Of particular interest to the ongoing debate surrounding *Darwinius masillae* Franzen *et al*., 2009, we house a number of Eocene primate types, such as those of the adapid *Caenopithecus lemuroides* Rütimeyer, 1862 (Fig. 1a) and *Cercamonius brachyrhynchus* Stehlin, 1912 (Fig. 1b) In addition, a high-quality coloured cast of *Darwinius masillae* plate A is available. We possess material of half of the reference localities of the European Eocene biochronological timescale: Dormaal, Avenay, Grauves, Egerkingen α + β, La Livinière 2, Robiac and La Débruge, sometimes with hundreds of well-preserved specimens. The NMB houses a collection from more than a 100 Eocene localities (Fig. 2), with highlights such as Cuis and Mancy near the late Palaeocene site of Cernay, Bouxwiller, Egerkingen, Euzet-les Bains, Gösgen-Kanal, Mormont-Eclepens and the famous Quercy represented by thousands of specimens. A total inventory of this collection is in progress. We have about 15 Eocene type localities with about 90 holotypes of mammal species together with their associated paratypes. It is noteworthy to add that an annotated geographic catalogue of the Swiss faunas (from the Palaeocene to the Pliocene) is available at the NMB, each site being described and located on maps with geographic coordinates. This catalogue was recently digitized.

We now have a special part of our collection dedicated to holotypes, and a database of the specimens with pictures was created. We plan to make it available in due course. A catalogue of the Eocene holotypes of mammals is in the making and should be published for the occasion of the 22nd International Senckenberg Conference in an open access journal.

The Basel collection houses largely unpublished material together with well-known and important specimens. This exceptional collection will provide original data for systematics, biogeographical, palaeoecological and biodiversity studies.

Figure 1. A, holotype of *Caenopithecus lemuroides* (NMB Ef.383) and original illustration in Rütimeyer (1862). B, holotype of *Cercamonius brachyrhynchus* (NMB Q.V.619) and original illustration in Stehlin (1912). Scale bar: 1 cm.

FRANZEN, J.L., GINGERICH, P.D., HABERSETZER, J., HURUM, J.H., KOENIGSWALD, W.V., SMITH, B.H. (2009). Complete primate skeleton from the Middle Eocene of Messel in Germany: Morphology and paleobiology. PlosOne 4(5): 1-27.

RÜTIMEYER, L. (1862). Eocaene Säugethiere aus dem Gebiet des Schweizerischen Jura. Neue Denkschriften der allgemeinen schweizerischen Gesellschaft für die gesamten Naturwissenschaften 19:1-98.

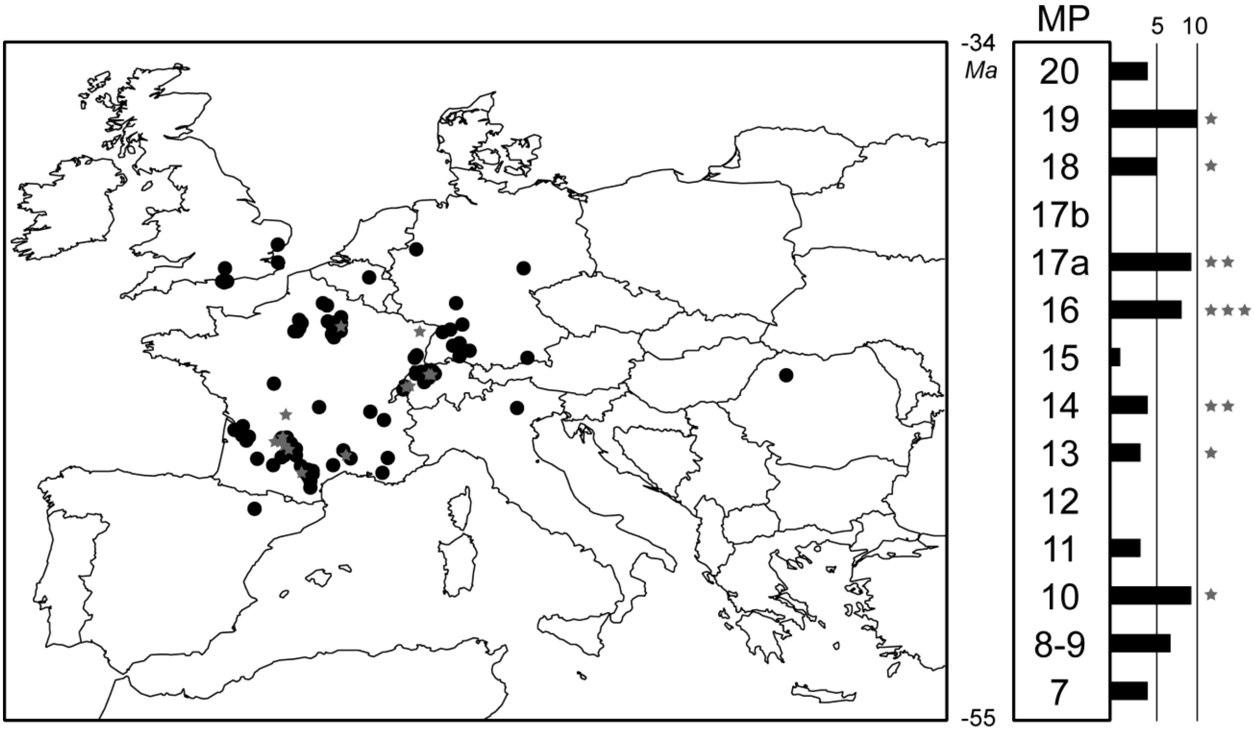

Figure 2. Geographic position of the Eocene localities stored at the NMB (extra-European localities (*ca.* 20: *e.g,* Big Horn Basin or Wasatch) are not represented). Black bars indicate the number of localities for each Eocene MP reference level (from 7 to 20); *ca.* 30 localities with indeterminate ages are also stored at the NMB. Grey stars represent localities with holotypes (3 localities of the Quercy are not represented since the old collections are not well dated).

RÜTIMEYER, L. (1891). Die eocäne Säugethier-Welt von Egerkingen. Abhandlungen der Schweizerischen Palaeontologischen Gesellschaft 18: 1-153.

STEHLIN, H.G. (1912). Die Säugetiere des schweizerischen Eocaens, Siebenter Teil, erste Hälfte: Adapis. Abhandlungen der Schweizerischen Palaeontologischen Gesellschaft 38: 1165-1298.

The haplorhine/strepsirhine position of *Darwinius masillae*: New insights based on the CT analysis of *Pronycticebus gaudryi* middle ear morphology

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The morphology of the middle ear in primates has been studied for a century (e.g., Gregory, 1915, 1920; Saban, 1963; Packer and Sarmiento, 1984; MacPhee and Cartmill, 1986). Middle ear and basicranial structures are commonly used for systematics (e.g., MacPhee and Cartmill 1986). Differences in morphology, pneumatization and vascularization are found between the two primate suborders and between the great clades within both suborders.

In 2009, Franzen *et al.* described an incredibly well-preserved primate from the middle Eocene of Germany. This specimen has been systematically ranked within the Cercamoniinae subfamily and thus linked to the genera *Cantius*, *Protoadapis*, *Europolemur*, *Agerinia*, *Pronycticebus*, etc. The importance of the discovery of *Darwinius masillae* for paleoprimatologists comes from the exceptional completeness of the specimen, one of the most complete

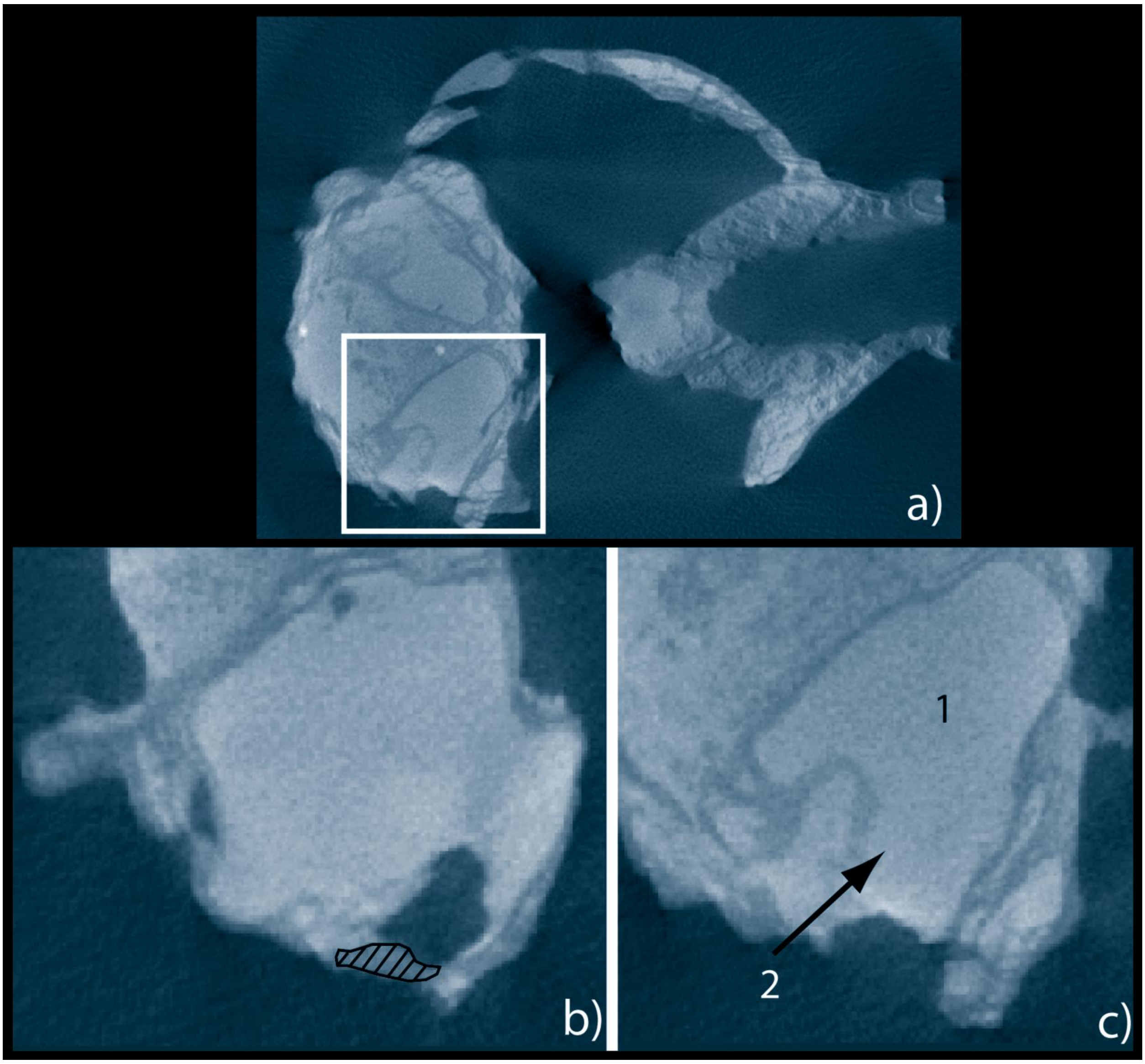

Figure 1. CT scans of *Pronycticebus gaudryi* in dorso-ventral plane (pixel size = 66.66 µm). a) Skull slice highlighting the left bulla illustrated in b) and c). b) Middle ear slice on which the free tympanic ring (hatched) is visible. c) Bulla slice displaying the large tympanic cavity (1) and the postero-lateral entry of the internal carotid (2 and arrow). The absence of an accessory anterior chamber delimited by a septum is notable.

fossil primates ever found. Furthermore, its study by Franzen *et al.* (2009) led these authors to propose that it and other adapoids are basal haplorhines, contrary to the more common view of Adapiformes being strepsirhines. Of the 30 anatomical characters on which Franzen *et al.* (2009) commented, only two (ectotympanic anatomy and promontorial/stapedial vascularization) concern the middle ear morphology. However, at least six middle ear characters are known as synapomorphies of crown haplorhines (Cartmill and Kay, 1978; MacPhee and Cartmill, 1986; Kay *et al.*, 1997; Williams *et al.*, 2010). This is probably due to the deformation of *Darwinius masillae* during fossilization, which does not facilitate the observation and reconstruction of intracranial structures. Williams *et al.* (2010), reconsidering the anatomical traits of *Darwinius*, supported its strepsirhine affinity and stated that a comparison with other Cercamoniinae crania would move the discussion forward.

The skull of *Pronycticebus gaudryi* is the only one currently known for European cercamoniines. It was carefully described by Le Gros Clark (1934) and reinterpreted by Simons (1962). Basicranial anatomical traits were studied, but access to the middle ear was very difficult, although one auditory bulla has been opened mainly for describing the ectotympanic morphology.

Materials and Methods

We studied the *Pronycticebus* middle ear with 3D micro-CT techniques. After segmentation, middle ear morphology, pneumatization and vascularization were described and compared to those of adapoids (*Adapis*), Lemuriformes (*Lemur*), and two haplorhines (*Tarsius* and *Cercopithecus*). We focused on internal carotid artery pathway, pneumatization of the tympanic cavity, and the attachment point for the eardrum, all characters which distinguish strepsirhines from haplorhines. A 3D reconstruction of these structures will be presented.

Results and Discussion

Ectotympanic morphology (tympanic ring), simple epitympanic recess, posterolateral internal carotid entry, and also the absence of an anterior accessory cavity indicate that, regarding middle ear morphology, Cercamoniinae are close to Adapinae and both adapoid subfamilies are very similar to extant strepsirhines (Fig. 1). Most of the analyzed traits are probably primitive for primates. However, there are no tangible arguments that would support the hypothesis linking Cercamoniinae to Haplorhini, which are characterized by a series of derived middle ear characters. Since the middle ear morphology of "Ida" is not available, we suggest that it very probably was similar to that of *Pronycticebus*, and this in turn makes it a very probable primitive strepsirhine, and not a haplorhine.

Acknowledgements

We thank Pascal Tassy and Christine Argot for giving access to the cranium of *Pronycticebus gaudryi.* We are grateful to Hugo Dutel and Olivier Lambert, who helped to perform the scan of *Pronycticebus,* and to the "ATM formes possibles", for financing that scan. We thank Eloïse Zoukouba for technical help. We express our gratitude to Marcia Ponce de León and Christoph Zollikofer (Anthropological Institute and Museum Zürich) for giving access to extant specimens and to scanning facilities. We thank Paul Tafforeau and the staff of beamlines ID19 and ID17 (European Synchrotron Radiation Facility).

Cartmill, M., Kay, R.F. (1978). Cranio-dental morphology, tarsier affinities and primate sub-orders. In: Chivers, D.J., Joysey, K.A. (eds) Recent Advances in Primatology. London, Academic Press, pp 205-214.

Franzen, J.L., Gingerich, P.D., Habersetzer, J., Hurum, J.H., von Koenigswarld, W. (2009). Complete primate skeleton from the Middle Eocene of Messel in Germany: Morphology and paleobiology. PLoS ONE 4*:*1-27.

Gregory, W.K. (1915). I: On the relationship of the Eocene Lemur *Notharctus* to the adapidae and the other Primates. II: On the classification and phylogeny of the Lemuroidea. Bulletin of the Geological Society of America 26: 419-446.

Gregory, W.K. (1920). On the structure and relations of *Notharctus*, an American Eocene primate. Bulletins of the American Museum of Natural History 42: 95-263.

Kay, R.F., Ross, C.F., Williams, B.A. (1997). Anthropoid origins. Science 275*:* 797-804.

Le Gros Clark, W.E. (1934). On the skull structure of *Pronycticebus gaudryi*. Proceedings of the Zoological Society of London 1*:* 19-27.

MacPhee, R.D.E., Cartmill, M. (1986). Basicranial structures in primates systematics. In: Swindler, D.R. (ed) Comparative Primate Biology Systematics, Evolution and Anatomy. New York: Liss, A.R. pp 219-275.

Packer, D.J., Sarmiento, E.E. (1984). External and middle ear characteristics of Primates with reference to Tarsier-Anthropoid affinities. American Museum Novitates 2787*:* 1-23.

Saban, R. (1963). Contribution a l'étude de l'os temporal des primates. Description chez l'homme et les prosimiens. Anatomie comparée et phylogénie. Mémoires du Muséum National d'Histoire Naturelle de Paris, série A, 29*:* 1-378.

Simons, E.L. (1962). A new Eocene primate genus, *Cantius*, and a revision of some allied European lemuroids. Bulletin of the British Museum (Natural History) Geology 7*:* 1-36.

Williams, B.A., Kay, R.F., Kirk, C.E., Ross, C.F. (2010). *Darwinius masillae* is a strepsirrhine: A reply to Franzen *et al.* (2009). Journal of Human Evolution 59: 567-573.

How a comprehensive analysis of feeding ecology, food properties, and tooth-use wear in an extant primate community can inform Eocene primate paleobiology

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Interpreting the ecology and behavior of extinct primates is dependent on a thorough understanding of comparable, living forms. Therefore, it is imperative that paleobiologists frame their work in the context of what is known about living animals, and it is the responsibility of those workers who study living organisms to conduct and produce meaningful research that allows those who study fossil forms to access and utilize these data. One of the primary goals of our research program is to do just that, to provide a context from extant primate ecology, biology, and behavior to interpret the biology of extinct Eocene (and other) fossil primates.

Beginning in 2003, we have been conducting a comprehensive study of the dental ecology of an extant lemur community in southwestern Madagascar. Among the ring-tailed lemurs (*Lemur catta*) at the Beza Mahafaly Special Reserve (BMSR), we have documented a pattern of frequent severe tooth wear, leading to the antemortem loss of teeth in more than 25% of the population (Fig. 1), which is not simply a result of studying “old” individuals (Cuozzo and Sauther, 2004, 2006; Cuozzo *et al.*, 2008, 2010). Rather, this pattern of wear is largely a product of this species consuming a fallback food with challenging mechanical and physical properties, including being the hardest, toughest and largest food consumed in this riverine gallery forest (Yamashita *et al.*, 2011). This food, the fruit of the tamarind tree (*Tamarindus indica*) also contains biogenic silica (opal phytoliths), which has recently been shown to produce enamel wear (Cuozzo *et al.*, submitted). Unlike omnivorous *Lemur catta*, sympatric folivorous sifaka (*Propithecus verreuaxi*) shows few individuals (< 5%) with severe wear and antemortem tooth loss (Cuozzo and Sauther, 2006). However, BMSR sifaka do display a high frequency of maxillary canines abscesses (~ 30%), a result of heavy wear of the canine crown, which exposes the pulp cavity (Fig. 2), resulting in decay and an eventual apical abscess, which, like severe wear and tooth loss in *Lemur catta*, does not occur solely in old-aged individuals.

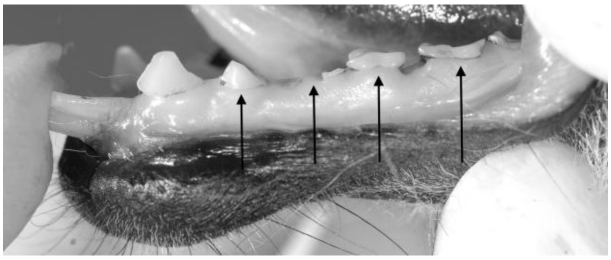

Figure 1. Severe wear and antemortem tooth loss in a BMSR ring-tailed lemur. Black arrows indicate worn and/or absent tooth positions.

What do these two dental patterns share? Although ring-tailed lemurs are mixed feeders at BMSR, consuming fruit, leaves, and on occasion, invertebrates, whereas sympatric verreaux’s sifaka are viewed as obligate folivores, both species frequently consume tamarind fruit, with ring-tailed lemurs using ripe fruit, and verreaux’s sifaka unripe fruit. Despite the different stages of ripeness used, this fruit generally maintains its challenging properties as it ripens, remaining both tough and hard (Yamashita *et al.*, 2011). This tree species also fruits asynchronously, therefore this food is available year round and readily accessible (Sauther and Cuozzo, 2009). Also in common is that these two dental patterns reflect the placement of tamarind fruit on the dental arcade. In ring-tailed lemurs, severe wear and tooth loss predominately occurs on the postcanine teeth where tamarind fruit is processed. In verreaux’s sifaka, with their reduced dental formula, foreshortened jaw, and limited gape, tamarind fruit is processed with the maxillary canines. Therefore, the use of this specific food is in large part responsible for two distinct, yet corresponding patterns of tooth-use wear in these sympatric lemur species, and provides an identifiable hard-tissue record of its use.

Assessing patterns of tooth-use wear in primate fossils has a long history. However, since its development in the 1970s and 1980s, analyses of dental

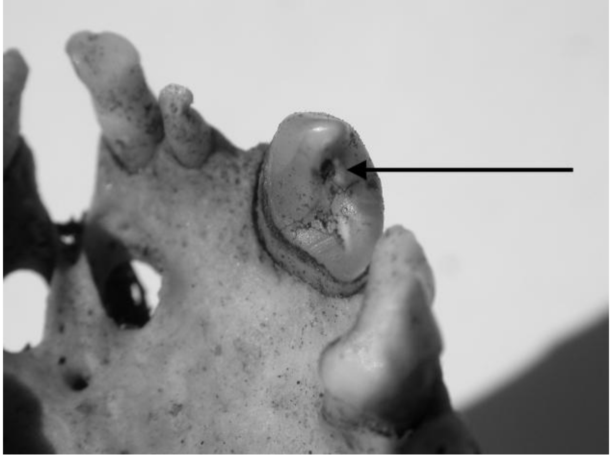

Figure 2. Heavy maxillary canine wear and exposed pulp cavity (black arrow) in BMSR verreaux’s sifaka.

microwear have dominated dental wear assessment, with patterns of overall or gross wear receiving far less attention (e.g., Ungar, 2002). Our long-term work combines data on feeding ecology and food properties in a single primate community to identify the proximate causes of primate tooth wear, and provides an interpretive framework for assessing patterns of gross wear in primate fossils. Specifically, we have documented identifiable patterns of tooth wear produced by consuming specific foods with particular properties. In numerous descriptions of Eocene primates (and many other early Tertiary mammals), specimens are often noted as displaying varying degrees of gross tooth wear, with authors commonly lamenting that "heavy" wear obscures dental traits needed for taxonomic identification. Yet, these patterns of heavy tooth wear can be quite informative in terms of assessing the behavior and ecology of extinct forms.

Among Eocene primates, several Southeast Asian anthropoid forms have been described as displaying varying degrees of "heavy" dental wear, at different tooth positions (e.g., Ciochon and Gunnell, 2004; Beard *et al.*, 2009). Beard *et al.*, (2009) describe a pattern of distinct, heavy wear in the mandibular canines of the newly named middle Eocene amphipithecid *Ganlea megacanina* from the Pondaung formation of Myanmar. Most striking is the pattern of heavy wear on the mandibular canines, which is interpreted as evidence of feeding on hard foods, similar to the extant New World pithecine. How do our data further inform this assessment? Gross tooth wear is a product of the overall use of the teeth, particularly the long-term use of specific foods. In this way, analyses of dental macrowear (i.e., gross wear) provide a very different view of an animal's ecology than microwear analyses, which reflect the most recent foods consumed. The pattern of tooth-use wear described for *G. megacanina* is similar to that of the BMSR sifaka, in which canines show marked abrasion, while the post-canine teeth display far less severe wear. As the canine wear pattern of BMSR sifaka reflects long-term use of a food that is not only hard and tough, but also laden with biogenic silica, it is also possible that *G. megacanina* regularly used a fallback food with similar mechanical and physical properties. Detailed work on living animals can thus add important detail to current discussions regarding the paleobiology of long-extinct primates.

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BEARD, K.C., MARIVAUX, L., CHAIMANEE, Y., JAEGER, J-J., MARANDAT, B., TAFFOREAU, P., SOE, A.N., TUN, S.T., KWAY, A.A. (2009). A new primate from the Eocene Pondaung Formation of Myanmar and the monophyly of Burmese amphipithecids. Proceedings of the Royal Society B 276: 3285-3294.

CIOCHON, R.L., GUNNELL, G.F. (2004). Eocene large-bodied primates of Myanmar and Thailand: Morphological considerations and phylogenetic affinities. In: Ross, C.F., Kay, R.F. (eds) Anthropoid origins: New visions. Kluwer/Plenum Press, New York, pp 249-282.

CUOZZO, F.P., SAUTHER, M.L. (2004). Tooth loss, survival, and resource use in wild ring-tailed lemurs (*Lemur catta*): Implications for inferring conspecific care in fossil hominids. Journal of Human Evolution 46: 625-633.

CUOZZO, F.P., SAUTHER, M.L. (2006). Severe wear and tooth loss in wild ring-tailed lemurs (*Lemur catta*): A function of feeding ecology, dental structure, and individual life history. Journal of Human Evolution 51: 490-505.

CUOZZO, F.P., SAUTHER, M.L, GOULD, L., SUSSMAN, R.W., VILLERS, L.M., LENT, C. (2010). Variation in dental wear and tooth loss in known-aged, older ring-tailed lemurs (*Lemur catta*): A comparison between wild and captive individuals. American Journal of Primatology 72: 1026-1037.

CUOZZO, F.P., SAUTHER, M.L., YAMASHITA, N., LAWLER, R.R., BROCKMAN, D.K., GODFREY, L.R., GOULD, L., JACKY YOUSSOUF, I.A., LENT, C., RATSIRARSON, J., RICHARD, A.F., SCOTT, J.R., SUSSMAN, R.W., VILLERS, L.M., WEBER, M.A., WILLIS, G. (2008). A comparison of salivary pH in sympatric wild lemurs (*Lemur catta* and *Propithecus verreauxi*) at Beza Mahafaly Special Reserve, Madagascar. American Journal of Primatology 70: 363-371.

CUOZZO, F.P., UNGAR, P.S., SAUTHER, M.L., MILLETTE, J.B., YAMASHITA, N. (submitted). Silica phytoliths as a source of primate tooth wear. American Journal of Physical Anthropology.

SAUTHER, M.L, CUOZZO, F.P. (2009). The impact of fallback foods on wild ring-tailed lemur biology: A comparison of intact and anthropogenically disturbed habitat. American Journal of Physical Anthropology 140: 671-686.

UNGAR, P.S. (2002). Reconstructing the diets of fossil primates. In: Plavcan, J.M., Kay, R.F., Jungers W.L., van Schaik, C.P. (eds) Reconstructing behavior in the fossil record. Kluwer Academic/Plenum Press, New York, pp 261-296.

YAMASHITA, N., CUOZZO, F.P., SAUTHER, M.L. (2011). Interpreting food processing through dietary mechanical properties: A *Lemur catta* case study. American Journal of Physical Anthropology DOI 10.1002/ajpa.21549.

A new Eocene locality from southern France sheds light on the basal radiation of Pachynolophinae (Mammalia, Perissodactyla, Equoidea)

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A new Eocene locality from Southern France, though yielding a poorly diversified vertebrate fauna, has yielded an abundant and varied material representing a new pachynoloph equoid. This new locality, Sainte-Eulalie, is located 30 km northeast of Carcassonne, within continental Cenozoic deposits of the Minervois (southernmost foothill of the Massif Central). They document vertebrate evolution from the earliest Ypresian to the Bartonian (e.g., Gervais, 1859; Hartenberger *et al.*, 1968; Marandat, 1986, 1987). More precisely, Sainte-Eulalie belongs to the “Grès et Argiles d'Assignan” formation, inserted between two other formations dated from MP7 and MP10 (Marandat, 1987). These data suggest a middle Ypresian age (MP8–9, estimated ca. 52–53 Ma; Escarguel *et al.*, 1997; Luterbacher *et al.*, 2004) for Sainte-Eulalie. This is consistent with the mammal fauna present at this locality (*Dissacus* sp., *Lophiaspis* sp., *Donrussellia* sp.).

Together with *Pachynolophus* sp. from La Borie (Laurent *et al.*, 2010), the new species is the oldest occurrence of the genus *Pachynolophus*. They are most likely close relatives as well. The new species, represented by 18 specimens of cranial, maxillary and upper dental material and 33 specimens of mandibular and lower dental material, is characterized by an incomplete postprotocrista on P^3; a subquadrangular P^4, displaying in most cases a complete postprotocrista and a relatively strong and continuous lingual cingulum; an extra cusp sometimes present on the lingual side of the metacone on P^4; the labial cingulum that can be interrupted at the paracone; the postcingulum expanded only on M^3; a “pseudomesostyle” (*sensu* Badiola *et al.*, 2005) often present on the upper molars; the paraconule weak to moderate; M^3 smaller than M^2; and the weak entoconid on P_4 not connected to the hypoconid (Fig. 1).

A phylogenetic analysis suggests the exclusion of *Pachynolophus hookeri* from the genus and the paraphyly of *Propachynolophus*. The diagnosis of the genus has therefore been emended. Thus, these small brachyodont equoids are characterized by non-molariform premolars, the absence of a true mesostyle on the upper molars, relatively weak cingula except for an important expansion of the postero-lingual cingulum on the P^4 and a medially oriented prehypoconulocristid on the M_3. According to this phylogenetic analysis, the genus *Pachynolophus* is monophyletic (to the exclusion of “*P*”. *hookeri*). The stem position of the new species is consistent with stratigraphy. The analysis also shows two or even three groups among *Pachynolophus* species, as already highlighted by Remy (1972) and Badiola *et al.* (2005). The first is formed by *P. bretovensis*, *P. garimondi*, *P. zambranensis*, and *P. lavocati*. *Pachynolophus boixedatensis* and *P. cesserasicus* make up the second group. Finally, Remy (1972) and Badiola *et al.* (2005) recognized a third group, comprising *P. livinierensis* and *P. duvali*, but their relationships are not resolved in the present analysis.

In the quite abundant and diverse material of *Pachynolophus* sp. nov., some variability appears, in particular on the cranium and the mandible. It is, however, consistent with only one species. Two morphs have been distinguished that are interpreted

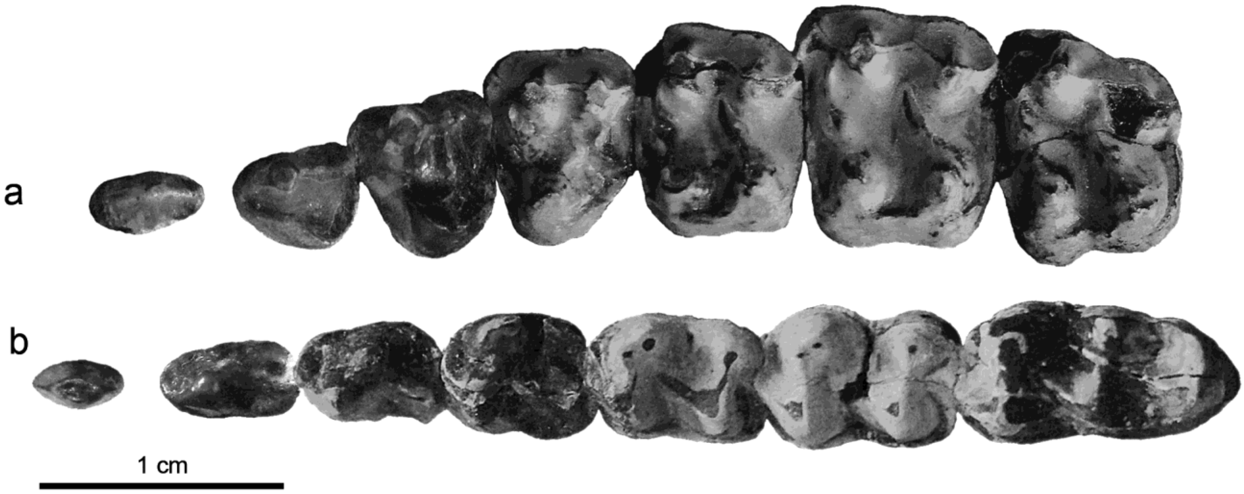

Figure 1. *Pachynolophus* sp. nov. a) Composite left upper tooth row, based on SEL-101 (holotype, P^4-M^3) and SEL-45 (P^1-P^3); b) Composite left lower tooth row, based on SEL-43 (paratype, P_3-M_3), SEL-05 (P_2) and SEL-08 (P_1).

as sexual dimorphism. Indeed, some crania are more robust. They mainly show larger canine alveoli, more powerful crests, a convex naso-frontal area (which is flat in the other morph), and a greater height between the larger jugal arch and the teeth row. These features were also found in *Hyracotherium* by Gingerich (1981). This author interpreted the robust forms as males and the slender ones as females. The same hypothesis is assumed here, but in contrast with *Hyracotherium*, in *Pachynolophus* sp. nov. the crania of males and females are similar in size.

Furthermore, on one cranium the organization of the muzzle bones is visible. This is, according to Remy (2004), an important character in distinguishing equoid groups. Indeed, in Equidae the premaxilla is always dorsally enlarged and the maxilla never extends to the rim of the nasal notch. In contrast, in Palaeotheriidae *s.l.* (Remy, 2004), the dorsal apophysis of the premaxilla is reduced and the maxilla reaches the nasal notch, more or less according to the taxon. In this new species a primitive configuration, consistent with its phylogenetic and stratigraphic position, is found, since the maxilla does not extend to the nasal notch and the premaxilla is reduced upward. The new material should thus help to solve the question of controversial systematics and phylogeny of pachynolophs (Savage *et al.*, 1965; Remy, 1967; Franzen, 1989; Hooker, 1989; Cuesta, 1994; Froehlich, 1999). Furthermore, these fossils will shed new light on the initial radiation of European equoids (Hooker, 1989; Froehlich, 2002). More advanced investigations, e.g. by CT scanning, are to be undertaken in the near future.

BADIOLA, A., PEREDA-SUBERBIOLA, X., CUESTA, M.A. (2005). Una nueva especie de *Pachynolophus* (Mammalia, Perissodactyla) de Zambrana (Álava, Región Vasco-Cantábrica). Análisis filogenético de *Pachynolophus* et primera cita en el Eoceno Superior de la Península Ibérica. Geobios 38: 1-16.

CUESTA, M.A. (1994). Los Pachynolophinae (Equoidea, Perissodactyla, Mammalia) del Eocéno de la Cuenca del Duero (Castilla y León, España). Studia Geologica Salmanticensia 30:21-63.

ESCARGUEL, G., MARANDAT, B., LEGENDRE, S. (1997). Sur l'âge numérique des faunes de mammifères du Paléogène d'Europe Occidentale, en particulier celles de l'Eocène Inférieur et Moyen. In: Aguilar, J.P., Legendre, S., Michaux, J. (eds) Actes du Congrès Biochrom'97, Montpellier. Volume 21. Mémoires et Travaux de l'Ecole Pratique des Hautes Etudes, Montpellier, pp 443-460.

FRANZEN, J.L. (1989). Origin and systematic position of the Palaeohteriidae. In: Prothero, D.R., Schoch, R.M. (eds) The Evolution of Perissodactyls. Oxford University Press, New York, pp 102-108.

FROEHLICH, D.J. (1999). Phylogenetic systematics of basal perissodactyls. Journal of Vertebrate Paleontology 19(1): 140-159.

FROEHLICH, D.J. (2002). Quo vadis *Eohippus*? The systematics and taxonomy of the early Eocene equids (Perissodactyla). Zoological Journal of the Linnean Society 134: 141-256.

GERVAIS, P. (1859). Zoologie et Paléontologie françaises (animaux vertébrés). Bertrand, Paris.

GINGERICH, P.D. (1981). Variation, sexual dimorphism, and social structure in the early Eocene horse *Hyracotherium* (Mammalia, Perissodactyla). Paleobiology 7(4): 443-455.

HARTENBERGER, J.L., SIGÉ, B., SUDRE, J. (1968). Nouveaux gisements de Vertébrés dans l'Eocène continental du Minervois. Compte Rendu Sommaire des Séances de la Société Géologique de France 1968: 22-23.

HOOKER, J.J. (1989). Character polarities in early perissodactyls and their signifiance for *Hyracotherium* and infraordinal relationships. In: Prothero, D.R., Schoch, R.M. (eds) The Evolution of Perissodactyls. Oxford University Press, New York, pp 79-101.

LAURENT, Y., ADNET, S., BOURDON, E., CORBALAN, D., DANILO, L., DUFFAUD, S., FLEURY, G., GARCIA, G., GODINOT, M., LE ROUX, G., MAISONNAVE, C., MÉTAIS, G., MOURER-CHAUVIRÉ, C., PRESSEQ, B., SIGÉ, B., SOLÉ, F. (2010). La Borie (Saint-Papoul, Aude): Un gisement exceptionnel dans l'Eocène basal du Sud de la France. Bulletin de la Société d'Histoire Naturelle de Toulouse 146: 89-103.

LUTERBACHER, H.P., ALI, J. R., BRINKHUIS, H., GRADSTEIN, F.M., HOOKER, J.J., MONECHI, S., OGG, J.G., POWELL, J., RÖHL, U., SANFILIPPO, A., SCHMITZ, B. (2004). The Paleogene period. In: Gradstein, F., Ogg, J., Smith, A. (eds) A Geologic Time Scale. Cambridge University Press, pp 384-408.

MARANDAT, B. (1986). Découverte d'une faune de micromammifères d'âge Cuisien Supérieur dans les marno-calcaires d'Agel à Azillanet (Minervois, Hérault). Géologie de la France 2: 197-204.

MARANDAT, B. (1987). La biostratigraphie mammalienne de l'Éocène continental du versant sud de la Montagne Noire. Reconsidération d'après les nouvelles données. Münchner Geowissenschaftliche Abhandlungen Reihe A 10: 149-158.

REMY, J.A. (1967). Les Palaeotheridae (Perissodactyla) de la faune de mammifères de Fons 1 (Écene Supérieur). Palaeovertebrata 1(1): 1-46.

REMY, J.A. (1972). Étude du crâne de *Pachynolophus lavocati* n. sp. (Perissodacyla, Palaeotheriidae) des Phosphorites du Quercy. Palaeovertebrata 5(2): 45-78.

REMY, J.A. (2004). Le genre *Plagiolophus* (Palaeotheriidae, Perissodactyla, Mammalia) : Révision systématique, morphologie et histologie dentaires, anatomie crânienne, essai d'interprétation fonctionnelle. Palaeovertebrata 33(1-4): 17-281.

SAVAGE, D.E., RUSSELL, D.E., LOUIS, P. (1965). European Eocene Equidae (Perissodactyla). University of California Publications in Geological Sciences 56: 1-94.

Echolocation, flight and inner-ear adaptation in bats

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Bats are globally one of the most successful mammalian orders, and records suggest that the number of extant bat species currently stands at over 1133 (Reeder *et al.*, 2007). Two of their key innovations are said to have aided their diversification: powered flight and sophisticated laryngeal echolocation. Whereas examination of early Eocene fossils has recently suggested that powered flight evolved prior to echolocation (Simmons *et al.*, 2008), little else is known regarding the exact timing and origins of these two features.

The auditory systems of laryngeal echolocating bats are remarkable among mammals, with the upper hearing limit of many species being above 100 kHz, five times that of humans. In order to receive and process the high-frequency sounds produced during echolocation, the inner-ears of bats have undergone substantial structural and functional modifications. Traditionally, studying these features has proved problematic, for several reasons. Past methods involved sacrificing live specimens followed by fixation, dissection and serial sectioning of the regions of interest. This destructive method is neither efficient nor practical, as results are unrepeatable, potential measurements are limited, and the endangered status of many bats limits its applicability. In order to overcome these problems, high-resolution micro-computer tomography (μCT) scans were taken of a variety of bat species from existing museum collections, representing a cross section of bat diversity in terms of echolocation call type, Old World / New World distribution and ecological preference, with the ultimate aim of exploring and documenting structural variation of inner-ears displayed across 16 bat families.

Following scanning, individual X-ray slices were aligned and 3D reconstructions of the regions of interest were formed. The internal void of the cochlea and associated semi-circular canals was then digitally dissected and extracted to produce complete 3D representations (Fig. 1). These volumes were then analysed in terms of the morphology of the cochlea and the semi-circular canals – the two key elements of the mammalian inner-ear responsible for audition and vestibular function, respectively.

By studying these morphological adaptations, inferences may be drawn regarding the associated adaptations of each of the major echolocation call types as well as understanding the evolutionary origins across the order. In particular, we aimed to determine whether the inner-ears of the two clades of echolocating bats (Yangochiroptera and echolocating Yinpterochiroptera) showed similar derived features not shared by non-echolocating Old World fruit bats. Signatures of convergence would support the hypothesis that high-frequency echolocation has evolved multiple times in bats, rather than that of loss in non-echolocating Old World fruit bats.

The two inner-ear components were analysed using linear and multivariate techniques, the results of which were then related to a variety of ecological characteristics. First, the gross morphology of the cochlea, i.e., overall size and number of turns, was compared between echolocating and non-echolocating bats, as well as with a number of other mam-

Figure 1. 3D reconstructions of the internal volumes of the inner-ear from three bat species – not to scale, (left to right: *Rhinolophus philippinensis*, *Centurio senex* and *Pteropus sp.*).

mals. The length of the basilar membrane – the structure supporting the hair cells – was estimated and correlated with hearing ranges, based on both audiogram data and echolocation call parameters. Second, semi-circular canal size was compared to published data from non-volant mammals in order to look for adaptations of powered flight in bats. Semi-circular size and shape in bats was studied to assess how these traits have been affected by changes in cochlea morphology associated with echolocation. Attempts were also made to relate morphological variation of the semi-circular canals to different wing morphologies and thus different flight capabilities.

Results show that inner-ear morphology is highly variable within and across different bat clades. No unifying adaptations of the semi-circular canals for flight were found, although given their body size, the bats of several families were found to have larger than expected canals. Further analyses suggest that the semi-circular canals of echolocating bats are influenced by cochlear expansion relating to echolocation, and this may mask the expected correlations with either body mass or agility.

In agreement with previous studies (for examples see Habersetzer and Storch, 1992; Pye, 1966) the cochleae of echolocating bats were found to be greatly expanded and structurally complex, and, therefore, support previous assertions of morphological convergence between echolocating clades. No clear evidence of relaxation or 'loss of function' was found in the Old World fruit bats. Therefore, our findings do not support a loss of echolocation in Old World fruit bats. We also suggest that different selective constraints have been acting on the two clades of echolocating bats. Our analyses of eco-morphological features of bats not only provide a unique insight into the remarkable diversity of modern bats, but will also provide a valuable resource for comparisons with early-bat fossils. From the anatomical features it may then be possible to reconstruct the behavioural and sensory capabilities in bat ancestors, which can then be used to 're-trace' the origins of echolocation.

Habersetzer, J., Storch, G. (1992). Cochlea size in extant chiroptera and Middle Eocene microchiropterans from Messel. Naturwissenschaften 79(10): 462-466.

Pye, A. (1966). The structure of the cochlea in chiroptera. I. Microchiroptera: Emballonuroidea and Rhinolophoidea. Journal of Morphology 118(4): 495-510.

Reeder, D.M., Helgen, K.M., Wilson, D.E. (2007). Global trends and biases in new mammal species discoveries. Occasional Papers, Museum of Texas Tech University 269: 1-36.

Simmons, N.B., Seymour, K.L., Habersetzer, J., Gunnell, G.F. (2008). Primitive Early Eocene bat from Wyoming and the evolution of flight and echolocation. Nature 451(7180): 818-821.

10th G.H.R. von Koenigswald Lecture

Paleoanthropology in 3D: A review of analysis and visualization of primate (especially human) evolution

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Nearly 100 years ago, D'Arcy W. Thompson published one of the first studies visualizing two-dimensional evolutionary morphology, comparing (among other examples) the shapes of crania in humans and apes and graphing the "distortions" that would permit one to transform into another. In the past 20 years, collaborations among mathematical biologists, morphologists, paleontologists and computer scientists have led to the rise of geometric morphometrics, which allows the sophisticated statistical analysis of shape in the biological world and the visualization of evolutionary shape change. Anthropologists have been at the forefront of such work, studying the cranium, dentition and postcranial elements of living and fossil humans and other primates in ways that would never have been imagined even 30 years ago.

This lecture will survey the methods and techniques of 3D GM (three-dimensional geometric morphometrics) and review some of the major results of analyses conducted to date by numerous researchers, especially my colleagues in the NYCEP Morphometrics Group (http://www.nycep.org/nmg). 3D GM requires the recording of landmarks on bony surfaces and may involve semi-landmarks placed between fixed landmarks. With new technology, data collection has evolved from the use of simple devices such as 3D digitizers to high-resolution surface scanners and CT scanners. Analytical methods have also become more complex, combining multivariate statistics, least-squares superimposition of datasets, splines and advanced visualization programs.

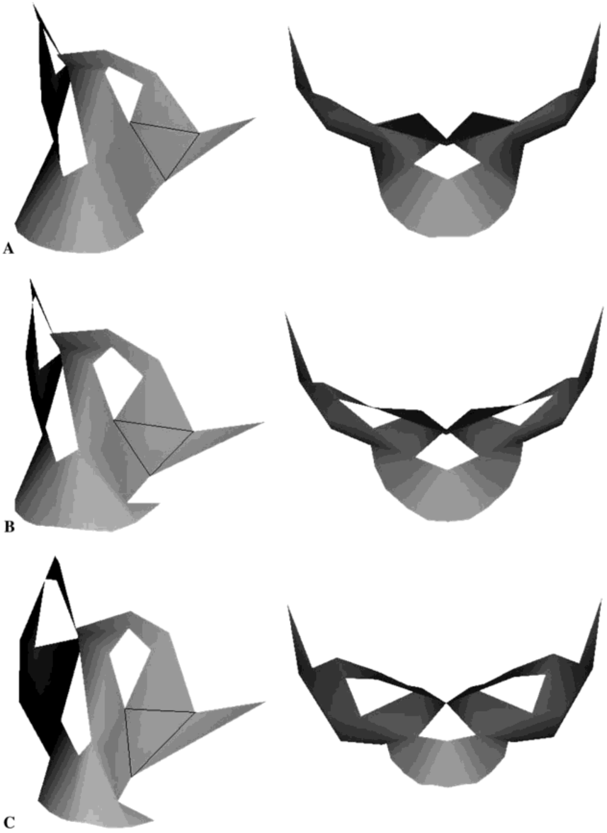

Figure 1. Wireframe views of a) Sts 5, b) Taung simulated as an adult, c) SK 48 (from McNulty *et al.*, 2006).

Among the many projects undertaken by numerous colleagues, not all of which can be discussed here, a few can be noted: 1) comparison of cranial shape variation in Neanderthals vs. modern humans, revealing that Neanderthals are more different from *Homo sapiens* than species of chimpanzees or macaques are from each other, thus supporting *Homo neanderthalensis* as a distinct species of hominin (Harvati *et al.*, 2004); 2) study of cranial shape variation in modern baboons, documenting a continuity of form with only slight "steps" at the boundaries of recognized varieties, suggesting that there is only one extant species of *Papio* with numerous subspecies, rather than multiple species (Frost *et al.*, 2003); 3) analysis of growth patterns in various primate species, revealing that the patterns are relatively consistent across closely related species and most cranial shape is fixed from a quite young age, so that juvenile individuals can be "grown up" along their ontogenetic trajectories to allow comparison of their inferred adult shape—this has been accomplished for individuals of such species as the fossil human *Australopithecus africanus* (Fig. 1) and the rare and newly recognized African monkey *Rungwecebus kipunji*, which have then been compared to adults of closely related species (McNulty *et al.*, 2006; Singleton *et al.*, 2010); 4) reconstruction of damaged individuals of such fossil hominins as *Sahelanthropus tchadensis*, *Homo neanderthalensis* and others using a "puzzle-piece" approach with CT scans and a computer visualization approach for other fossil species (Ponce de Leon and Zollikofer, 2001; Zollikofer and Ponce de Leon, 2005; Zollikofer *et al.*, 2005; Fig. 2, Delson *et al.*, in prep.); 5) analysis of shape variation in crania of *Homo erectus* and related fossil humans leading to the recognition that such variation is within the expected range for a single species and that additional species such as *H. ergaster*, *H. georgicus* and *H. soloensis* can be accomodated within *H. erectus* (Baab, 2008); 6) a comparison of

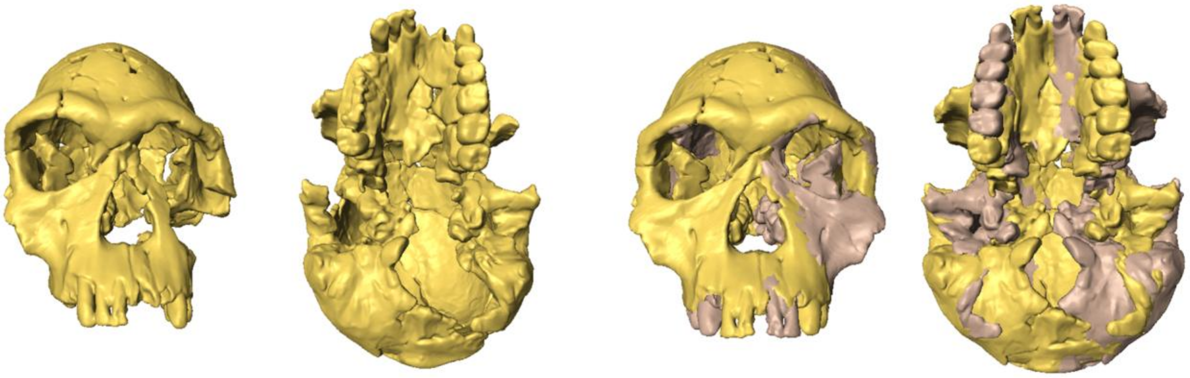

Figure 2. Virtual reconstruction and "retrodeformation" of KNM-ER 1813, cranium of *Homo habilis*. On the left are basal and frontal views of 1813, rendered from CT scan data of the original fossil. On the right, the digitally restored skull includes regions that were mirrored from left to right (and vice versa) as well as parts that were symmetrized by a newly developed process, which combines local retrodeformation with a global approach to non-linear symmetry restoration: the researcher indicates corresponding right and left landmarks in our Landmark Editor software and then defines a local neighborhood of fixed radius around each landmark. Based on deformation of right-left landmark pairs within the local neighborhood, new software estimates a local stretch that would restore symmetry. In a second step, a global least-squares optimization is applied to the local stretches and aligns the local planes of symmetry with a common midline plane. We assume the final symmetry of the result as a tight constraint, subject to which we maintain the distances between neighboring landmark points on the surface using the least-squares criterion. Lastly, the software restores those pieces of the cranium indicated by the researcher to be damaged or missing by reflecting the data from the other side of the specimen. (Research in progress by E. Delson, N. Amenta, S. Frost, D. Ghosh, F.J. Rohlf, W.E.H. Harcourt-Smith, L. Tallman and K. St-John).

scanned articulating tibial and talar surfaces using semi-landmark grids with the aim of distinguishing species and individuals (Harcourt-Smith *et al.*, 2008); and 7) an ongoing study of Old World monkey cranial shape change through time, combining a baseline molecular phylogeny with laser scans of extant and fossil species' crania, reconstruction of damaged fossils, inference of cranial shape at any point on the tree, and placement of fossils close to the most similar inferred shape (Delson *et al.*, in prep.).

Research underway by members of the NYCEP Morphometrics Group is aimed at reconstructing and visualizing the pattern and history of cranial shape variation in Old World monkeys and hominins, combining the above approaches with new ones to be discussed in this talk.

BAAB, K.L. (2008). The taxonomic implications of cranial shape variation in *Homo erectus*. Journal of Human Evolution 54: 827-847.

FROST, S.R., MARCUS, L.F., REDDY, D.P., BOOKSTEIN, F., DELSON, E. (2003). Cranial allometry, phylogeography and systematics of large bodied papionins (Primates: Cercopithecinae) inferred from geometric morphometric analysis of landmark data. Anatomical Record 275A: 1048-1072.

HARCOURT-SMITH, W.E., TALLMAN, M., FROST, S.R., WILEY, D.F., ROHLF, F.J., DELSON, E. (2008). Analysis of selected hominoid joint surfaces using laser scanning and geometric morphometrics: A preliminary report. In: Sargis, E.J., Dagosto, M. (eds) Mammalian Evolutionary Morphology: A Tribute to Frederick S. Szalay; Springer, Dordrecht, pp 373-383.

HARVATI, K., FROST, S.R., MCNULTY, K.P. (2004). Neanderthal taxonomy reconsidered: Implications of 3-D primate models of intra- and interspecific differences. Proceedings of the National Academy of Sciences, USA 101: 1147-1152.

MCNULTY, K.P., FROST, S.R., STRAIT, D.S. (2006). Examining affinities of the Taung child by developmental simulation. Journal of Human Evolution 51:274-296.

PONCE DE LEÓN, M.S., ZOLLIKOFER, C.P.E. (2001). Neanderthal cranial ontogeny and its implications for late hominid diversity. Nature 412: 534-538.

SINGLETON, M., MCNULTY, K.P., FROST, S.R., SODERBERG, J., GUTHRIE, E.H. (2010). Bringing up Baby: Developmental simulation of the adult cranial morphology of *Rungwecebus kipunji*. Anatomical Record 293: 388-401.

ZOLLIKOFER, C.P.E., PONCE DE LEÓN, M.S. (2005). Virtual Reconstruction: A Primer in Computer-Assisted Paleontology and Biomedicine. Wiley, New York. 288pp.

ZOLLIKOFER, C.P.E., PONCE DE LEÓN, M.S., LIEBERMAN, D.E., GUY, F., PILBEAM, D., LIKIUS, A., MACKAYE, H. T., VIGNAUD, P., BRUNET, M. (2005). Virtual cranial reconstruction of *Sahelanthropus tchadensis*. Nature 434: 755-759.

Carnivorous mammal faunas in the Paleogene of East Asia: Timing of faunal turnovers and geographical differences

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East Asia is known to have provided rich fossil evidences for Paleogene mammals. However, a large portion of the fossil remains has come from northern East Asia, such as Mongolia and Inner Mongolia of China. Information on mammal fossils from southern East Asia has been rare. During the past decade or so, intensive paleontological expeditions to Eocene localities in Southeast Asian countries such as Myanmar and Thailand have augmented the terrestrial mammalian fossil records from low-latitude East Asia (southern China and Southeast Asia). In addition, re-examination of carnivorous mammals from the late Eocene of Mongolia revealed the presence of species that are new taxa or are taxa previously unknown to the area. In this study, using updated information on the carnivorous mammal fossil records in the Paleogene of East Asia, we attempted to evaluate chronological changes and geographical (latitudinal) differences among various carnivorous mammal faunas.

In our analyses, approximately 60 faunas were included. They are grouped into three geographical regions: northern (Inner Mongolia of China, and Mongolia), middle (middle-latitude China), and southern (southern China, and southeast Asia) faunas (Fig. 1). The relative ages, or East Asian Land Mammal Ages, for most of the localities have been determined by Tsubamoto *et al.* (2004) using the Appearance Event Ordination Method based on the whole mammal faunal list of localities.

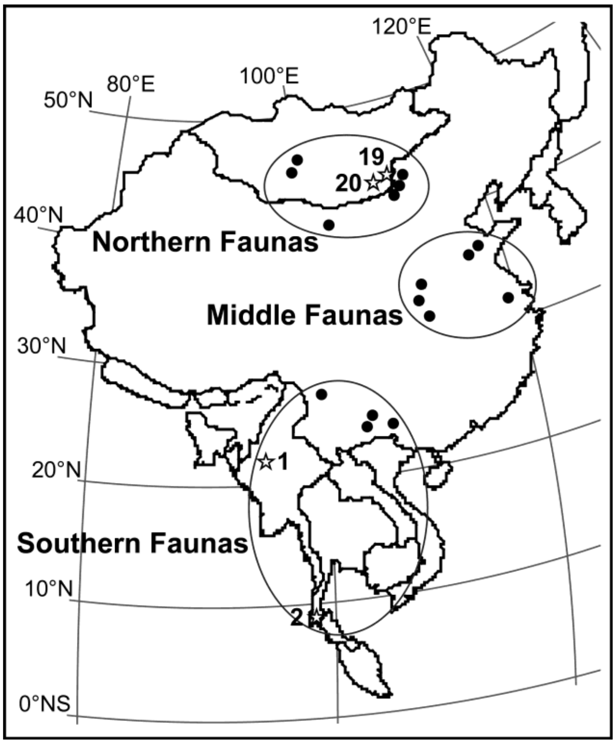

Figure 1. Distribution of the Paleogene mammalian faunas in East Asia. Only the middle to late Eocene localities are indicated (*i.e.*, Paleogene, early Eocene, and Oligocene localities are not shown). Localities mentioned in the text: 1, middle Eocene Pondaung (Myanmar); 2, late Eocene Krabi (Thailand); 19, Ergilin at Khoer Dzan (Mongolia); 20, Ergilin at Ergilin Dzo (Mongolia).

Mammalian faunal lists of all except four localities were compiled from the published data (e.g., Tsubamoto *et al.*, 2004 and cited therein; Peigné *et al.*, 2006). The exceptions are the middle Eocene Pondaung fauna and the late Eocene Krabi, Khoer Dzan, and Ergilin Dzo faunas; the occurrences of carnivorous mammals from these localities have been revised by adding the unpublished materials from recent expeditions. The Pondaung fauna comprises approximately 40 genera of mammals. Half of the carnivorous mammals are hyaenodontid creodonts: four genera of proviverrines and one hyaenaelurine. Seven carnivorans (carnivoramorphs sensu Wesley-Hunt and Flynn, 2005) have been also collected: one miacid, two amphicyonids, one arctoid, two nimravids, and one cf. stenoplesictid. The Krabi fauna consists of more than 25 genera of mammals, yielding carnivorans only (nimravid genera, one miacid, and two arctoids, one of which is a mustelid). The Khoer Dzan fauna includes more than 20 genera of mammals. The locality yields *Hyaenodon* species (hyaenodontid creodonts) of various body sizes, four carnivorans (two nimravids and two stenoplesictids), and one mesonychid. The Ergilian Dzo fauna consists of approximately 20 genera of mammals, among which *Hyaenodon* and three other genera of carnivorans (nimravid, stenoplesictid, and amphicyonid) have been found.

Carnivorous mammals in our comparison are from three orders: Carnivora (or Carnivoramorpha), Creodonta, and Mesonychia. In East Asia, mesonychians were at first more dominant than other carnivorous mammals, with carnivorans becoming dominant during the later part of the Paleogene. The carnivorans in the Paleocene were represented by the Viverravidae, and then the Miacidae appeared in the early Eocene. Southern East Asian faunas differ from the northern traditional Asian faunas in several respects. First, mesonychians were dominant until the late Eocene in the northern area, whereas in the southern area they decreased during the middle Eocene. Second, in the northern faunas hyaenodontid creodonts are *Hyaenodon* and its relatives, surviving until the end of the Oligocene, whereas hyaenodontids in the southern faunas are proviverrines of Indian affinities and a hyaenaelurine, becoming extinct during the late Eocene. Third, carnivorans were rare or absent before the late Eocene in the northern area, while in the southern area they had been common elements of the fauna since the middle Eocene.

Although there is a general trend of faunal turnovers from mesonychians to carnivorans in the Paleogene of East Asia, the timings of first and last appearances of the carnivorous mammal groups differ from area to area. The turnover occurred earlier in the lower latitude faunas than in the higher latitude ones. Such latitudinal differences in the timing of faunal turnovers have been known also in large herbivorous mammals (perissodactyl to artiodactyl transition; Tsubamoto *et al*., 2004). The timing of the faunal turnover is not the same across different mammals, however: Meng and McKenna (1998) suggested that the turnover of perissodactyl-dominant to rodent/lagomorph-dominant faunas occurred at the Eocene/Oligocene boundary in northern East Asia, whereas our comparison suggested that the carnivorans had already started to replace the others in the late Eocene.

Carnivoran species from the Paleogene of East Asia tend to be cosmopolitan, suggesting an interchange or radiation across East Asia. In contrast, hyaenodontid creodonts suggest that the faunas contain elements of geographically different origins: hyaenodontids from the southern faunas have relatives in India and Africa (Egi *et al*., 2005; Borths *et al*., 2010; but there are differing opinions, e.g., Peigné *et al*., 2007), while those from the northern faunas (e.g., *Hyaenodon*) are genera known from North America and Europe. In East Asia, latitudinal differences in composition of terrestrial carnivorous mammalian faunas had been present at least since the middle Eocene, well before the formation of present-day biogeographical regions.

Borths, M., Seiffert, E., Goodenberger, K., Simons, E. (2010). The oldest Fayum creodont: Dental and humeral morphology of a new proviverrine hyaenodontid from the earliest late Eocene of Egypt. Journal of Vertebrate Paleontology – Society of Vertebrate Paleontology, Program and Abstracts Book, 2010, 63A.

Egi, N., Holroyd, P.A., Tsubamoto, T., Aung-Naing-Soe, Takai, M., Ciochon, R.L. (2005). Proviverrine hyaenodontids (Creodonta: Mammalia) from the Eocene of Myanmar and a phylogenetic analysis of the proviverrines from the Para–Tethys area. Journal of Systematic Palaeontology 3: 337-358.

Meng, J., McKenna, M.C. (1998). Faunal turnovers of Paleogene mammals from the Mongolian Plateau. Nature 394: 364-367.

Peigné, S., Chaimanee, Y., Yamee, C., Srisuk, P., Marandat, B., Jaeger, J.-J. (2006). A new member of the Mustelida (Mammalia: Carnivora) from the Paleogene of Southeast Asia. Journal of Vertebrate Paleontology 26: 788-793.

Peigné, S., Morlo, M., Chaimanee, Y., Ducrocq, S., Soe-Thura-Tun, Jaeger, J.-J. (2007). New discoveries of hyaenodontids (Creodonta, Mammalia) from the Pondaung Formation, middle Eocene, Myanmar: Paleobiogeographic implications. Geodiversitas 29: 441-458.

Tsubamoto, T., Takai, M., Egi, N. (2004). Quantitative analysis of biogeography and faunal evolution of middle to late Eocene mammals in East Asia. Journal of Vertebrate Paleontology 24: 657-667.

Wesley-Hunt, G.D., Flynn, J.J. (2005). Phylogeny of the Carnivora: Basal relationships among the Carnivoramorpha, and assessment of the position of “Miacoidea” relative to Carnivora. Journal of Systematic Palaeontology 3: 1-28.

Origins of early Eocene Hippomorpha of Europe and North America

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Owing to its rich fossil record, the evolution of hippomorpha is well documented and has become a prime example for evolution in general. Nonetheless many questions are still unanswered, especially those concerning the early phase of the development of this taxon occurring mainly in the Eocene. It is widely accepted that Equidae as well as Palaeotheriidae are nested within Hippomorpha, but the particular phylogenetic relationships for the very early forms are not clear. In addition, their ancestor is unknown and controversial (Hooker, 1994; Franzen, 1995). Connected to this is the question about the taxonomic and paleogeographic origin of Hippomorpha in general. In this study, those questions will be addressed by investigating the external skull morphology as well as the endocranial cavity. Brain cases of various early Hippomorpha or potential ancestral genera from North America, Europe, and Asia (*Cardiolophus, Eurohippus parvulus, Hallensia matthesi, Hyracotherium leporinum, Phenacodus, Pliolophus vulpiceps*, *Propalaeotherium voigti, Radinskya yupingae*) are scanned with micro-CT. Subsequently, their endocranial cavity is virtually reconstructed in order to compare the different taxa. The aim of this study is also to analyse the endocranial anatomy of European Hippomorpha and to compare it to the paleoneurologic studies of North American Hippomorpha as established by Edinger (1948) and Radinsky (1976). The first results of this study are presented here (Fig. 1), and will help to learn more about the taxonomical and phylogenetic relationships between Equidae and Palaeotheriidae, as well as between European and North American Eocene Equidae.

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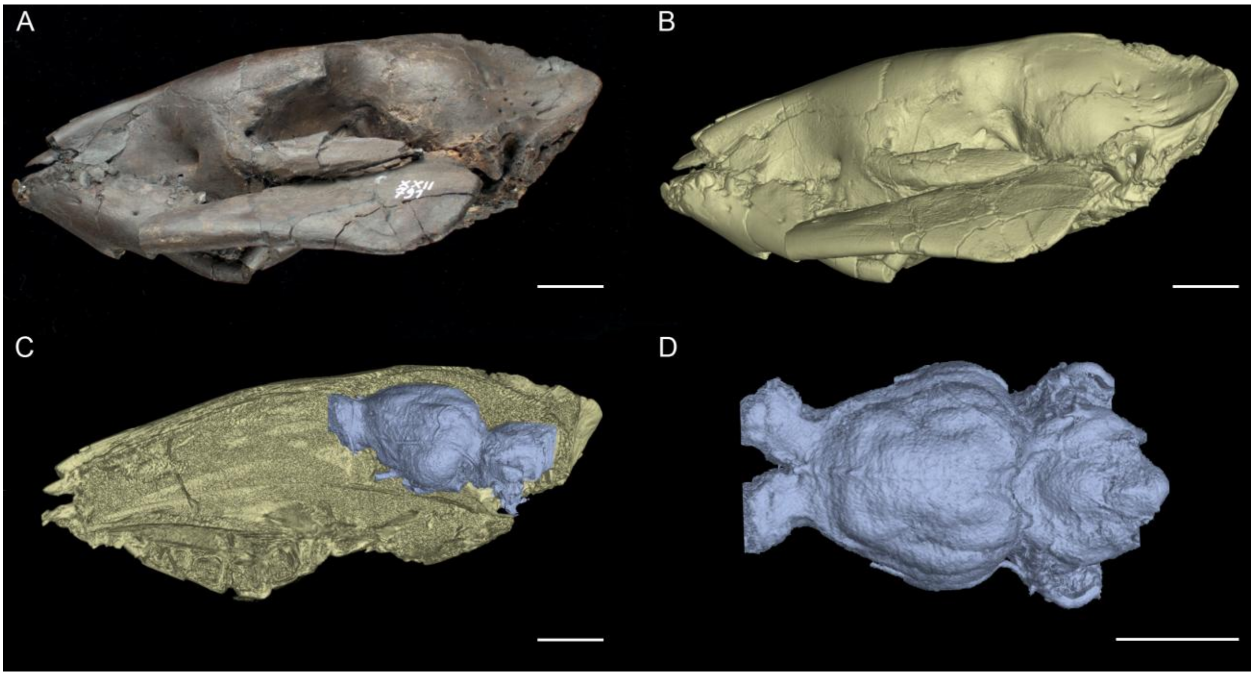

Figure 1. *Hallensia matthesi* (Geiseltalmuseum XXII791). A) Original fossil specimen. B) Virtual skull model reconstructed through micro-CT scanning. C) Reconstructed cranial endocast (blue) in its natural position in the skull of *Hallensia*. D) Dorsal view of the reconstructed cranial endocast. Scale bar 2 cm.

EDINGER, T. (1948). Evolution of the Horse Brain. Memoir 25, Geological Society of America; Waverly Press, Baltimore, 177pp.

FRANZEN, J.L. (1995). Die Equoidea des europäischen Mittzeleozäns. Hallesches Jahrbuch für Geowissenschaften, Reihe B: Geologie, Paläontologie, Mineralogie, 17: 31-45.

HOOKER, J.J. (1994). The beginning of the equoid radiation. Zoological Journal of the Linnean Society, 112: 29-63.

RADINSKY, L. (1976). Oldest horse brains: More advanced than previously realized. Science 194: 626-627.

New data on the early Eocene frogs from Vastan, Gujarat, India

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The lower Eocene (Ypresian) Cambay Shale Formation at Vastan Lignite Mine, located north-east of Surat in Gujarat, western India, has recently received particular attention for its rich vertebrate assemblage, including the earliest birds (Mayr *et al.*, 2007) and modern mammals of the Indian subcontinent (Rana *et al.*, 2004, 2005, 2008; Bajpai *et al.*, 2005; Smith *et al.*, 2007; Rose *et al.*, 2006, 2008, 2009; Kumar *et al.*, 2010). Among the herpetological remains discovered, snakes (Rage *et al.*, 2008) and lizards (Prasad and Bajpai, 2008) have already been described. Amphibians have also been reported (Bajpai and Kapur, 2008; Folie *et al.*, 2008).

About 380 well-preserved, three-dimensional isolated frog remains such as ilia and vertebrae have been found. No remains of caudates nor caecilians are known from Vastan; all of the amphibian remains belong to anurans. Four anuran taxa are recognized: the most abundant is a particular frog, characterized by a strange pattern of inter-vertebral articulation similar to a zygosphene-zygantrum complex, that represents the oldest record of the "archaeobatrachian" Bombinatoridae; a "mesobatrachian" frog attributed to the genus *Eopelobates* (Pelobatidae) and resembling the middle Eocene *E. wagneri* from Messel (Wuttke, 1992) is identified based on a single nearly complete ilium; and an abundant ranid (*sensu lato*) and a rhacophorid are the earliest record of both families, illustrating the "neobatrachian" Ranoidea. The most famous Indian fossil frog, *Indobatrachus pusillus* from the Maastrichtian of Bombay, seems not present at Vastan.

The oldest mentioned occurrence of pelobatids is the Maastrichtian of North America (Estes and Sanchiz, 1982), and the earliest confirmed pelobatids are in the middle Eocene of Europe and North America (Rocek and Rage, 2000; Henrici and Haynes, 2006). The oldest record of the bombinatorids is in the Miocene of Germany (Sanchiz and Schleich, 1986). The other two families have not recorded in Europe before the late Eocene (Holman and Harrison, 1999). A ranoid frog has been mentioned from the Cenomanian of Africa (Baez and Werner, 1996). Thus the pelobatid suggests Laurasian affinities, whereas the ranoids and maybe the bombinatorid support a Gondwanan origin, with dispersal to Eurasia via Greater India, as suggested by molecular phylogenies (Bossuyt *et al.*, 2006).

Baez, A.M., Werner, C. (1996). Presencia de anuros Ranoideos en el Cretacico de Sudan. Ameghiniana 33: 460.

Bajpai, S., Kapur, V.V. (2008). Earliest Cenozoic frogs from the Indian subcontinent: Implications for out-of-India hypothesis. Journal of the Palaeontological Society of India 53: 65–71.

Bajpai, S., Kapur V.V., Das D.P., Tiwari, B.N., Saravanan, N., Sharma, R. (2005). Early Eocene land mammals from Vastan Lignite Mine, District Surat (Gujarat), western India. Journal of the Palaeontological Society of India 50: 101–113.

Bossuyt, F., Brown, R.M., Hillis, D.M., Cannatella, D.C., Milinkovitch, M.C. (2006). Phylogeny and biogeography of a cosmopolitan frog radiation: Late Cretaceous diversification resulted in continent-scale endemism in the family Ranidae. Systematic Biology 55: 579–594.

Estes, R., Sanchiz, B. (1982). New discoglossid and palaeobatrachid frogs from the Late Cretaceous of Wyoming and Montana, and a review of other frogs from the Lance and Hell Creek Formations. Journal of Vertebrate Paleontology 2: 9-20.

Folie, A., Rana, R.S., Sahni, A., Rose, K.D., Smith, T. (2008). Frogs (Anura) from the early Eocene of Vastan Lignite Mine, Gujarat, India. Journal of Vertebrate Paleontology 28: 79A

Henrici, A.C., Haynes, S.R. (2006). *Elkobatrachus brocki*, a new pelobatid (Amphibia: Anura) from the Eocene Elko Formation of Nevada. Annals of Carnegie Museum 75: 11–35.

Holman, J.A., Harrison, D.L. (1999). *Rana* (Amphibia: Ranidae) from the upper Eocene (MP17a) Hordle Cliff Locality, Hampshire, England. Palaeovertebrata 28: 47–51.

Kumar, K., Rose, K.D., Rana, R.S., Singh, L., Smith, T., Sahni, A. (2010). Early Eocene artiodactyls (Mammalia) from India. Journal of Vertebrate Paleontology 30: 1245–1274.

Mayr, G., Rana, R.S., Sahni, A., Smith, T. (2007). Oldest fossil avian remains from the Indian subcontinental plate. Current Science 92: 1266–1269.

Prasad, G.V.R., Bajpai, S. (2008). Agamid lizards from the early Eocene of western India: Oldest Cenozoic lizards from South Asia. Palaeontologia Electronica 11: 19pp.

Rage, J.-C., Folie, A., Rana, R.S., Singh, H., Rose, K.D., Smith, T. (2008). A diverse snake fauna from the early Eocene of Vastan Lignite Mine, at Gujarat, India. Acta Palaeontologica Polonica 53: 391–403.

Rana, R.S., Kumar, K., Escarguel, G., Sahni, A., Rose, K.D., Smith, T., Singh, H., Singh, L. (2008). An ailuravine rodent from the lower Eocene Cambay Formation at Vastan, western India, and its palaeobiogeographic implications. Acta Palaeontologica Polonica 53: 1-14.

Rana, R.S., Kumar, K., Singh, H. (2004). Vertebrate fauna from the subsurface Cambay Shale (Lower Eocene), Vastan Lignite Mine, Gujarat, India. Current Science 87: 1726–1732.

Rana, R.S., Singh, H., Sahni, A., Rose, K.D., Saraswati, P.K. (2005). Early Eocene chiropterans from a new mammalian assemblage (Vastan lignite mine, Gujarat, western peninsular margin): Oldest known bats from Asia. Journal of the Palaeontological Society of India 50: 93–100.

Rocek, Z., Rage, J.-C. (2000). Tertiary Anura of Europe, Africa, Asia, and North America. In: Heatwole, H., Carroll, R.L. (eds) Amphibian Biology, vol. 4 Palaeontology. Surrey Beatty and Sons, Shipping Norton, pp 1332–1387.

ROSE, K.D., DELEON, V.B., MISSIAEN, P., RANA, R.S., SAHNI, A., SINGH, L., SMITH, T. (2008). Early Eocene lagomorph (Mammalia) from western India and the early diversification of Lagomorpha. Proceedings of the Royal Society of London B 275: 1203–1208.

ROSE, K.D., RANA, R.S., SAHNI, A., KUMAR, K., MISSIAEN, P., SINGH, L., SMITH, T. (2009). Early Eocene primates from Gujarat, India. Journal of Human Evolution 56: 366–404.

ROSE, K.D., SMITH, T., RANA, R.S., SAHNI, A., SINGH, H., MISSIAEN, P., FOLIE, A. (2006). Early Eocene (Ypresian) continental vertebrate assemblage from India, with description of a new anthracobunid (Mammalia, Tethytheria). Journal of Vertebrate Paleontology 26: 219–225.

SANCHIZ, B., SCHLEICH, H.H. (1986). Erstnachweis der Gattung *Bombina* (Amphibia: Anura) in Untermiozän Deutschlands. Mitteilungen Bayerischen Staatssammlung Paläontologie Historische Geologie 26: 41–44.

SMITH, T., RANA, R., MISSIAEN, P., ROSE, K.D., SAHNI, A., SINGH, H., SINGH, L. (2007). High bat (Chiroptera) diversity in the early Eocene of India. Naturwissenschaften 94: 1003–1009.

WUTTKE, M. (1992). Amphibia at Lake Messel: Salamanders, toads, and frogs. In: Schaal, S., Ziegler, W. (eds) Messel: An Insight into the History of Life and of the Earth. Clarendon Press, Oxford, pp 95-98.

Strepsirrhine or haplorhine?

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In determining whether Eocene primate *Darwinius* from Grube Messel (Franzen *et al.*, 2009) is a strepsirrhine or not, we have to base arguments on living strepsirrhines such as Lemuriformes and Lorisiformes (which includes Galagidae) in order to avoid a circulus vitiosus. The reason is that in the suborder Strepsirrhini as defined by Hoffstetter (1977), Adapiformes – the superfamily *Darwinius* belongs to – is already included. We should also avoid using characters as Seiffert *et al.* (2009: 1120) and Williams *et al.* (2010:569) did, because their method does not distinguish between advanced (synapomorphic) and primitive (plesiomorphic) characters, between characters that belong to the same functional complex and those that evolve independently. What then is a character? A character is a feature regarded as typical for a certain systematic unit. Biologically, however, characters do not develop for systematic purposes. Biologically, a character is an anatomical construction or part of one that helps an organism to survive (Franzen, 2010: 81). Therefore, it is necessary to know the function(s) of a character in order to determine the direction and level of its phylogenetic development, and to decide whether it is plesio- or apomorphic. Consequently, splitting a functioning system and counting and treating its various characters statistically in order to reveal systematic units and their evolution is biologically questionable. Even worse, this method opens the door for manipulation, because one functioning unit can be split into as many characters as needed to support a favoured hypothesis.

Investigating adapiforms and living strepsirrhines under these preconditions has led to new insights. One concerns the incisor system. A central-incisal diastema and a toothcomb represent character complexes unique for all living strepsirrhines. But don't they belong to the same functional complex, the frontal dentition? In order to understand whether diastema and toothcomb are functionally correlated (e.g., by interlocking), I measured and compared 33 skulls of extant strepsirrhines. The results show no correlation (Fig. 1). It is obvious that both represent synapomorphies that are functionally independent of each other. A third independent synapomorphy of living strepsirrhines is the grooming claw on the second toe. In the form and function of the astragalus, *Darwinius* belongs to the haplorhines, but contrary to Gebo (1986) this functional complex is not synapomorphic but plesiomorphic (Williams *et al.*, 2010; Gingerich *et al.*, 2010). The structure of the middle and inner ear (MacPhee and Cartmill, 1986; Lebrun *et al.*, 2010) is not preserved in *Darwinius*. In any

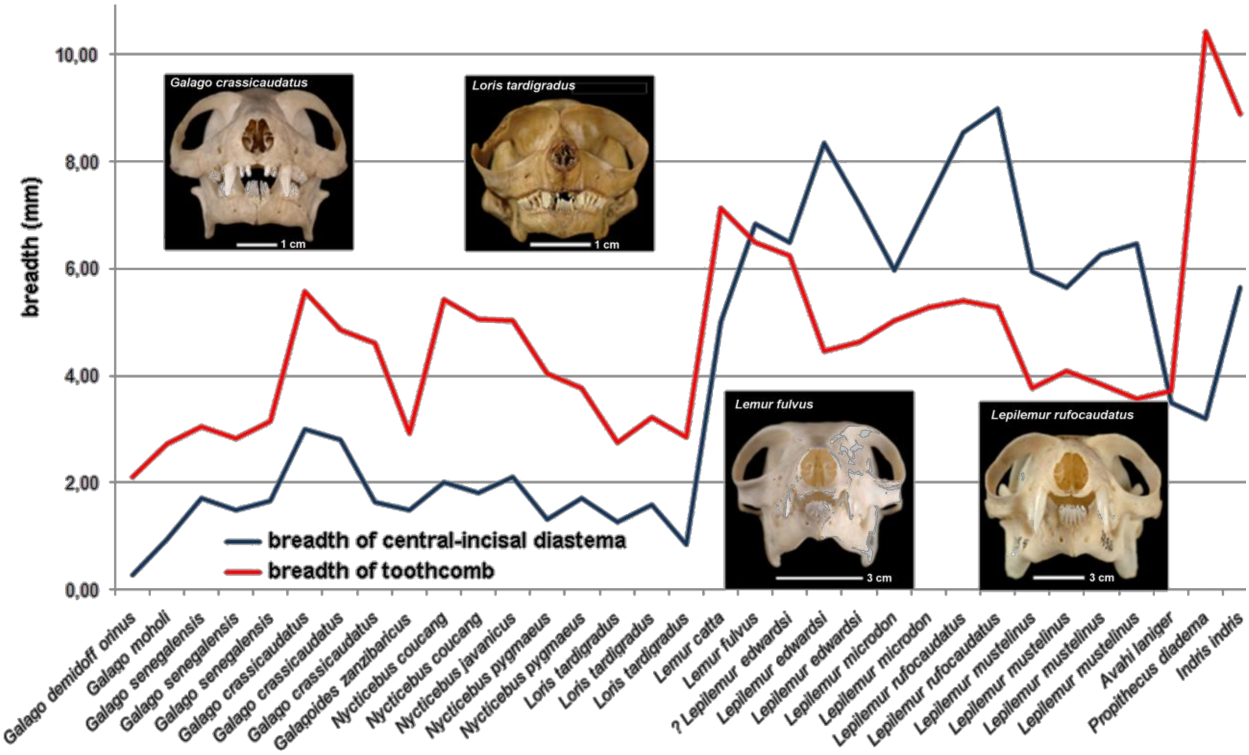

Figure 1. Breadth of central-incisal diastema in the upper jaw versus breadth of toothcomb in the mandible in extant lemuriforms. Except for *Lemur fulvus* and *Avahi laniger* the breadths of central-incisal diastema and toothcomb do not correspond with each other. Consequently, both appear not to be functionally correlated. Diagram: author.

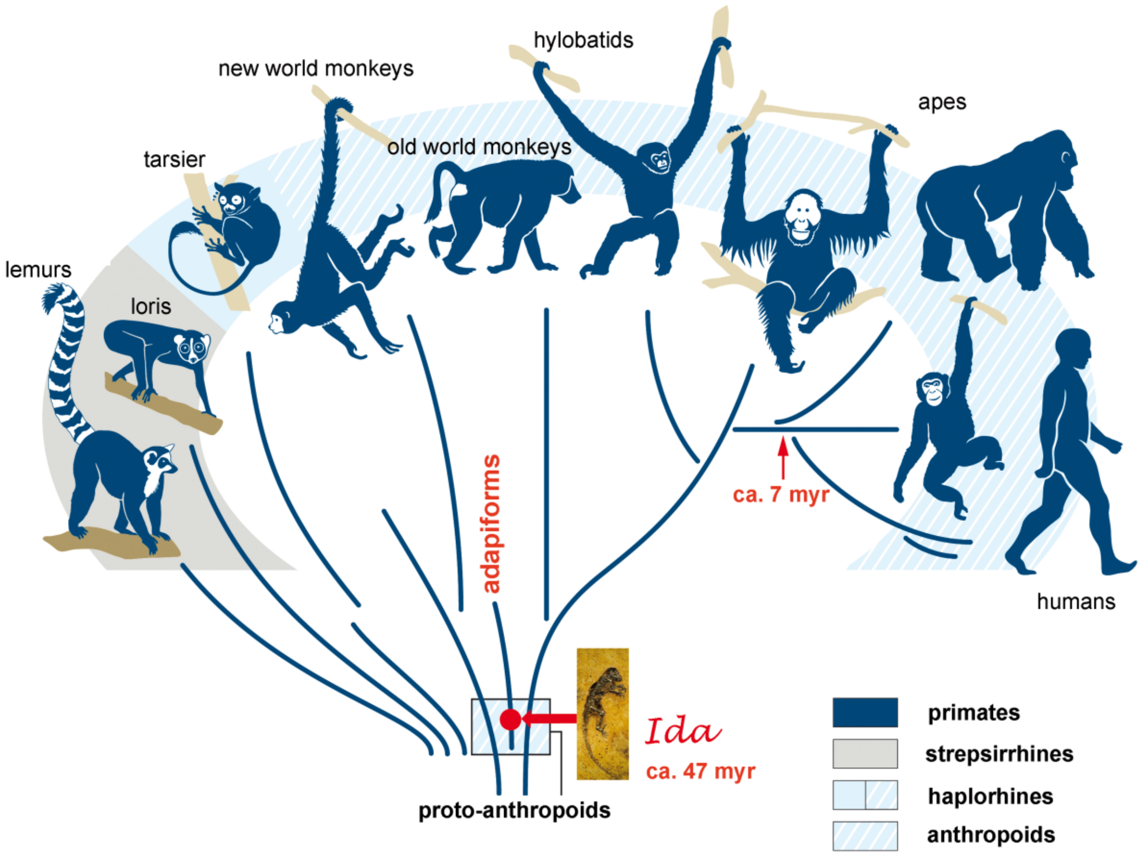

Figure 2. Position of “Ida” (*Darwinius masillae*) in the primate phylogenetic tree. Here in context with *Darwinius*, the adapiforms shift from strepsirrhines to haplorhines. Graphics: Stelzner Illustration and author.

case, the three synapomorphies mentioned above must have been present before the lemuriform clade radiated into lemurids, galagids and lorisids. This had occurred at the latest when lemurids arrived on Madagascar by island hopping or rafting. An estimate based on a molecular clock dates the initial radiation of the lemuriform clade at approximately 62 my (Yoder and Yang, 2004). This would be a minimum age for the invasion of Madagascar. Consequently, a central-incisal diastema, a toothcomb, and a grooming claw should be present in *Darwinius* and adapiforms if they are strepsirrhines. Considering *Darwinius* and adapiforms as stem strepsirrhines would require deriving the toothcomb structure of extant strepsirrhines from that of the frontal dentition of *Darwinius* and adapiforms as a whole, which is hard to imagine. Therefore, I conclude that *Darwinius* and adapiforms are not strepsirrhines, not even stem strepsirrhines (Fig. 2). In 1994, I had already regarded adapiforms as an early offshoot of protoanthropoids once living in sub-Saharan Africa (Franzen, 1994), although at that time no protoanthropoids were known from that area and time period. This, however, may have changed by the discovery of *Namaia bogenfelsi* from the early middle Eocene of Namibia (Pickford *et al*., 2008).

Franzen, J.L. (1994). The Messel primates and anthropoid origins. In: Fleagle, J.F., Kay, R.F. (eds) Anthropoid Origins. Plenum Press, New York, pp 99-122.

Franzen, J.L. (2010). The Rise of Horses: 55 Million Years of Evolution. The Johns Hopkins University Press, Baltimore, 211pp.

Franzen, J.L., Gingerich, P.D., Habersetzer, J., Hurum, J.H., Koenigswald, W.v., Smith, B.H. (2009). Complete primate skeleton from the middle Eocene of Messel in Germany: Morphology and paleobiology. PLoS ONE 4 (5): 1-27.

Gebo, D. (1986). Anthropoid origins – The foot evidence. Journal of Human Evolution 15: 421-430.

Gingerich, P.D., Franzen, J.L., Habersetzer, J., Hurum, J.H., Smith, B.H. (2010). *Darwinius masillae* is a haplorhine – Reply to Williams *et al.* (2010). Journal of Human Evolution 59: 574-579.

Hoffstetter, R. (1977). Primates: Filogenia e historia biogeographica. Studia Geologicos 13: 211-253.

Lebrun, R., León, M. de, Tafforeau, P., Zollikofer, C. (2010). Deep evolutionary roots of strepsirrhine primate labyrinthine morphology. Journal of Anatomy 216: 368-380.

MacPhee, R.D.E., Cartmill, M. (1986). Basicranial structures and primate systematics. In: Swindler, D.R., Erwin, J. (eds) Comparative Primate Biology. 1: Systematics, Evolution and Anatomy. Alan R. Liss, New York, pp 219-275.

Pickford, M., Senut, B., Morales, J., Mein, P., Sanchez, I.M. (2008). Mammalia from the Lutetian of Namibia. Memoir of the Geological Survey of Namibia 20: 465-514.

Seiffert, E.R., Perry, J.M.G., Simons, E.L., Boyer, D.M. (2009). Convergent evolution of anthropoid-like adaptations in Eocene adapiform primates. Nature 461: 1118-1121.

Williams, B.A., Kay, R.F., Kirk, E.C., Ross, C.F. (2010). *Darwinius masillae* is a strepsirrhine – A reply to Franzen *et al.* (2009). Journal of Human Evolution 59: 567-573.

Yoder, A.D., Yang, Z. (2004). Divergence dates for Malagasy lemurs estimated from multiple gene loci: Geological and evolutionary context. Molecular Ecology 13: 757-773.

Palaeopathology of *Darwinius masillae* (Mammalia, Primates)

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47 Myr ago a young female primate fell from a tree, broke her right wrist, drowned, and ended up in the abyss of Eocene Lake Messel, where she became fossilized in unique quality. This dated scenario is based on the external morphology of the primate and 2D radiographs (Franzen *et al.*, 2009: 15; Franzen, 2010: 19–23). However, in palaeopathology a major focus is to distinguish between fractures that occurred during lifetime from those that resulted from post-mortem compaction. The only way to distinguish between these possibilities is by determining whether callus had developed.

Therefore, we applied micro-CT analyses of the structure of the bones, particularly of those parts that were embedded in polyester during transfer preparation. Through the existence of a large excrescence of bone overgrowing most of the wrist as well as the proximal metacarpals and distal radius and ulna, we confirmed that the right wrist had been fractured. This can be seen in a film sectioning through the

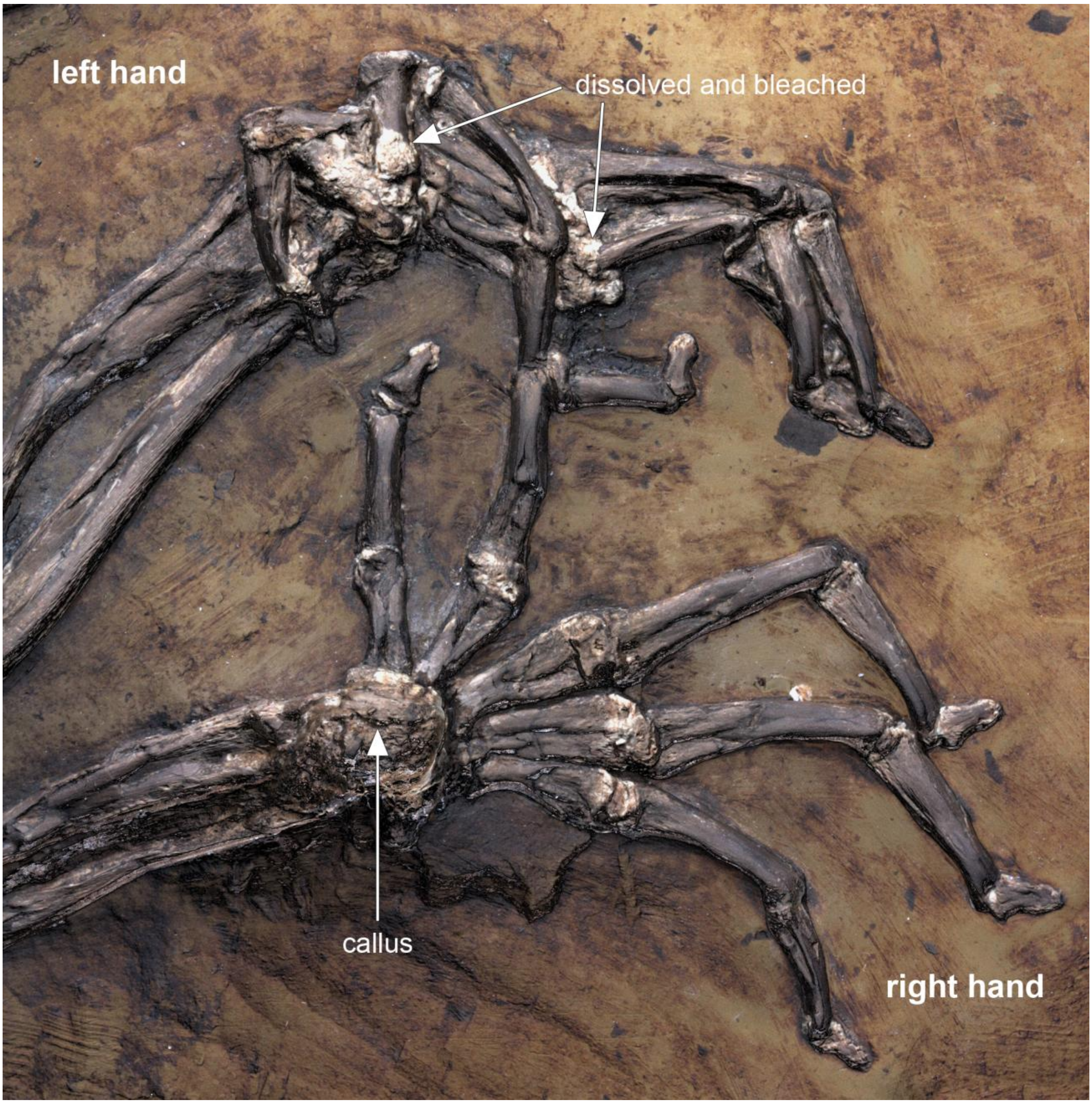

Figure 1. Dorsal view of both hands of “Ida” (*Darwinius masillae*). Strong development of callus on the wrist of the right hand indicates that this was broken in vivo (below). The left hand (above) was not affected.– Photo: Øyvind Hammer, Natural History Museum Oslo.

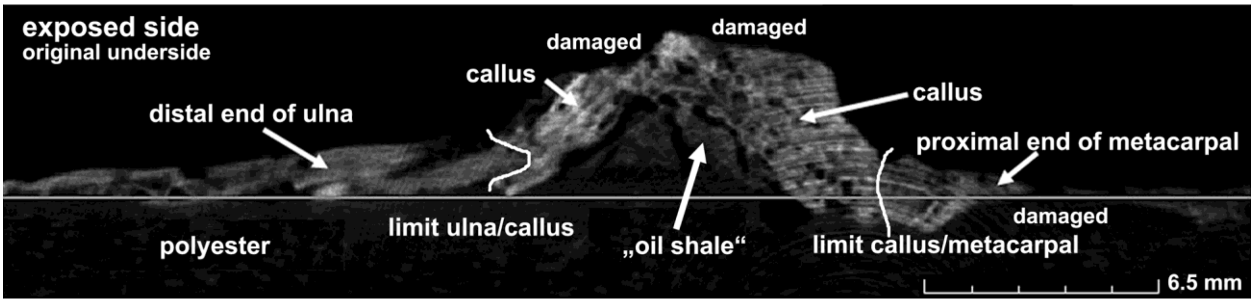

Figure 2. Micro-CT cross section through the right hand. The fine horizontal white line approximates the border between the exposed side (original underside) above and the polyester plate below. The callus bridges the gap between the distal zeugopodium and the metacarpals. Obviously, the carpals were not yet ossified. They are therefore not identifiable. The whole hand is crippled. At some places the specimen seems to be damaged in the course of preparation. Micro-CT: Jörg Habersetzer, Senckenberg Forschungsinstitut Frankfurt am Main.

region of the wrist from dorsal to ventral. This film and additional micro-CTs leave no doubt that the first and only specimen of *Darwinius masillae* suffered from a severe trauma to its right forearm that affected the wrist and the distal radius and ulna, and that lead to an excessive development of callus (Figs. 1–2). Evidently, the young primate survived the accident for more than one month: human pathology demonstrates that such an amount of time is needed for the development of callus (Thomas, 1992: 298). That the female survived the accident is also proven by the fact that, in contrast to the carpals, the tarsals were already more or less ossified when she died. This is possible only if a considerable time span passed during which the callus formed on the right hand. This means that the wrist still consisted more or less of cartilage when the young primate suffered a mishap. At this time, the carpals were developed only as cores, which became overgrown by the callus; their outline is therefore not identifiable. Micro-CT of the whole skeleton revealed that the broken hand was the only trauma that occurred during life. Its consequences, however, were severe. The metacarpals were rendered immovable, and the right hand was seriously crippled (Fig. 2). *Darwinius* was obviously no longer able to climb and live in trees. Forced to stay on the ground, the animal was exposed to the same dangers as other ground-dwelling animals, such as occasional post-volcanic exhalations, particularly of carbon dioxide. *Darwinius* got into such a layer of poisonous gas, perhaps while drinking, lost consciousness, fell into the water, drowned, and drifted as a cadaver out into Eocene Lake Messel. There, the young primate sank to the bottom, where it became fossilized under very calm anoxic conditions.

The scenario developed above is, of course, a hypothesis. At first sight, other hypotheses might appear possible. For example, the hand could have been broken in some other, less traumatic kind of accident, although it is highly questionable that this would result in such an amount of callus. Also, primates are known today to climb with broken limbs, though ones that eventually healed (e.g., Currey, 2006). In the case of *Darwinius*, however, the hand was not just broken, but became seriously crippled, making it impossible for *Darwinius* to climb and live in trees. There are also alternative hypotheses as to why Lake Messel became a trap for vertebrates. Koenigswald *et al.* (2004) thought that it was not the air but the epilimnion that was poisoned by cyanobacteria from time to time during seasonal blooms. But this hypothesis does not explain why flying organisms are so abundant among the Messel fossils, and why low-flying bats are far more frequent than high-flying ones. Neither does this explain why layers paved with fish, which should occur under such conditions, have never been discovered during decades of excavation. Finally, this does not explain why primate specimens in particular are rare at Messel, even though a rain forest of tropical character existed as an optimal biotope in the surroundings.

Currey, J.D. (2006). Bones: Structure and Mechanics. Princeton University Press, Princeton and Oxford, 436 pp.

Franzen, J.L (2010). *Darwinius masillae*. Darwins Halbaffe und die Primatenfunde aus der Grube Messel. Natur und Museum 140 (1/2): 12-29.

Franzen, J.L., Gingerich, P.D., Habersetzer, J., Hurum, J.H., Koenigswald, W.v., Smith, B.H. (2009). Complete primate skeleton from the middle Eocene of Messel in Germany: Morphology and paleobiology. PLoS ONE 4 (5): 1-27, e5723.

Koenigswald, W.v., Braun, A., Pfeiffer, T. (2004). Cyanobacteria and seasonal death: A new taphonomic model for the Eocene Messel lake. Paläontologische Zeitschrift 78 (2): 417-424.

Thomas, C. (1992). Histopathologie. Lehrbuch und Atlas für die Kurse der allgemeinen und speziellen Pathologie. 11th Edition; Schattauer, Stuttgart, New York, 387pp.

A short account on the Eocene fish fauna from Huadian, Jilin Province, China

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The vertebrate fossil site Huadian, Gonglangtou, is situated in the People's Republic of China, Jilin Province. Vertebrates have been found in the Paleogene oil-shale sediments of the Huadian Formation. The first detailed report on the vertebrate fossils is that of Zhang *et al.* (1986).

During new field work in the years 2006 to 2009 it was possible to visit the mines for some weeks together with colleagues of Jilin University, Changchun, and to collect vertebrate specimens, including fishes, reptiles (Smith *et al.*, 2011), bird eggs and mammals. The mammals are represented mainly by erinaceids, soricids, and rodents. The tarsiiform primate *Asiomomys*, which was described by Beard and Wang (1991), suggests an age of the Gonglangtou fauna slightly younger than early Uintan, probably corresponding to the late Uintan, or late middle Eocene. This age estimation is supported by the anatomy of the other small mammals (Wang and Li, 1990). Wang *et al.* (2005) interpreted the fossiliferous oil-shale units as representing a semi-deep to deep lacustrine environment.

COMPOSITION OF THE HUADIAN FISH FAUNA

Along with many other fossils, the Huadian mine has yielded fish remains which generally consist of isolated bones. The first mention of the fishes from the Huadian Formation was made by Zhou and Sun (1985), who reported the occurrence of Amiiformes, Cypriniformes (represented by Catostomids), and Clupeiformes. Later, Chang *et al.* (2001) figured the pharyngeal bone-bearing teeth of an undetermined catostomid from Huadian. The same bone was again figured by Chang and Chen (2008) in their review of the fossil Cypriniformes from China.

Although we have not identified any bone of Clupeiformes among the examined material from Huadian, we could identify at least three taxa.

1) An amiiforme which clearly belongs to the genus *Cyclurus* Agassiz, as undoubtedly shown by a lower jaw exhibiting on its mesial surface coronoids bearing blunt teeth. This taxon is represented by many isolated cephalic bones: opercula, a frontal, maxillaries, dentaries, a gular, etc., and an isolated scale.

2) A cypriniforme belonging to the catostomids, as demonstrated by an operculum showing a typical antero-dorsal process, which is strongly projected dorsally, and an isolated pharyngeal bone bearing about 50 teeth.

3) A perciforme, which is represented by isolated fin spines and a small preoperculum ornamented by some forward-oriented spines, as in percichthyids and moronids.

PALAEOECOLOGICAL SIGNIFICANCE OF THE HUADIAN FISH FAUNA

According to the studied material, the fish fauna from Huadian is undoubtedly a lacustrine one, as demonstrated by the occurrence of the genus *Cyclurus* Agassiz and of catostomids. Additionally, it is oligospecific, as only three taxa could be identified. The small number of taxa is reminiscent of the situation known in several fossiliferous lacustrine localities of the European Palaeocene and Eocene, such as Menat (Central France, Palaeocene: three taxa according to Gaudant, 1979), Eckfeld (Germany, middle Eocene: four taxa according to Micklich and Wuttke, 1988), Kutschlin (upper Eocene, Czech Republic: four taxa according to Reuss, 1844; von Meyer, 1851), Geiseltal (Germany: five taxa according to Voigt, 1934; Jerzmanska, 1977; Gaudant and Haubold, 1995) and Messel (Germany: eight taxa according to Kinkelin, 1884; Andreae, 1895; Weitzel, 1933; Micklich, 1978, 1985; Gaudant and Micklich, 1990; Micklich and Klappert, 2001).

A similar situation is known in the middle Eocene of British Columbia, where Wilson (1977) identified five taxa at Driftwood Creek and in the surroundings of Princeton, and four at Horsefly Mine that he had personally excavated.

PALAEOBIOGEOGRAPHICAL ASPECTS OF THE HUADIAN FISH FAUNA

Among the identified taxa, at least one (a catostomid) suggests a close trans-Pacific relationship with the North American fish fauna, where this family is widespread throughout the whole continent. However, this family has still living representatives in recent freshwaters of Eastern Siberia (Berg, 1948) and in the Yangtse drainage (Chang *et al.*, 2001). Additionally, it has been widely distributed in Central Asia since Eocene times, as illustrated by Hussakof (1932), who figured two opercula from the Eocene (Ulan Shireh beds) of Inner Mongolia, and Sytchevskaya (1986), who described isolated pharyngeal teeth from the Zaissan depression (Eastern Kazhakstan), as well as articulated skeletons from the Vladivostok region.

The genus *Cyclurus* Agassiz has a typical laurasiatic distribution (Grande, 1998). Additionally to Huadian, it is present in at least two other localities of China – in the late Palaeocene or early Eocene of Shandong Province and in the middle Eocene of Hunan Province (Chang *et al.*, 2010) – and in the Palaeocene and Eocene of Western Europe (Menat, Messel, Eckfeld, Geiseltal, Kutschlin, etc.), the Eocene of Southeast Kazakhstan and of Central China, the upper Palaeocene of the Southern Gobi desert (Mongolia), the upper Cretaceous of Alberta (Canada), and the middle Eocene of the Green River Formation (Wyoming, USA).

CONCLUSION

Our temporary work in Jilin, Huadian, has shown that some coal mines of Gonglangtou and its surroundings contain many well-preserved vertebrate remains. They offer a limited but mentionable potential for palaeobiological and taxonomical research of fossil fishes and other vertebrates. A sustained palaeontological research programme may help increase the presently known biodiversity of the Huadian Fm oil shales.

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ANDREAE (1895). Beiträge zur Kenntniss der fossilen Fische des Mainzer Beckens. Abhandlungen der senckenbergischen naturforschenden Gesellschaft 18: 351-365.

BEARD, K.C., WANG, B.Y. (1991). Phylogenetic and biogeographic significance of the tarsiiform primate *Asiomomys changbaicus* from the Eocene of Jilin Province, People's Republic of China. American Journal of Physical Anthropology, 85: 159-166.

BERG, L.S. (1948). Freshwater fishes of the USSR and adjacent countries. Israel Program for Scientific Translations, Jerusalem, 3: 1962-1965.

CHANG, M.-M., CHEN, G. (2008). Fossil Cypriniformes from China and its adjacent areas and their palaeobiogeographical implications. In: Cavin, L., Longbottom, A., Richter, M. (eds) Fishes and the breakup of Pangaea. Geological Society, London, Special Publications 295: 337-350.

CHANG, M.-M., MIAO, D., CHEN, Y., ZHOU J., CHEN P. (2001). Suckers (Fish, Catostomidae) from the Eocene of China account for the family's current disjunct distributions. Science in China (D) 44 (7): 577-586.

CHANG, M.-M., WANG, N., WU, F.-X. (2010). Discovery of *Cyclurus* (Amiinae, Amiidae, Amiiformes, Pisces) from China. Vertebrata Palasiatica 48 (2): 85-100.

GAUDANT, J. (1979). Mise au point sur l'ichthyofaune paléocène de Menat. Comptes Rendus de l'Académie des Sciences, Paris 288 (D): 1461-1464.

GAUDANT, J., HAUBOLD, H. (1995). Ein Lepisosteide (Pisces, Ginglymodi) aus dem Mittel-Eozän des Geiseltales bei Halle (Sachsen-Anhalt, Deutschland. Neues Jahrbuch für Geologie und Paläontologie Monatshefte 1995(5): 271-278.

GAUDANT, J., MICKLICH, N. (1990). *Rhenanoperca minuta* nov. gen., nov. sp., ein neuer Percoide (Pisces, Perciformes) aus dem Messel-Formation (Mittel-Eozän, Unteres Geiseltalium). Paläontologische Zeitschrift. 64: 269-286.

GRANDE, L. (1998). A comprehensive phylogenetic study of Amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. Society of Vertebrate Paleontology, Memoir 4: 1-690.

HUSSAKOF, L. (1932). The fossil fishes collected by the Central Asiatic Expeditions. American Museum Novitates 553: 1-19.

JERZMANSKA, A. (1977). The freshwater fishes from the Middle Eocene of Geiseltal. In Matthes, H.W., Thaler, B. (Hrsg.). Eozäne Wirbeltiere des Geiseltales, M.-L. Universität Halle-Wittenberg, Wissenschaftliche Beiträge 1977/2 (P5), Halle (S.): 41-65.

KINKELIN, F. (1984). Über Fossilien aus Braunkohlen der Umgebung von Frankfurt am Main. Bericht über die senkenbergische naturforschende Gesellschaft 1883-1884: 165-182.

MEYER H. VON (1851). Beschreibung der fossilen Decapoden, Fische, Batrachier und Säugetiere aus den tertiären Süsswassergebilden des nördl. Böhmens. In Reuss, A.E., Meyer, H. von (Hrsg.). Die tertiären Süsswassergebilde des nördlichen Böhmens und ihre fossilen Thierreste. Palaeontographica 2: 43-73.

MICKLICH, N. (1978). *Palaeoperca proxima*, ein neuer Knochenfisch aus dem Mittel-Eozän von Messel bei Darmstadt. Senckenbergiana lethaea 59 (4/6): 483-501.

MICKLICH, N. (1985) Biologisch paläontologische Untersuchungen zur Fischfauna der Messeler Ölschiefer (Mittel-Eozän, Lutetium). Andrias 4: 1-171.

MICKLICH, N., KLAPPERT, G. (2001) *Masillosteus kelleri*, a new gar (Actinopterygii, Lepisosteidae) from the Middle Eocene of Grube Messel (Hessen, Germany). Kaupia – Darmstädter Beiträge zur Naturgeschichte 11: 73-81.

MICKLICH, N., WUTTKE, M. (1988). Weitere Fischfunde aus dem Eozän von Eckfeld bei Manderscheid (SW-Eifel, Bundesrepublik Deutschland). Mainzer Naturwissenschaftliches Archiv 26: 107-149.

REUSS, A.E. (1844). Geognostiche Skizzen aus Böhmen. Bd. II: Die Kreidegebilde des westlichen Böhmens, ein monographischer Versuch. V.W. Medau, Prag, pp 304.

SMITH, K.T., SCHAAL, S.F.K., SUN, W., LI, C. (2011). Acrodont iguanians (Squamata) from the Middle Eocene of the Huadian Basin of Jilin Province, China, with a critique of the taxon *Tinosaurus*. Vertebrata Palasiatica, 49: 69-84.

SYTCHEVSKAYA, E.K. (1986). Palaeogene freshwater fish fauna of the USSR and Mongolia. The Joint Soviet-Mongolian Palaeontological Expedition Transactions, 29: 1-157.

VOIGT, E. (1934). Die Fische aus der mitteleozänen Braunkohle des Geiseltales mit besonderer Berücksichtigung der erhaltenen Weichteile. Nova Acta Leopoldina (N.F.) 2: 21-146.

WANG, B.Y., LI, C. (1990). First Paleogene mammalian fauna from northeast China. Vertebrata Palasiatica, 28(3): 165-205. (in Chinese with English summary)

WANG, Y.L., LIU, Z.J., JING, H.L., ZHANG, H.-L., ZHANG, J. (2005). Sedimentary characteristics of oil shale deposit of the Huadian Formation of Paleogene in Huadian Basin. Journal of Jilin University (Earth Sciences Edition), 35(6): 720-724. (in Chinese with English summary)

WEITZEL, K. (1933). *Amphiperca multiformis* n. g. n. sp. und *Thaumaturus intermedius* n. sp., Knochenfische aus dem Mitteleozän von Messel. Notizblatt des Vereins für Erdkunde und der hessischen Landes-Anstalt zu Darmstadt 5: 89-97.

WILSON, M.V.H. (1977). Middle Eocene freshwater fishes from British Columbia. Life Sciences Contributions, Royal Ontario Museum 113: 1-61.

ZHANG, P., LU, B., LI, C., SUN, J., LIU, A. (1986). Discovery of the Huadian fauna of the early Tertiary and its geological significance. Jilin Geology, 12(4): 1-14. (in Chinese with English summary)

ZHOU, J.J., SUN, J.R. (1985). The fossil fish fauna from the Huadian basin of the Jilin Province. Vertebrata Palasiatica 23: 190. (in Chinese)

Mouse lemurs as model primate ancestors: The evolution of body size in Cheirogaleidae

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The currently popular model of a small, nocturnal primate ancestor was largely inspired by a living family of Malagasy lemurs, the Cheirogaleidae, which includes the smallest living lemurs (30–400 g). Mouse lemurs (*Microcebus* spp.), in particular, are believed to have retained a suite of primitive characters associated with their very small size: nocturnality, insectivorous/omnivorous diet, fast life history, nest-building, altricial infants carried by mouth, solitary social structure, and a promiscuous mating system (Charles-Dominique and Martin, 1970; Cartmill, 1992). Here we report the results of a morphometric study conducted to investigate the evolution of body size within Cheirogaleidae and the closely related family Lepilemuridae, analysed within the context of recent phylogenetic reconstructions for the lemuriforms (DelPero *et al*., 2006; Chatterjee *et al*., 2010).

We collected 15 craniodental measurements from each of 83 adult cheirogaleid and 24 adult lepilemurid skulls, and 4 hind limb measurements from 51 cheirogaleid and lepilemurid skeletons housed in the Natural History Museum (London) and the Muséum National d'Histoire Naturelle (Paris). We also measured 5 juvenile/subadult skulls of *Lepilemur ruficaudatus* that covered the growth trajectory of the species. We used data from the literature to investigate the allometry of gestation periods in *Lepilemur* and the cheirogaleid taxa compared with other primates, and the climatic predictability of Madagascar (Dewar and Richard, 2007).

Phylogenetic reconstructions of lemuriform relationships (Fig. 1a) indicate that Lepilemuridae and Cheirogaleidae are sister taxa, and that the evolution of body size in this clade has involved at least 4 independent dwarfing events. A discriminant function analysis showed that lepilemurids and cheirogaleids fall readily into three size-related groups which do not reflect their sister-group affiliations (Fig. 1b). *Cheirogaleus major s.l.*, *Mirza* and *Phaner*, the greater cheirogaleids – the "dwarfs" – share similar size/shape relationships to one another, as do *C. medius s.l., Microcebus* and *Allocebus* – the "hyper-dwarfs". Decreasing body size in cheirogaleid taxa is associated with decreasing gestation periods not explained by the allometric effect of body size. Moreover, the smaller forms of *Lepilemur* and Cheirogaleidae are found in regions characterised by very high levels of environmental variability, suggesting that dwarfing in this group allowed an acceleration of life history and increased fecundity (Dewar and Richard, 2007). Finally, we tested Gould's (1977) hypothesis of paedomorphic dwarfing, and showed that cheirogaleid body-size reduction has

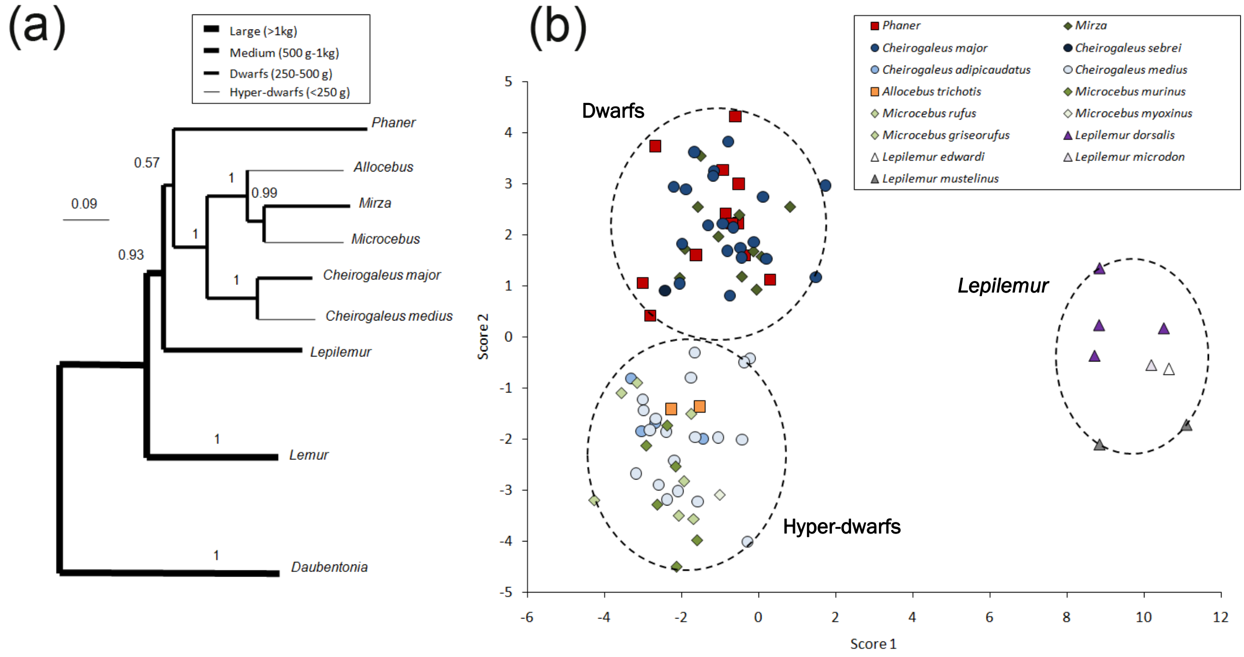

Figure 1. (a) Phylogeny based on combined mtDNA + morphological data (majority-rule consensus tree, excerpted from Masters et al., in prep.). Posterior probabilities are shown at nodes. Scale units are substitutions/site. (b) Discriminant Function Analysis based on 15 cranial variables and 107 adult specimens attributed to 16 species of Lepilemuridae and Cheirogaleidae.

involved a truncated ontogeny, or progenesis, revealed by the association between static allometries and growth allometries (*Lepilemur* growth trajectory and three juvenile specimens of *Phaner*, *Mirza* and *Microcebus*). We identified two major allometries resulting from heterochrony in cheirogaleids: first, a parallel reduction of the body and limbs in the dwarf forms (*Phaner*, *Mirza* and *Cheirogaleus major s.l.*); and second, parallel changes in cranial shape in the hyper-dwarf forms (lesser forms of *Cheirogaleus*, *Allocebus* and *Microcebus*). Cheirogaleids are a potential example of island dwarfing in lemurs.

The small size of mouse lemurs is hence not ancestral, but part of a suite of adaptations to relatively recent climatic fluctuations. The climatic conditions envisaged for the early evolution of primates (e.g., Sussman, 1991) are vastly different, and Eocene primates are associated with mesic forest environments. The adaptations of ancestral primates are unlikely to have been driven by selective pressures similar to those that drove the cheirogaleid radiation, and mouse lemurs in particularly make poor model primate ancestors. Many characters co-vary with body size (e.g., life history parameters, diet, use of heterothermy, and, at least partially, activity rhythm), and any similarities that might exist between the biology of cheirogaleids and that of a small primate or lemur ancestor would be homoplastic, rather than plesiomorphic, if indeed ancestral primates were small. Dwarfing has apparently occurred many times during primate evolution, complicating the reconstruction of ancestral body size. The argument for a small-sized primate ancestor requires a firmer data base.

Cartmill, M. (1992). New views on primate origins. Evolutionary Anthropology 1: 105-111.
Charles-Dominique, P., Martin, R.D. (1970). Evolution of lemurs and lorises. Nature 227: 257-260.
Chatterjee, H.J., Ho, S.Y.W., Barnes, I., Groves, C. (2009). Estimating the phylogeny and divergence times of primates using a supermatrix approach. BMC Evolutionary Biology 9: 259.
Delpero, M., Pozzi, L., Masters, J.C. (2006). A composite molecular phylogeny of living lemuroid primates. Folia Primatologica 77: 434-445.
Dewar, R.E., Richard, A.F. (2007). Evolution in the hypervariable environment of Madagascar. Proceedings of the National Academy of Sciences, USA. 104: 13723-13727.
Gould, S.J. (1977). Ontogeny and Phylogeny. Belknap Press, Cambridge, MA.
Sussman, R.W. (1991). Primate origins and the evolution of angiosperms. American Journal of Primatology 23: 209-223.

Primates in the Eocene

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The Eocene, like many epochs, started in crisis. The first evidence of the crisis came in Wyoming with discovery of a distinct basal-Wasatchian Wa-0 mammalian fauna that included some seemingly dwarfed species of lineages present before and after (Gingerich, 1989). The best-documented lineage with dwarfing is that of *Ectocion*, where *E. osbornianus* was replaced briefly by *E. parvus*. Stable isotope studies later linked the dwarfing of *Ectocion* in Wyoming to the extinction of benthic foraminifera in the world's oceans, and tied both to a global greenhouse warming event now known as the Paleocene-Eocene thermal maximum or PETM (Kennett and Stott, 1991; Koch *et al.*, 1992; Clyde and Gingerich, 1998; reviewed in Gingerich, 2006). The Wa-0 crisis fauna includes the first representatives of the important mammalian orders Artiodactyla, Perissodactyla, and modern Primates ('Euprimates') to be found in North America. Two Wa-0 primates are known: *Cantius torresi* Gingerich, 1986 and *Teilhardina brandti* Gingerich, 1993.

Teilhardina and *Cantius* represent different superfamilies of primates, Tarsioidea and Adapoidea, respectively, that have never been found in older Paleocene strata but were seemingly cosmopolitan from very early in the Eocene (Gingerich, 1986; Smith *et al.*, 2006). Early tarsioids and adapoids have the same dental formula, 2.1.4.3 / 2.1.4.3, and similar upper and lower cheek teeth. They are generally distinguished by size and by the relative length of the premolars. Tarsioids are smaller, generally below 500 g in estimated body weight, and adapoids are larger, generally above 500 g in estimated body weight. Premolars in tarsioids are short anteroposteriorly and compact, while those of adapoids are more elongated anteroposteriorly. However, premolars of *Cantius torresi* are similar to those of early omomyid tarsioids (Gingerich, 1986).

Rose and Bown (1991, p. 101) developed this theme, writing of early adapoids and omomyid tarsioids:

> *Although adapids and omomyids have generally been placed in separate higher taxa of primates (e.g., suborders), the earliest members of each group are in fact very similar both dentally and postcranially—sufficiently so that diagnoses of these two families have been chronically vague, and confusion has surrounded the proper family assignment of such taxa as* Donrussellia *(*D. gallica*, the type species of* Donrussellia*, was initially allocated questionably to* Teilhardina*). As our knowledge of the earliest euprimates has improved, the number of characters distinguishing adapids and omomyids has steadily declined, making separation of Omomyidae from Adapidae exceedingly difficult on dental characters alone (dentitions constitute by far the principal fossil remains for most early euprimates). In view of the primitive characteristics of* Steinius vespertinus*, there remains only one distinctive dental trait separating basal omomyids from primitive adapids: a one-rooted (vs. two-rooted)* P_2.

Given their similarity in space, time, and form, it is natural to group Tarsioidea and Adapoidea together as sister taxa and difficult to imagine that they are anything but closely related. Both superfamilies were forged in the PETM and seemingly cast from the same mold.

From this very similar beginning, Tarsioidea and Adapoidea diversified through the Eocene on all three northern continents. Tarsioidea and Adapoidea are known from the Eocene of Africa as well (Hartenberger and Marandat, 1992; Pickford *et al.*, 2008; Seiffert *et al.*, 2009; Jaeger *et al.*, 2010), which may be their center of origin. By the late Eocene, the oldest anthropoids, Parapithecoidea, are known from Africa (Bonis *et al.*, 1988; Seiffert *et al.*, 2005; Jaeger *et al.*, 2010). Africa is the logical place to search for the origin of anthropoid or higher primates, but the Eocene fossil record there is still inadequately studied.

Eocene primates are best known from the northern continents, where they are represented by something on the order of a hundred thousand specimens. Most are isolated teeth or teeth in jaws, but there are also crania and partial skeletons. The advantage of having Eocene primates by the thousands is that in favorable stratigraphic settings large numbers of specimens enable lineages to be traced through long intervals of time. Fossils, even fragmentary fossils, are important for understanding geographic distributions, ecological associations, and environmental constraints.

The advantage of crania and partial skeletons is that they provide more information about the animals as a whole, which is necessary to constrain hypotheses of relationship to living primates. This is where Messel specimens are so important. *Europolemur* and *Darwinius* are each known from exceptional specimens preserving crania and articulated postcranial elements, sometimes in association (e.g., Koenigswald, 1979; Franzen, 1987; Franzen *et al.*, 2009). *Darwinius* is particularly interesting in being so complete. Integrating *Darwinius* into a phylogeny of living primates indicates that it groups with higher primates (Gingerich et al., 2010).

Putting all of this together (Fig. 1), we have a phylogeny of higher primates, or Anthropoidea, including the superfamilies Ceboidea, Cercopithecoidea, and Hominoidea. Anthropoidea originated and diversified sometime near the end of the Eocene. Combining Anthropoidea with Adapoidea and Tarsioidea, we have a more inclusive group, Haplorhini, that origi

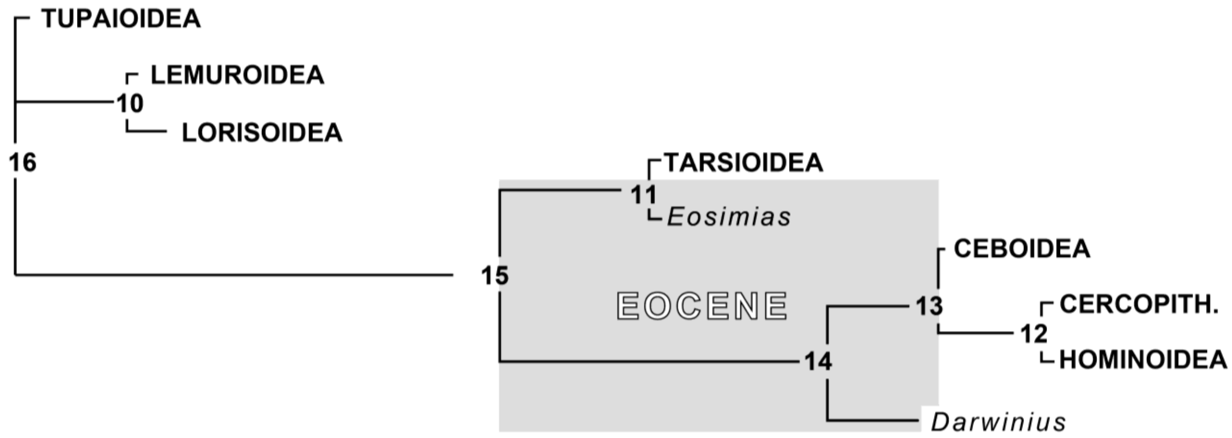

Figure 1. Phylogram showing the relationships of Eocene Tarsioidea (including *Eosimias*) and Adapoidea (including *Darwinius*), in the shaded box, to more primitive Strepsirrhini (Lemuroidea and Lorisoidea) and more derived Anthropoidea (Ceboidea, Cercopithecoidea, and Hominoidea). Analysis follows Gingerich *et al.* (2010).

nated and diversified sometime near the beginning of the Eocene. The Eocene can be viewed as the age of Tarsioidea and Adapoidea. *Darwinius* is an adapoid and phylogenetically also a stem anthropoid. The designation 'stem anthropoid' is misleading for *Darwinius*, as it is for most stem taxa, because it has none of the characteristics that would make it a true anthropoid. The sister group to Haplorhini, Strepsirrhini, including Lemuroidea and Lorisoidea, has a deeper root and, by inference, may go back to the early part of the Paleocene (no Paleocene strepsirrhines are known).

Acknowledgments

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Bonis, L.D., Jaeger, J.-J., Coiffait, B., Coiffait, P.-E. (1988). Decouverte du plus ancien primate Catarrhinien connu dans l'Eocene superieur d'Afrique du Nord. Comptes Rendus de l'Académie des Sciences Série II 306: 929-934.

Clyde, W.C., Gingerich, P.D. (1998). Mammalian community response to the latest Paleocene thermal maximum: An isotaphonomic study in the northern Bighorn Basin, Wyoming. Geology 26: 1011-1014.

Franzen, J.L. (1987). Ein neuer Primate aus dem Mitteleozän der Grube Messel (Deutschland, S-Hessen). Courier Forschungsinstitut Senckenberg 97: 151-187.

Franzen, J.L., Gingerich, P.D., Habersetzer, J., Hurum, J.H., Koenigswald, W.v., Smith, B.H. (2009). Complete primate skeleton from the middle Eocene of Messel in Germany: Morphology and paleobiology. PLoS One 4 (e5723): 1-27.

Gingerich, P.D. (1986). Early Eocene *Cantius torresi* – Oldest primate of modern aspect from North America. Nature 320: 319-321.

Gingerich, P.D. (1989). New earliest Wasatchian mammalian fauna from the Eocene of northwestern Wyoming: composition and diversity in a rarely sampled high-floodplain assemblage. University of Michigan Papers on Paleontology 28: 1-97.

Gingerich, P.D. (1993). Early Eocene *Teilhardina brandti*: Oldest omomyid primate from North America. Contributions from the Museum of Paleontology, University of Michigan 28: 321-326.

Gingerich, P.D. (2006). Environment and evolution through the Paleocene-Eocene thermal maximum. Trends in Ecology and Evolution 21: 246-253.

Gingerich, P.D., Franzen, J.L., Habersetzer, J., Hurum, J.H., Smith, B.H. (2010). *Darwinius masillae* is a haplorhine – Reply to Williams et al. (2010). Journal of Human Evolution 59: 574-579.

Hartenberger, J.-L. Marandat, B. (1992). A new genus and species of an early Eocene primate from North Africa. Human Evolution 7: 9-16.

Jaeger, J.-J., Beard, K.C., Chaimanee, Y., Salem, M., Benammi, M., Hlal, O., Coster, P., Bilal, A.A., Duringer, P., Schuster, M., Valentin, X., Marandat, B., Marivaux, L., Métais, E., Hammuda, O., Brunet, M. (2010). Late middle Eocene epoch of Libya yields earliest known radiation of African anthropoids. Nature 467: 1095-1098.

Kennett, J.P., Stott, L.D. (1991). Abrupt deep-sea warming, palaeoceanographic changes and benthic extinctions at the end of the Paleocene. Nature 353: 225-229.

Koch, P.L., Zachos, J.C., Gingerich, P.D. (1992). Correlation between isotope records in marine and continental carbon reservoirs near the Palaeocene-Eocene boundary. Nature 358: 319-322.

Koenigswald, W.v. (1979). Ein Lemurenrest aus dem eozänen Ölschiefer der Grube Messel bei Darmstadt. Paläontologische Zeitschrift 53: 63-76.

Pickford, M., Senut, B., Morales, J., Mein, P., Sanchez, I.M. (2008). Mammalia from the Lutetian of Namibia. Memoir of the Geological Survey of Namibia 20: 465-514.

Rose, K.D., Bown, T.M. (1991). Additional fossil evidence on the differentiation of the earliest euprimates. Proceedings of the National Academy of Sciences USA 88: 98-101.

Seiffert, E.R., Perry, J.M.G., Simons, E.L., Boyer, D.M. (2009). Convergent evolution of anthropoid-like adaptations in Eocene adapiform primates. Nature 461: 1118-1121.

Seiffert, E.R., Simons, E.L., Clyde, W.C., Rossie, J.B., Attia, Y., Bown, T.M., Chatrath, P., Mathison, M.E. (2005). Basal anthropoids from Egypt and the antiquity of Africa's higher primate radiation. Science 310: 300-304.

Smith, T., Rose, K.D., Gingerich, P.D. (2006). Rapid Asia-Europe-North America geographic dispersal of earliest Eocene primate *Teilhardina* during the Paleocene-Eocene Thermal Maximum. Proceedings of the National Academy of Sciences USA 103: 11223-11227.

Tarsals of European Cercamoniinae (Primates, Adapiformes) and their phylogenetic implications

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The Cuisian fauna of Prémontré contains remains of a variety of mammals and other vertebrates, including numerous pantolestids, rodents and primates. The preliminary faunal list included a small *Nannopithex* and several cercamoniines, *Cantius* sp., *Protoadapis* aff. *curvicuspidens*, *Protoadapis* sp., cf. *Periconodon*, gen. et sp. nov. (Dégremont *et al.*, 1985). The dental material is under study. A series of tarsal bones can be confidently ascribed to the cercamoniines of the locality, because they have a typical euprimate notharctid anatomy and have the right size. An astragalus from Egerkingen tentatively ascribed to *Caenopithecus lemuroides* (Stehlin, 1916) does not pertain to a primate (Decker and Szalay, 1974). Therefore these bones are the first tridimensional uncrushed tarsals that appear to represent European cercamoniines. At least two species are represented, which share a global pattern but have differences of probable systematic significance. We describe here the more common morphology for both types of bones.

The calcaneus is slender (Fig. 1). Its proximal part is slightly bent medially. In profile views, the plantar border of the body shows a long slight concavity and the plantar border of the tuber calcanei is curved. On the plantar side, the anterior plantar tubercle is well delineated. The peroneal tubercle is damaged; its broken base shows that it was small, low, and placed along the distal extremity of the posterior calcaneal facet. On the dorsal side, the posterior astragalar facet is short and its long axis is approximately anteroposterior; it separates a relatively short posterior part and a moderately elongated anterior part. The sulcus calcanei is wide. The sustentacular facet has a rounded outline with a well-defined distal rim; however, a narrow articular surface continues and broadens distally into the anterior calcaneal facet, which interrupts before reaching the distal rim. The cuboid facet is ovoid and tansversally elongated. Its long axis is oriented dorsomedially. On the articular facet, it is possible to distinguish a semicircular ribbon, narrow dorsally and broadening laterally, and a large semiconical central pit, having its deepest point at the plantar margin of the facet and close to the extremity of the anterior plantar tubercle.

The astragalus has a relatively elongated body and a moderately long talar neck, medially inclined, which broadens distally until the head. The tibial trochlea is elongated, shallow, slightly broadening distally, not expanded onto the neck, and posteriorly extended on a well-developed posterior trochlear shelf. The posterior groove for the tendon of the flexor fibularis is laterally offset relative to the axis of the trochlea. On the medial side, the tibial facet is excavated, cup-like, and salient at its plantar rim. The lateral side is high and moderately sloping ventrolaterally, showing an anterior fibular facet, the deep pit for the posterior talofibular ligament, and probably a small posterior fibular facet. On the ventral side, the proximal calcaneal facet is oblique, broad under the fibular facets, and narrower under the ligament pit (as in notharctids). The sustentacular facet is continuous with the anterior calcaneal, spring ligament and navicular facets. The lateral nonarticular surface broadens distally until it reaches the navicular facet. In distal view, the head is rounded, slightly transversely elongated and higher on its lateral side; its long axis is barely dorsomedially inclined. On the posterior side, the trochlear articular facet continues after narrowing between the lateral and medial ligamentous insertion zones. It reaches close to the groove for the flexor fibularis tendon, which is well extended on this side.

The overall morphology of these bones is very close to that described in fossil notharctids. They were likewise very probably predominantly above-branch arboreal quadrupeds (Gebo, 1988). Some differences can be noted. On the calcaneus, *Cantius* and asiadapines have a more elongated posterior astragalar facet, extending further anteriorly in *Cantius*, probably a larger peroneal tubercle, and small differences in the shape of the cuboid facet (Gebo, 1988; Rose *et al.*, 2009). The astragalus differs from that of *Cantius* through its more elongated body and tibial trochlea. It differs from asiadapines through its sustentacular facet, which is narrower and less extended toward the medial side (possibly also less inclined). The astragalus of *Notharctus* differs more markedly from that of European cercamoniines through its higher body and more laterally protruding lateral side, accompanied by a more extended posterior fibular facet (derived characters in *Notharctus*).

It is clear that the astragali of these European cercamoniines present the typical strepsirhine characters of the lateral sloping of the fibular facet and the offset between the trochlear axis and the groove for the tendon of the flexor fibularis. However, these characters are not strongly expressed. The offset is recognizable in dorsal view, but it is much less conspicuous on the posterior view owing to the progressive attenuation of the articular characters of the surface, which extends directly toward the groove. The lateral sloping of the fibular facet is often illustrated in lemurids, in adapines and in *Notharctus*, in which it is strongly expressed. However, this sloping

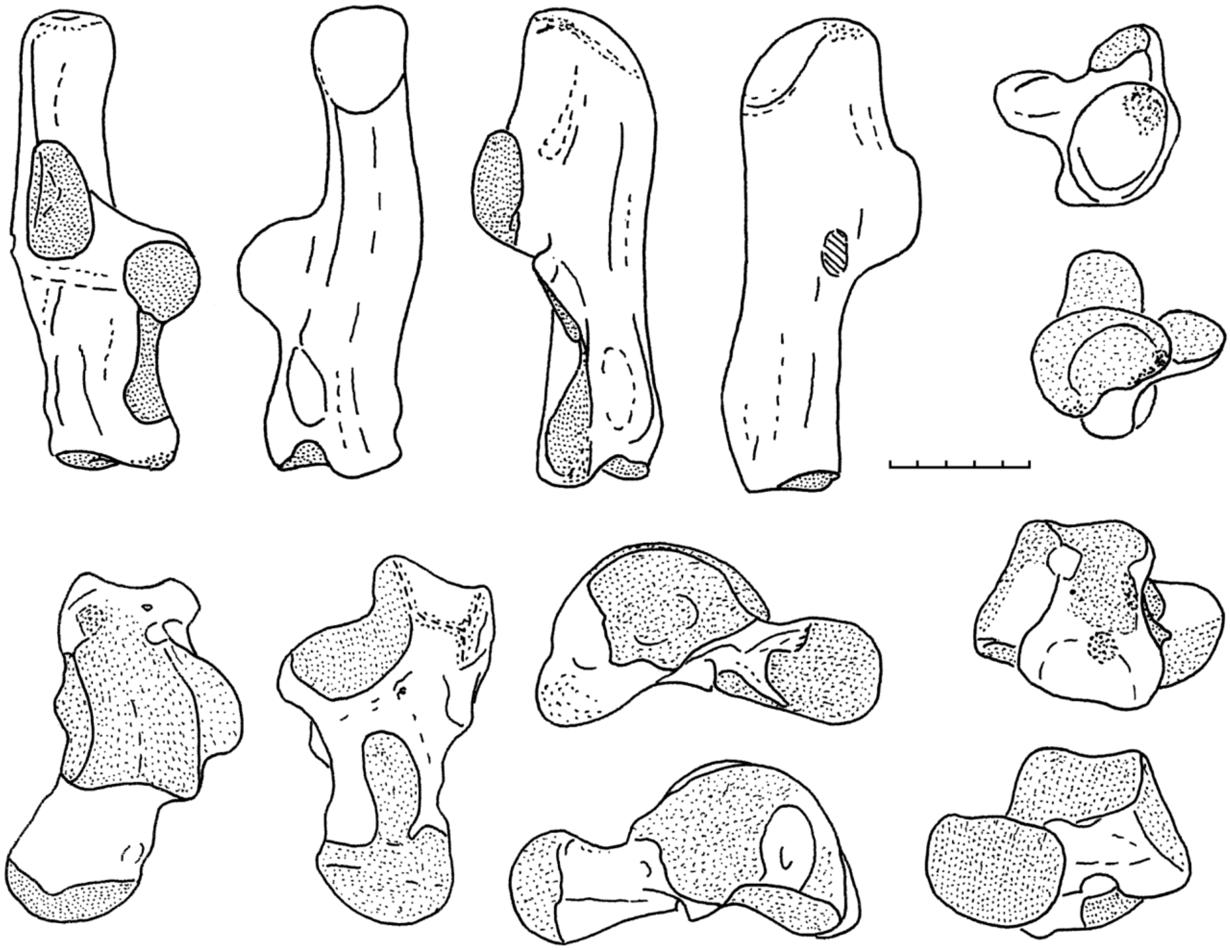

Figure 1. Calcaneus and astragalus of a cercamoniine from Prémontré. Above, calcaneus in (left to right) dorsal, plantar, medial, lateral, proximal and distal views. Below, astragalus in dorsal, plantar, medial, lateral, proximal and distal views. Scale bar is 5 mm.

is less accentuated in some cheirogaleids, in asiadapines and in European cercamoniines. We think that this much less laterally protruding lateral side (Fig. 1) probably partly explains the difficulty in recognizing it on the skeleton of *Darwinius masillae* (Franzen *et al.*, 2009). A weak lateral sloping is likely to be primitive in strepsirhines, reducing the morphological gap with haplorhines or primitive primates. It confirms the increase in this character already admitted as probably convergent between *Notharctus* and lemurids-indriids. Correlatively, this diminishes the value of the character as it would apply to the most primitive strepsirhines.

Because *Darwinius* has been described as a cercamoniine (Franzen *et al.*, 2009), it very probably had a tarsal anatomy similar to that of the Cuisian cercamoniines from Prémontré, which are close in age. The latter include a new species of *Agerinia* which shows important dental similarities with *Darwinius*. These arguments emphasize the probable strepsirhine affinities of the latter. At the same time, these tarsals call attention to the character states of primitive strepsirhines, different from those which have been considered the most typical for the group until now, and less contrasted with those of haplorhines.

Decker, R.E., Szalay, F.S. (1974). Origins and function of the pes in the Eocene Adapidae (Lemuriformes, Primates). In: Jenkins, F.A. (ed) Primate Locomotion. Academic Press, New York, pp 261-291.

Degremont, E., Duchaussois, F., Hautefeuille, F., Laurain, M., Louis, P., Tetu, R. (1985). Paléontologie: Découverte d'un gisement du Cuisien tardif à Prémontré (Aisne). Bulletin d'Information des Géologues du Bassin de Paris 22: 11-18.

Franzen, J.L., Gingerich, P.D., Habersetzer, J., Hurum, J.H., Koenigswald, W.v, Holly Smith, B. (2009). Complete primate skeleton from the Middle Eocene of Messel in Germany: Morphology and paleobiology. PLoS ONE 4(5): 1-27.

Gebo, D.L. (1988). Foot morphology and locomotor adaptation in Eocene Primates. Folia Primatologica 50: 3-41.

Rose, K.D., Rana, R.S., Sahni, A., Kumar, K., Missiaen, P., Singh, L., Smith, T. (2009). Early Eocene Primates from Gujarat, India. Journal of Human Evolution 56: 366-404.

Stehlin, H.G., (1916). Die Säugetiere des schweizerischen Eocaens. Abhandlungen der schweizerischen paläontologischen Gesellschaft 41: 1299-1552.

Shedding new light on the phylogeny and historical biogeography of *Hoya* (Apocynaceae)

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The Indomalesian and Australasian region is nowadays characterized by high levels of species richness and endemism in plants (Myers *et al.*, 2000), which is partly attributed to its dynamic and complex climatic and geological history throughout the Cenozoic (for detailed discussion see Sodhi *et al.*, 2004, or Morley, 2003). One of the three tectonic events which may have had an important impact on trans-oceanic angiosperm dispersal routes was the collision of the Indian Plate with Asia during the Middle Eocene (50–39 Ma; Morley, 2003). Although there have been numerous opportunities for dispersal across geographical barriers during geological time or overseas (reviewed in Moss and Wilson, 1998), Wallace’s line may represent a significant barrier for some plant groups (van Welzen *et al.*, 2005) and therefore is the focus of biogeographical studies. The fossil record as well as geological events can be used to set temporal constraints at nodes in molecular phylogenetic trees and make predictions for expected topologies and to some extent the timing of diversification events. It has been shown that, in this target region, such dated phylogenetic trees are a powerful instrument for reconstructing dispersal and migration routes (*e.g.*, shown in Muellner *et al.*, 2008).

The genus *Hoya* of the family Apocynaceae contains more than 200 species. Its distribution ranges from India to the Pacific Islands (see Fig. 1) and covers five of the currently recognized World Biodiversity hotspots – Sundaland, Wallacea, the East Malesian Islands, the Philippines, and the Queensland wet tropics (compare Myers *et al.*, 2000; *Biodiversity Hotspots*, Center for Applied Biodiversity Science at Conservation International http://www.biodiversity-hotspots.org/Pages/default.aspx).

Almost 600 species names are attributed to *Hoya* (The Plant Names Project, 1999), and the last taxonomic revision was done by Hooker (1885) and completed by Schlechter (1913, 1916), who proposed ten sections within the genus. To unravel the relationships between *Hoya* and related genera as well as relationships between and within the currently recognized infrageneric sections, we have recently

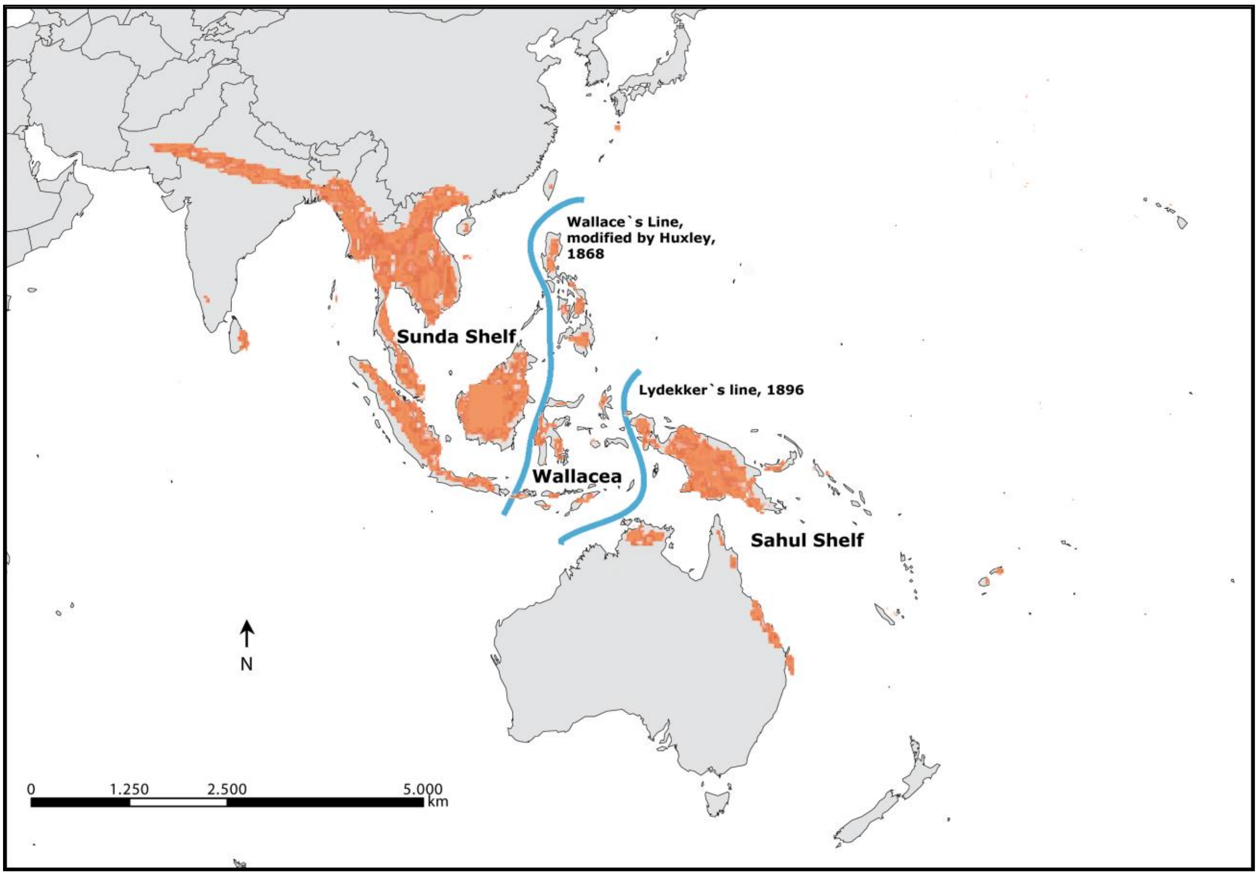

Figure 1. Geographical distribution of *Hoya* (orange), Wallace’s Line (modified by Huxley) and Lydekker’s line (blue) (redrawn from Pannell, 1998, Muellner *et al.*, 2009 and Wanntorp *et al.*, 2006).

undertaken molecular phylogenetic studies (e.g., Wanntorp, 2009, Wanntorp *et al.*, 2011), which are currently under further progress. So far, we have analysed samples of various species of *Hoya*, as well as several samples of *Dischidia* and *Marsdenia*, with nuclear and plastid DNA markers. The resulting phylogenetic reconstructions will ultimately provide important information for a modern taxonomic revision of *Hoya* and help to unravel the biogeographic history of this widely distributed genus.

However, the monophyletic character of *Hoya* is still unclear, and the relationships between some of the major clades identified as well as the exact relationship between *Hoya* and some related taxa (e.g., *Dischidia* and *Clemensiella*) are only partly resolved. This underlines the need of further studies on phylogenetic relationships and generic delimitations within the tribe Marsdenieae (Wanntorp *et al.*, 2011).

Here, we present a new dated phylogenetic hypothesis based on further information on the fossil record and geological events (from the middle Eocene to present) to help in resolving the unclear taxonomic boundaries in *Hoya* and understanding the diversification of flowering plants in the Indomalesian and Australasian region. Dated phylogenetic trees also have the potential to contribute to geological and climatological studies by providing temporal information on, e.g.*,* island emergence in the Indomalesian and Australasian region and the development of different climatic zones. Future collaboration between systematists, palaeobiologists, palaeoclimatologists and geologists will provide a clearer picture of both the biotic and abiotic history of this highly diverse region.

Hooker, J.D. (1885). Asclepiadeae. In: Hooker, J.D. (ed) Flora of British India: Volume 4. Reeve, London, pp 1-78.

Morley, R.J. (2003). Interplate dispersal paths for megathermal angiosperms. Perspectives in Plant Ecology, Evolution and Systematics 6: 5-20.

Moss, S.J., Wilson, M.E.J. (1998). Biogeographic implications of the Tertiary palaeogeographic evolution of Sulawesi and Borneo. In: Hall, R., Holloway, J.D. (eds) Biogeography and Geological Evolution of SE Asia. Backhuys Publishers, Leiden, pp 133-163.

Muellner, A.N., Greger, H., Pannell, C.M. (2009). Genetic diversity and geographic structure in *Aglaia elaeagnoidea* (Meliaceae, Sapindales), a morphologically complex tree species, near the two extremes of its distribution. Blumea 54: 207-216.

Muellner, A.N., Pannell, C.M., Colemann, A., Chase, M.W. (2008). The origin and evolution of Indomalesian, Australasian and Pacific island biotas: Insights from Aglaieae (Meliaceae, Sapindales). Journal of Biogeography 35: 1769-1789.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J. (2000). Biodiversity hotspots for conservation priorities. Nature 403: 853-858.

Pannell, C.M. (1998). Taxonomy, ecology and reproductive biology of *Aglaia* (Meliaceae). In: Hopkins, H.C.F., Huxley, C.R., Pannell, C.M., Prance, G.T., White, F. (eds) The Biological Monograph: The Importance of Field Studies and Functional Syndrome for Taxonomy and Ecolution of Tropical Plants. A Festschrift for Frank White. Royal Botanic Gardens Kew, London, pp 59-77.

Schlechter, R. (1913). Die Asclepiadaceen von Deutsch-Neu-Guinea. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 50: 81-164.

Schlechter, R. (1916). Neue Asclepiadaceen von Sumatra und Celebes. Beihefte zum Botanischen Centralblatt 34: 1-18.

Sodhi, N.S., Koh, L.P., Brook, B.W., Ng, P.K.L. (2004). Southeast Asian biodiversity: An impending disaster. TRENDS in Ecology and Evolution 19: 654-660.

The Plant Names Project (1999). International Plant Names Index. http://www.ipni.org (accessed Nov. 2009).

Wanntorp, L. (2009). Phylogenetic systematics of *Hoya* (Apocynaceae). Blumea 54: 228-232.

Wanntorp, L., Gotthardt, K., Muellner, A.N. (2011). Revisiting the wax plants (*Hoya*, Marsdenieae, Apocynaceae) phylogenetic tree using the *matK* gene and *psbA-trnH* intergenic spacer. Taxon 60: 4-14.

Wanntorp, L., Kocyan, A., Renner, S.S. (2006). Wax plants disentangled: A phylogeny of *Hoya* (Marsdenieae, Apocynaceae) inferred from nuclear and chloroplast DNA sequences. Molecular Phylogenetics and Evolution 39: 722-733.

Welzen, P.C. van, Slik, J.W.F., Alahuhta, J. (2005). Plant distribution patterns and plate tectonics in Malesia. Biologiske Skrifter 55:199-217.

Primitive chiropteran teeth – The complete dentition of the Messel bat *Archaeonycteris trigonodon*

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The bat component of the Messel mammalian assemblage is represented by seven species, all but one (the emballonurid *Tachypteron franzeni*) belonging to the archaic bat families Archaeonycteridae, Palaeochiropterygidae, and Hassianycteridae (Habersetzer and Storch, 1987; Storch *et al.*, 2002). Collectively, the Messel bats represent some of the best-preserved and most complete skeletons known for fossil chiropterans anywhere, often preserving soft tissue body outlines and stomach contents. However, one of the great ironies of such exquisite preservation is that some anatomical features traditionally used by mammalian systematists – such as details of dental morphology – are often obscured because the skeletons are articulated and the dentitions are in occlusion. Due to advances in CT-scanning technology, it is now possible to examine details of dental anatomy even in specimens where the upper and lower jaws are in tight occlusion. Herein we described the complete dentition of one of the most primitive members of the Messel bat community, *Archaeonycteris trigonodon* (HLMD 16069, Fig. 1), and compare its dental anatomy with that of the most primitive bat known from North America, *Onychonycteris finneyi* (Simmons *et al.*, 2008).

Archaeonycteris trigonodon has the presumably primitive chiropteran dental formula of 2.1.3.3/ 3.1.3.3. Upper incisors (Fig. 1B–C) are single-cusped, appressed and separated from C^1 by a diastema. I^1 extends farther ventrally, while I^2 is slightly broader and has a small posterolabial cuspule at the base of the crown. C^1 is relatively blunt, elongate, and bilaterally compressed with a sharply defined posterior crest and a weak but continuous basal cingulum. P^2-P^3 are reduced in size compared to P^4. P^2-P^3 are relatively short (barely extending beyond the C^1 cingulum) with a single, sharp cusp. P^2 is single-rooted, P^3 double-rooted, and both teeth have relatively robust and continuous basal cingula. P^4 is dominated by a tall paracone with a steep preparacrista and a slightly less steep, non-blade-like postparacrista, both of which extend to the relatively weak, non-continuous basal cingulum. A weak and low anterior shelf is present, as is a larger but equally low protocone shelf that extends only a short distance lingually but not posterolingually. M^1-M^2 are similar with well-developed and equally high proto-, para- and metacones. M^1-M^2 lack hypocone shelves and conules, have relatively broad stylar shelves and precingulae, lack mesostyles, have weakly formed parastyles with weak parastylar hook, have preparacristae that extend nearly to the labial margin, a relatively labiolingually compressed protofossa with the postpara- and premetacristae joining labially well short of the labial margin. M^1 differs from M^2 in having a distinct, relatively deeply excavated ectoflexus and in having weaker postcingulum. M^3 has a greatly extended parastylar lobe with a strong preparacrista extending the length of the lobe, a reduced metacone with no postmetacrista, a relatively lower protocone and a more abbreviated protofossa.

Lower incisors (Fig. 1DE) are small, nearly equivalent in size, tricuspate, appressed, with I_3 tightly appressed to the anterior base of the C_1. The lower canine is mesiodistally shorter and less robust than C^1. The anterior lower premolars ($P_{2\text{-}3}$) are much less reduced than their upper counterparts, P_2 being single-rooted and P_3 double-rooted. P_2-P_3 are dominated by a tall, pointed protoconid extending from which are a relatively short preprotocristid and a more elongate postprotocristid, both extending to the pre- and postcingulid, respectively. The cingulid is continuous labially, but there is no lingual cingulid. Neither P_2 nor P_3 have a talonid developed, but each has a short basal distal projection formed by a broadened postcingulid. Both P_2 and P_3 lack para- and metaconids, resulting in flattened and smooth lingual surfaces. P_4 is a more complex version of P_3 with a distinct but low paraconid and an equally developed but somewhat higher metaconid. P_4 lacks a distinct talonid, but the distal surface is extended into a sloping shelf that is restricted lingually by a postprotocristid extending to the postcingulid. There is a distinct labial cingulid, a short precingulid that is truncated by the paraconid and no lingual cingulid. Lower molars are six-cusped, with M_1 and M_2 of subequal size and M_3 somewhat smaller. The labial cusps (protoconid and hypoconid) are taller than the lingual cusps. Molar paraconids are located at the mesiolingual corner of the trigonid, are relatively small, and project mesially. The metaconids are larger and more robust than the paraconids, are somewhat taller (but not as tall as the protoconid), and are positioned at the distolingually corner of the trigonid, just distal to the protoconid. Trigonids are open mesially, distally, and lingually and are moderately compressed mesiodistally. The talonids are about as wide as the trigonids on $M_{1\text{-}2}$, while the talonid is narrower on M_3. Hypoconids are prominent; entoconids are low and small on $M_{1\text{-}2}$, and nearly absent on M_3. Hypoconulids are located just lingual of center, are as high as the entoconid, and are only weakly differentiated from the entoconid,

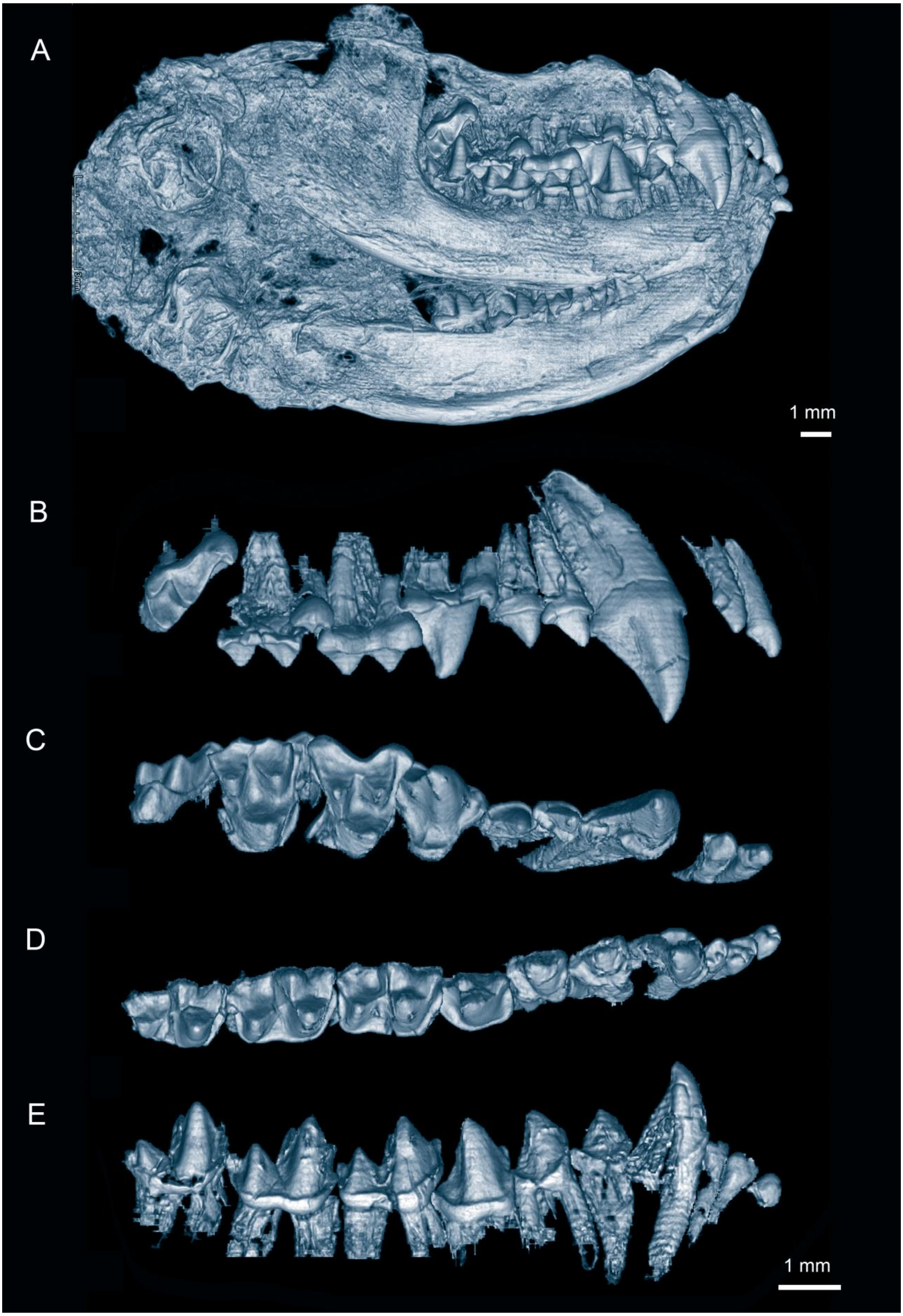

Figure 1. Skull and dentition of *Archaeonycteris trigonodon* (HLMD 16069). A) skull in lateral view. B-C) upper dentition in labial and occlusal views. D-E) lower dentition in occlusal and labial views.

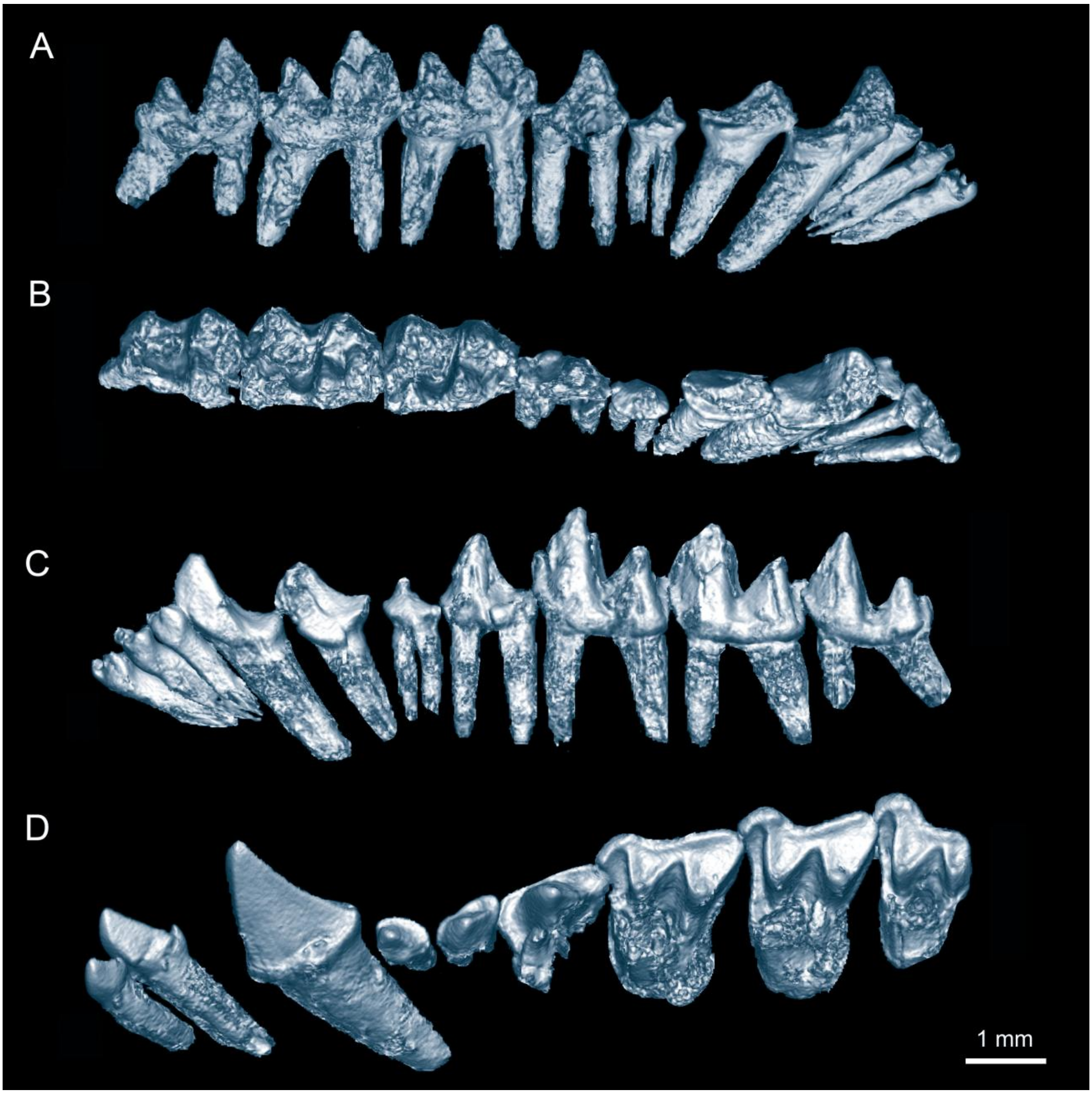

Figure 2. Dentition of *Onychonycteris finneyi* (ROM 55351A-B). A-C) lower dentition in lingual, occlusal and labial views. D) upper dentition in occlusal view.

essentially being tribosphenic. The entocristid is low and does not wall off the talonid lingually. The cristid obliqua joins the postvallid just labial of center, producing a relatively deep hypoflexid, even on M_3. There are strong pre-, post- and labial cingulids on $M_{1\text{-}2}$, with labial and postcingulids being weaker on M_3.

In comparison with the primitive North American bat *Onychonycteris finneyi* (Simmons *et al.*, 2008; Fig. 2), *A. trigonodon* differs in having I^1 and I^2 more similar in size and aligned mesiodistally (*O. finneyi* has I^2 noticeably larger than I^1 and the teeth are offset); C^1 more elongate and labiolingually compressed; P^2 and P^3 homodont (*O. finneyi* has P^3 with a blade-like postparacrista that is lacking on P^2) and more mesiodistally appressed; upper molars with broader stylar shelves, weaker parastylar hooks, and M^1 with a much deeper ectoflexus; M^3 with much more elongate parastylar region, a weaker metacone, and lacking a postmetacrista (*O. finneyi* has a shorter and broader parastyle, postmetacrista still present and a more distinct metacone); P_2 and P_3 similar in size and morphology and both unreduced (*O. finneyi* with P_3 reduced and simple, P_2 relatively large and similar in morphology to C_1); C_1 relatively larger and more projecting; P_4 with distinct para- and metaconids (*O. finneyi* apparently lacked both cusps on P_4); molar trigonids undifferentiated (*O. finneyi* with M_1 trigonid more open while $M_{2\text{-}3}$ trigonids are more mesiodistally compressed); cristid obliqua joins postvallid more lingually producing deeper hypoflexid.

Archaeonycteris and *Onychonycteris* are two of the most primitive fossil bats known – based entirely on skeletal features, *O. finneyi* represents the basalmost bat yet discovered (Simmons *et al.*, 2008). *O.*

finneyi differs substantially in dental morphology from *A. trigonodon*, indicating that establishing a bat dental morphotype will require more information. For example, *O. finneyi* lacks a paraconid and metaconid on P_4 while *A. trigonodon* has both developed – which of these represents the primitive condition? The disposition of molar hypoconulids has also been used as an arbiter of more plesiomorphic vs. more apomorphic taxa. In general, taxa with a tribosphenic pattern (hypoconulid centered on postcristid) are viewed as most primitive, those showing a nyctalodont pattern (hypoconulid lingual and connected to hypoconid) as more derived and those with a myotodont pattern (hypoconulid lingual and isolated, postcristid connects hypoconid to entoconid) as most derived (Menu and Sigé, 1971). However, *Archaeonycteris* and *Onychonycteris* differ in hypoconulid structure: *A. trigonodon* can be best described as tribosphenic, while *O. finneyi* might well be myotodont (difficult to tell with certainty on the CT scans). These observations suggest that the early evolution of the chiropteran dentition was mosaic in nature, and that assumptions about the primitive chiropteran dental morphotype need to be carefully evaluated.

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The authors thank N. Micklich and G. Gruber (Hessisches Landesmuseum Darmstadt) and K. Seymour (Royal Ontario Museum, Toronto) for access to specimens.

HABERSETZER, J., STORCH, G. (1987). Klassifikation und funktionelle Flügelmorphologie paläogener Fledermäuse (Mammalia, Chiroptera). Courier Forschungsinstitut Senckenberg 91: 117–150.

MENU, H., SIGÉ, B. (1971). Nyctalodontie et myotodontie, importants caractères de grades évolutifs chez les chiroptères entomophages. Comptes Rendus de l'Académie des Sciences, Paris 272: 1735-1738.

SIMMONS, N. B., SEYMOUR K. L., HABERSETZER, J., GUNNELL, G. F. (2008). Primitive early Eocene bat from Wyoming and the evolution of flight and echolocation. Nature 451: 818–822.

STORCH, G., SIGÉ, B., HABERSETZER, J. (2002). *Tachypteron franzeni* n. gen., n. sp., earliest emballonurid bat from the Middle Eocene of Messel (Mammalia, Chiroptera). Paläontologische Zeitschrift 76: 189–199.

Morphological specializations of the shoulder joints in extant and fossil bats

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The elements of the shoulder joint of modern Microchiroptera show remarkable morphological variation related to function, for instance in the complex shapes of the humeral head and secondary articulations (Schliemann and Schlosser-Sturm, 1999). Differently specialized and well-preserved shoulder joints have also been described for 47-Mya-old specimens of *Palaeochiropteryx, Archaeonycteris* and *Hassianycteris,* all known from the Eocene Messel Pit (Habersetzer and Storch, 1987).

Initial studies have been made to compare the internal bone structure of the shoulder joints in bats (Swartz *et al.*, 1998). In the present study the shoulders of *Archaeonycteris trigonodon* (Archaeonycterididae), *Rhinopoma hardwickei* (Rhinopomatidae), *Tachypteron franzeni, Taphozous melanopogon* (Emballonuridae), and *Molossus ater* (Molossidae) were investigated by means of micro-CT technology.

As extant functional models with known histology are required for comparisons with fossils, three modern bats were selected. The first, *Rhinopoma*, is a member of the extant Rhinopomatidae, which are considered basal Microchiroptera. Its shoulder joint morphology similar to that of the Megachiroptera. No functional specialisations are detectable externally. The two other modern bats, *Taphozous* and *Molossus*, are derived in this respect, and represent two differently specialised shoulder joint types among modern Microchiroptera. Of the two fossil species, *Archaeonycteris* is the more primitive taxon, whereas *Tachypteron* is closely related to the extant *Taphozous* (Storch *et al.*, 2002).

In the humerus and the scapula of all specimens studied, various types of cancellous bone can be distinguished, including trabecular struts and plates, honeycomblike spongiosa, and a zone of transition, the last immediately adjacent to the cortical bone (Habersetzer *et al.*, 2011).

The unspecialised *Rhinopoma* shows only struts and plates, whereas all tissues mentioned above are found in the derived shoulders of *Molossus* only. All other species in the sample lack the zone of transition.

For extant bats, standard 3D histomorphometrical data were recently presented (Habersetzer and Schlosser-Sturm, 2010). Differences in trabecular thickness, number and spacing led to the conclusion that the internal shoulder region of *Rhinopoma* is more robust and less differentiated than in other bat species. There are no further hints as to internal functional specialisations in this species.

Rhinopoma hardwickei appears to be a good extant model for *Archaeonycteris trigonodon*. In the humeral head of *R. hardwickei* (Fig. 1) the spongiosa consists of only a few but very robust trabeculae, as well as plates, which are numerous and multiply connected, and a few struts. In the shaft (left part of image) two single struts are shown. In the scapula (right part) only a few trabeculae are found beneath the joint surface; in deeper parts, long plates radiate into the shoulder blade. *Archaeonycteris* has a

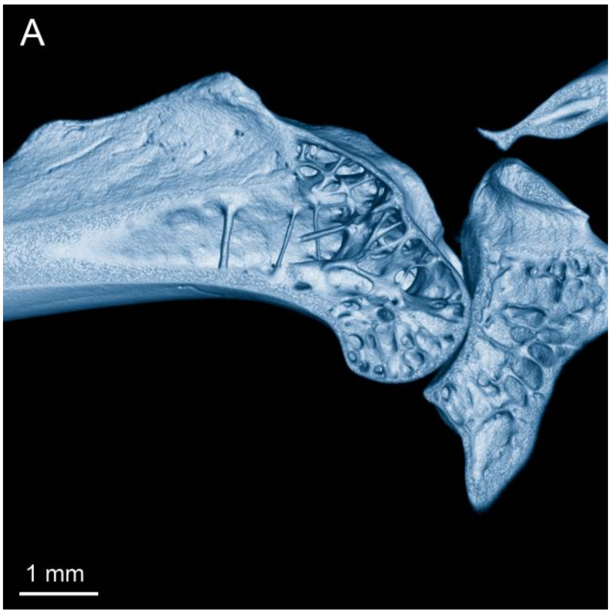

Figure 1. Abducted left shoulder joint of *Rhinopoma hardwickei,* an example for an unspecialised shoulder joint. Dorsal view, virtually cut in horizontal plane.

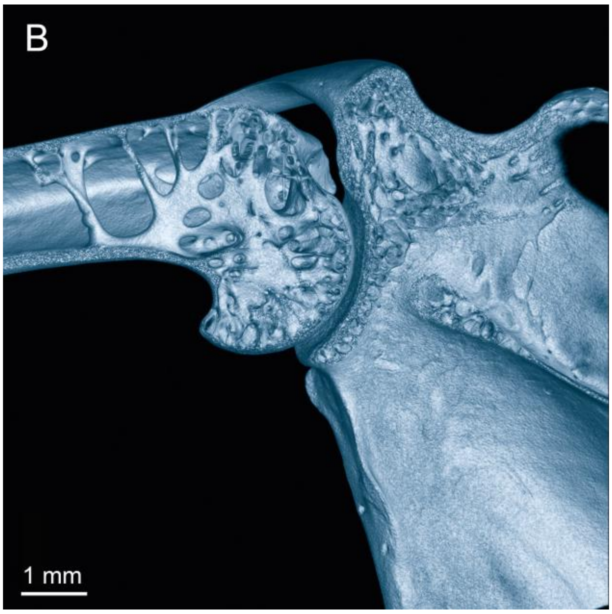

Figure 2. Abducted left shoulder joint of *Taphozous melanopogon,* an example for a derived shoulder joint. Virtually cut and oriented like Fig. 1.

similarly shaped humeral head and a similar trabecular pattern. However, a modern character of *Archaeonycteris* is the honeycomblike spongiosa under both articular surfaces (humerus/scapula), similar to the specialised *Tachypteron franzeni* and its extant relative *Taphozous melanopogon* (Fig. 2). In the middle of its humeral shaft and humeral head a large bracing trabecular plate is prominent. Plates dominate, but struts and honeycomblike spongiosa are also visible. They all form a dense spongiosa. In the scapula (right) a layer of honeycomblike spongiosa is present directly underneath the cortical bone of the glenoid cavity. The functional significance of these results will be discussed and detailed histomorphometrical analyses presented.

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HABERSETZER, J., SCHLOSSER-STURM, E. (2010). Primitive and derived shoulder joints of Messel bats. In: Horacek, I., Benda, P. (eds) 15th International Bat Research Conference, Prague 2010. Prague, pp 159-160.

HABERSETZER, J., SCHLOSSER-STURM, E., STORCH, G., SIGÉ, B. (2011). Shoulder joint and inner ear of *Tachypteron franzeni*, an emballonurid bat from the middle Eocene of Messel. In: Gunnell, G.F., Simmons, N.B. (eds) Evolutionary History of Bats: Fossils, Molecules and Morphology. Cambridge University Press, Cambridge (in press).

HABERSETZER, J., STORCH, G. (1987). Klassifikation und funktionelle Flügelmorphologie paläogener Fledermäuse (Mammalia, Chiroptera). Forschungsergebnisse zu den Grabungen in der Grube Messel bei Darmstadt. Courier Forschungsinstitut Senckenberg 91: 117-150.

SCHLIEMANN, H., SCHLOSSER-STURM, E. (1999). The shoulder joint of the Chiroptera – Morphological features and functional significance. Zoologischer Anzeiger 238 (1-2): 75-86.

STORCH, G., SIGÉ, B., HABERSETZER, J. (2002). *Tachypteron franzeni* n. gen., n. sp., earliest emballonurid bat from the Middle Eocene of Messel (Mammalia, Chiroptera). Paläontologische Zeitschrift 76 (2): 189-199.

SWARTZ, S.M., PARKER, A., HUO, C. (1998). Theoretical and empirical scaling patterns and topological homology in bone trabeculae. Journal of Experimental Biology 201: 573-590.

Eocene biogeography of eastern Gondwanan bats

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The presence of the archaic bat *Australonycteris clarkae* in the 55-million-year-old Tingamarra Local Fauna of south-eastern Queensland indicates that dispersal routes to Australia were available for bats in the earliest Eocene and that these bat faunas were shared globally (Hand *et al*., 1994). At that time Australia, as part of Gondwana, was latitudinally 25° further south and c. 3000 km more distant from northern continents than it is today (Fig. 1). Throughout the Eocene, Australia, Antarctica and South America remained connected, and this southern landmass was characterized by a cool temperate rainforest flora (Francis *et al*., 2008).

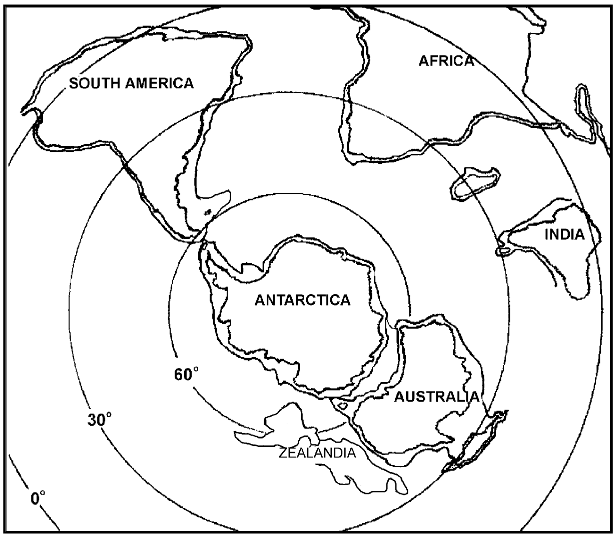

Figure 1. Early Cenozoic (c. 52 Ma) palaeogeographic reconstruction of the southern continents (after Sigé *et al*., 2009).

A corridor between South America and Australia across ice-free Antarctica in the Late Cretaceous to early Paleogene enabled dispersals of small terrestrial mammals including marsupials (Beck *et al*., 2008; Sigé *et al*., 2009; Nilsson *et al*., 2010). With the final breakup of Gondwana and establishment of fully marine conditions in the Drake Passage and Tasman Gateway c. 35 Ma (Brown *et al*., 2006), the Antarctic Circumpolar Current steadily increased in strength, conditions changed from greenhouse to icehouse in the Southern Hemisphere, and major Antarctic ice sheets developed by the earliest Oligocene (Exon *et al*., 2004). Steadily improving fossil records in South America, Antarctica, Australia and New Zealand (e.g., Trejedor *et al*., 2005; Hand *et al*., 2007) indicate that for bats and other good dispersers such as birds, insects and some plants, a trans-Antarctic corridor remained open throughout the Eocene and possibly longer, at least while climatic conditions remained favourable, and particularly along the Antarctic coastline. This fossil record, together with improved phylogenetic understanding about modern lineages, also indicates that, in the post-Gondwanan world, dispersal patterns in the Southern Ocean driven by the Antarctic Circumpolar Current /West Wind Drift may well have overwritten more ancient ones derived from a Gondwanan ancestry.

BECK, R.M.D., GODTHELP, H., WEISBECKER, V., ARCHER, M., HAND, S.J. (2008). Australia's oldest marsupial fossils and their biogeographical implications. PLoS ONE 3(3): e1858.

BROWN, B., GAINA, C., MÜLLER, R.D. (2006). Circum-Antarctic palaeobathymetry: Illustrated examples from Cenozoic to recent times. Palaeogeography, Palaeoclimatology, Palaeoecology 231: 158-168.

EXON, N.F., KENNETT, J.P. MALONE, M.J. (2004). The Cenozoic Southern Ocean: Tectonics, Sedimentation and Climate Change between Australia and Antarctica. American Geophysical Union, Washington, DC. 366pp.

FRANCIS, J.E., ASHWORTH, A., CANTRILL, D.J. CRAME, J.A., HOWE, J., STEPHENS, R. TOSOLINI, A.-M., THORN, V. (2008). 100 million years of Antarctic climate evolution: Evidence from fossil plants. In: Cooper, A.K., Barrett, P.J., Stagg, H., Storey, B., Stump, E., Wise, W. (eds) Antarctica: A Keystone in a Changing World. Proceedings of the 10th International Symposium on Antarctic Earth Sciences. The National Academies Press, Washington, DC, pp 19-27.

HAND, S.J., BECK, R.M.D., WORTHY, T.H., ARCHER, M., SIGÉ, B. (2007). Australian and New Zealand fossil bats: The origin, evolution, and extinction of bat lineages in Australasia. Journal of Vertebrate Paleontology 27 (Suppl.): 86A.

HAND, S., NOVACEK, M., GODTHELP, H., ARCHER, M. (1994). First Eocene bat from Australia. Journal of Vertebrate Paleontology 14: 375–381.

NILSSON, M.A., CHURAKOV, G., SOMMER, M., TRAN, N.V., ZEMANN, A., BROSIUS, J., SCHMITZ, J. (2010). Tracking marsupial evolution using archaic genomic retroposon insertions. PLoS Biology 8(7): e1000436.

SIGÉ, B., ARCHER, M., CROCHET, J-Y GODTHELP, H., HAND, S.J., BECK, R.M.D. (2009). *Chulpasia* and *Thylacotinga*, late Paleocene–earliest Eocene trans-Antarctic Gondwanan bunodont marsupials. Geobios 42: 813-823.

TEJEDOR, M.F., CZAPLEWSKI, N.J., GOIN, F.J., ARAGON, E. (2005). The oldest record of South American bats. Journal of Vertebrate Paleontology 25: 990–993.

A new species of *Agerinia* (Primates, Adapiformes) and its bearing on the phylogenetic affinities of *Darwinius masillae*

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The early Eocene locality of Condé-en-Brie, in the Paris Basin, is usually considered very close in age to the reference locality of MP 8–9, Avenay (Louis, 1966). Its fauna is partially published (e.g., Escarguel, 1999). The primates are under study. Three species have been identified: one *Donrussellia*, one *Cantius*, and one new species referable to *Agerinia* (Szalay, 1971). This allows the description of the thus far unknown upper dentition of a species of *Agerinia*. This dentition in turn reveals many similarities to that of *Darwinius masillae*, thus allowing a better assessment of the phylogenetic affinities of the latter.

The upper molars have relatively pointed cusps. Protocone, paracone and metacone have the same height on M^1, and the metacone is slightly lower than the others on M^2 and M^3. The trigon basin is transversely more elongated on M^2 than on M^1, linked to a greater transverse extension of the crown (Fig. 1). Some M^2 have a posterior part narrower than the anterior, associated with a variable lingual shift of the metacone. A continuous crista obliqua joins the protocone and the metacone; the metaconule is absent on M^3, and is variable, sometimes small and well formed, on M^2 and M^1. The paraconule is usually recognizable, situated on a preparaconule crista which joins the anterior rim of the molars. A groove separates it from the well-formed hypoparacrista descending lingually from the paracone summit. A hypocone varies from a relatively big cusp on some M^2 to a smaller one on many M^2 and M^1 to sometimes absent from the lingual extremity of the large posterior cingulum. It is usually crestiform. The anterior cingulum is also well developed, slightly ascending lingually, sometimes thickened at its extremity, to the extreme of forming a real pericone on several M^2. In these cases, the two lingual cusps can become very close to each other. The lingual cingulum varies from largely discontinuous to showing a small interruption, to continuous on some M^1 and M^2, and all M^3. One or two lingual cusps are also often present on the M^3 (when it is large it recalls more a central pericone than a hypocone). The ectocingulum is also variable, continuous or discontinuous, thin or thick, rarely almost lacking.

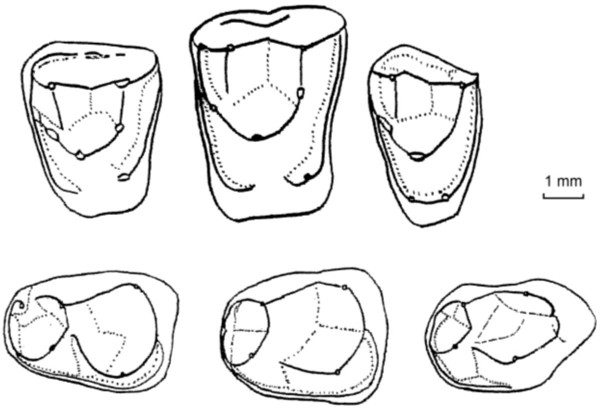

Figure 1. Isolated molars of a new species of *Agerinia* from Condé-en-Brie. Above, left upper molars, left to right M^1, M^2, M^3. Below, left lower molars, left to right M_1, M_2, M_3.

All lower molars have a large, transversely broad talonid basin, and a smaller trigonid (Fig. 1). The trigonid of the M_1 is the largest, with a paraconid small to moderate in size, and a trigonid basin anteroposteriorly longer than on M_2 and M_3. Most M_1 and all M_2 and M_3 have a premetacristid. On M_2 and M_3, it joins the paralophid and makes an almost continuous anterior link between protoconid and metaconid, which is deeply ventrally curved; only one or two small grooves and sometimes a very small, barely recognizable paraconid, interrupt the paralophid. On the M_1, a larger groove usually separates the paraconid and the base of the premetacristid lingually. The hypoconid is very high, voluminous, and pointed. The cristid obliqua is more lingual on M_1, sometimes joining the summit of the metaconid; it is labial on M_2 and M_3, sometimes curving toward the summit of the protoconid on M_3. There is a well-formed labial cingulid, sometimes interrupted at the base of the hypoconid, and, on a few teeth, curving dorsally and creating a very small hypoconulid on the posterior rim. The M_3 has always a long and broad third lobe, with a high hypoconulid summit.

The continuous paralophid of the M_2 and M_3 is typical of *Agerinia roselli* among known cercamoniines, even if the trigonid is anteroposteriorly narrower on the Spanish species. The paraconid is also lost on M_1 in the Spanish species, which is more advanced. Both species share a short and transversely broad talonid basin on M_2, which is derived relative to other cercamoniine genera. Paralophid morphology and talonid proportions refer the new species from Condé-en-Brie to *Agerinia*. The new species illustrates a more primitive stage than *A. roselli*, and more importantly it reveals the upper dentition of a species of *Agerinia*, unknown until now. The upper molars, especially the M^2 with a pericone, show some convergence in characters with species of *Periconodon*. The relationships between the two genera will have to be scrutinized. Importantly enough, many of the peculiar characters found on the molars of *Darwinius masillae* (Franzen *et al.*, 2009) also remarkably resemble those of *Agerinia*. Both share the pointed cusps of the upper molars, the continuous crista obliqua, a continuous lingual cingulum (variable in Condé-en-Brie) bearing a hypocone and a pericone, and on the lower molars a very high hypoconid, a talonid basin much larger and broader than the trigonid, and the almost continuous paralophid on M_2. The two species differ by the loss of the paraconid and the presence of a mesostylid on M_1 in *D. masillae*, both derived characters of the Lutetian species. However, a marked overall similarity and the sharing of derived characters typical of *Agerinia* suggest that *Darwinius* must be phylogenetically very close to *Agerinia*. This hypothesis will have to be scrutinized and tested by further 3D reconstructions of other teeth of *D. masillae*, as well as by further study of the premolars of the Paris Basin species of *Agerinia*. In any case, these similarities confirm the placement of *Darwinius* within the European Cercamoniinae (Franzen *et al.*, 2009). A close affinity of *Darwinius* with *Afradapis* and other primitive adapids was proposed (Seiffert *et al.*, 2009). It seems to us unlikely because the fossils described here do not present the typical adapid dental characters (especially their paralophid). A close affinity of *Agerinia* and *Pronycticebus* was tentatively proposed by Godinot (1998); however, this does not appear straightforward. A more precise placement of *Darwinius* within the European Cercamoniinae will require a more detailed and complete phylogenetic analysis of the subfamily.

ESCARGUEL, G. (1999). Les rongeurs de l'Eocène inférieur et moyen d'Europe occidentale. Systématique, phylogénie, biochronologie et paléobiogéographie des niveaux-repères MP 7 à MP 14. Palaeovertebrata 28: 89-351.

FRANZEN, J.L., GINGERICH, P.D., HABERSETZER, J., HURUM, J.H., KOENIGSWALD, W.V., HOLLY SMITH, B. (2009). Complete primate skeleton from the Middle Eocene of Messel in Germany: Morphology and paleobiology. PLoS ONE 4(5): 1-27.

GODINOT, M. (1998). A summary of adapiform systematics and phylogeny. Folia Primatologica 69 (Sup 1): 218-249.

LOUIS, P. (1966). Note sur un nouveau gisement situé à Condé-en-Brie (Aisne) et renfermant des restes de mammifères de l'Eocène inférieur. Annales de l'Université et de l'A.R.E.R.S. (Reims) 4: 108-118.

SEIFFERT, E.R., PERRY, J.M.G., SIMONS, E.L., BOYER, D.M. (2009). Convergent evolution of anthropoid-like adaptations in Eocene adapiform primates. Nature 461: 1118-1121.

SZALAY, F.S. (1971). The European adapid primates *Agerina* and *Pronycticebus*. American Museum Novitates 2466: 1-19.

Swiss terrestrial mammalian palaeoecosystems from the Eocene: A new submitted SNF project

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At the European scale, most of the Eocene mammal faunas have not been revised for almost twenty years. Most recent faunal lists are mainly compiled into symposium volumes (Schmidt-Kittler *et al.*, 1987; Aguilar *et al.*, 1997), whereas the last taxonomic results are compiled into collective synthesis (Prothero and Schoch, 1989; Prothero and Foss, 2007) or unpublished PhD theses (e.g., Blondel, 1996). All these works represent a good basis for the review of the Swiss faunas, but a greater investigation is necessary for the systematics.

The Swiss Eocene mammal localities are found mostly in the fissure-fillings of the Jura Mountains (NW Switzerland). Among the most important are some renowned localities such as Egerkingen, Dielsdorf and Mormont. The two latter localities were recently reviewed by Rosselet (1991) and Hooker and Weidmann (2000), respectively. However, the last published faunal list of Egerkingen was by Hartenberger in 1970. Despite the importance of this locality for the Eocene fossil record in Europe, no review has been published yet. Indeed, some mammal orders, such as Cetartiodactyla, have not been reviewed since Stehlin (1903–1916), at the beginning of the last century. Additionally, other Eocene mammal localities, such as la Verrerie de Roche in Canton Jura, have been identified but still remain unpublished.

"Terrestrial Palaeoecosystems of Mammals from Eocene: Biodiversity, Biogeochemistry and Biotic/Abiotic Events" is a new project, submitted to the Swiss National Science Foundation (SNF) as the continuation of SNF projects 115995 and 126420 ("Terrestrial Palaeoecosystems of Large Mammals from the Early Oligocene to Early Miocene: Biodiversity, Biogeochemistry and Biotic/Abiotic Events"). This project will focus on the Swiss mammal fossil record from the middle and late Eocene, specifically on the artiodactyls, perissodactyls, and primates, and aims to explore their ecological evolution during this time period and their significance at the scale of Western Europe by comparison with other European localities. The comprehensive study of Egerkingen, partially contemporaneous with the MECO (Middle-Eocene Climatic Optimum; Bohaty and Zachos, 2003), and its comparison with other coeval and younger localities (Fig. 1) will provide additional insight into evolutionary responses to changing environmental conditions and will allow us to question the influence of climatic events on the evolutionary patterns of mammal communities during the Eocene.

A wide array of proxies, such as taxonomy, body mass, locomotion type, diet, species richness, and commonness, will be characterized through anatomical comparison and dental meso- and microwear, as well as through biogeochemical analyses. The taxonomical studies will concentrate primarily on Swiss mammal remains, but will also be extended to other significant European material. The commonness of a species includes its relative abundance at a fossil locality and its locality coverage. Species richness will be treated at both local and Western European scales. The results will then be compared with the main mammal localities of Switzerland and Western Europe from the early Oligocene and studied in the frame of previous SNF projects.

Aguilar, J.-P., Legendre, S., Michaux, J. (1997). Actes du congrès Biochrom'97. Mémoires et Travaux de l'Ecole pratique des Hautes Etudes, Institut de Montpellier 21, 805 pp.

Blondel, C. (1996). Les ongulés à la limite Eocène/Oligocène et au cours de l'Oligocène en Europe occidentale: analyses faunistiques, morpho-anatomiques et biogéochimiques (d^{13}C, d^{18}O). Implications sur la reconstitution des paléoenvironnements. PhD Thesis, University of Montpellier II, France, 119 pp.

Bohaty, S.M., Zachos, J.C. (2003). Significant Southern Ocean warming event in the late middle Eocene. Geology 31: 1017-1020.

Cande, S.C., Kent, D.V. (1995). Revised calibration of the geomagnetic polarity time scale. Journal of Geophysical Research 100: 6093–6095.

Franzen, J.L. (2005). The implication of the numerical dating of the Messel fossil deposit (Eocene, Germany). Annales de Paléontologie, Volume 91(4): 329-335.

Gradstein, F.M., Ogg, J.G., Smith, A.G. (2004). A Geological Time Scale. Cambridge University Press, Cambridge, 589pp.

Grimes, S.T., Hooker, J.J., Collinson, M.E., Matthey, D.P. (2005). Summer temperatures of late Eocene to early Oligocene freshwaters. Geology 33(3): 189-192.

Hartenberger, J.-L. (1970). Les mammifères d'Egerkingen et l'histoire des faunes de l'Écène d'Europe. Bulletin de la Société géologique de France 12: 886-893.

Hooker, J.J., Collinson, M.E., Sille, N.P. (2004). Eocene–Oligocene mammalian faunal turnover in the Hampshire Basin, UK: Calibration to the global time scale and the major cooling event. Journal of the Geological Society 161: 161-172.

Hooker, J.J., Weidmann, M. (2000). The Eocene mammal faunas of Mormont, Switzerland. Mémoires suisses de Paléontologie 120: 1-143.

Mosbrugger, V., Utescher, T., Dilcher, D.L. (2005). Cenozoic continental climatic evolution of Central Europe. Proceedings of the National Academy of Sciences of the United States of America 102(42): 14964-14969.

Prothero, D.R., Foss, S.C. (2007). The Evolution of Artiodactyls. The Johns Hopkins University Press, Baltimore. 367pp.

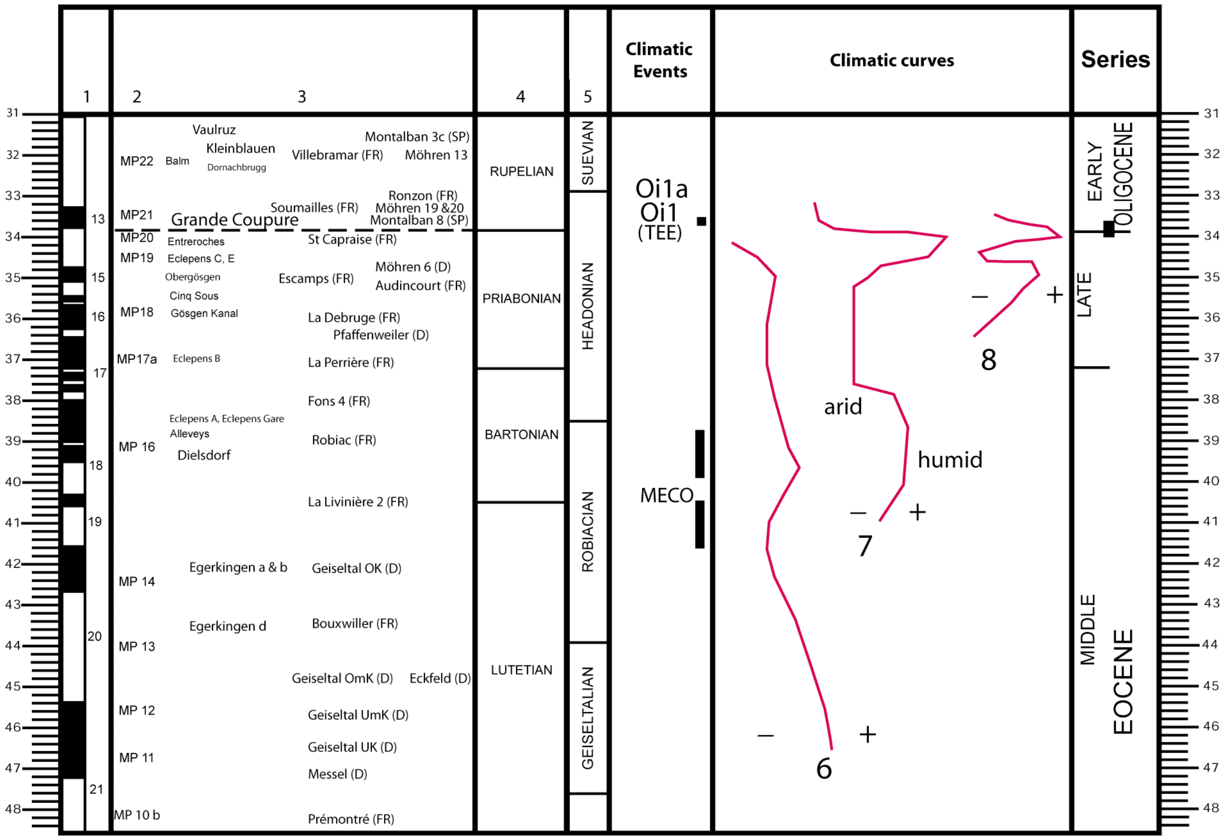

Figure 1. Stratigraphical chart of the Eocene. 1) Magnetostratigraphy (Cande and Kent, 1995); 2) European Land Mammal Zones (Hooker *et al.*, 2004; Franzen, 2005); 3) Swiss and some other European localities (Aguilar *et al.*, 1997); 4) Mediterranean stages (Gradstein *et al.*, 2004); 5) European Land Mammal Ages (ELMA; Gradstein *et al.*, 2004); 6) continental temperature evolution in Lower Rhine Graben (Mosbrugger *et al.*, 2005); 7) continental temperature and precipitation evolution in NW China (Yunfa *et al.*, 2008); 8) continental temperature evolution in Hampshire (Grimes *et al.*, 2005); climatic events (Bohaty and Zachos, 2003).

Prothero, D.R., Schoch, R.M. (1989). The Evolution of Perissodactyls. Clarendon Press, Oxford University Press, New York, Oxford. 537pp.

Rosselet, C. (1991). Die Fauna des Spaltenfüllungen von Dielsdorf (Eozän, Kanton Zürich). Documenta naturae 64: 1-177.

Schmidt-Kittler, N., Brunet, M., Godinot, M., Franzen, J. L., Hooker, J. J., Legendre, S., Vianey-Liaud, M. (1987). European reference levels and correlation tables. In: Schmidt-Kittler, N. (ed) International Symposium on Mammalian Biostratigraphy and Paleoecology of the European Paleogene. Münchner Geowissenschaftliche Abhandlungen Reihe A, Geologie und Paläontologie 10, pp 13–31.

Stehlin, H.G. (1903-1916). Die Säugetiere des schweizerischen Eocäns. Kritischer Katalog der Materielen. I-VII. Mémoires suisses de Paléontologie 30-33, 35-36, 38, 41: 1-1552.

Yunfa, M., Fang, X., Song, Z., Wu, F., Han, W., Dai, S., Song, C. (2008). Late Eocene pollen records and palaeoenvironmental changes in northern Tibetan Plateau. Science in China Series, Earth Sciences 51(8): 1089-1098.

Cranial morphology of the Eocene primate *Darwinius masillae*

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Darwinius masillae, nicknamed "Ida", is an almost complete primate skeleton from the Messel quarry (Franzen *et al.*, 2009). The age and the completeness of the specimen make it an important landmark for any evolutionary study of primate hands and feet (Fleagle, 2010), but so far the skull has been regarded as very difficult to interpret beyond detecting most of the sutures between the skull bones.

In the cladistic analysis of Gingerich *et al.* (2010) the basicranial characters of *Darwinius* were not scored in the matrix. Damage due to compression of the bulla and the splitting of the plates destroyed most of the details. A first interpretation of parts of the basicranium with the right petrosal partly preserved on Plate A is now achievable (Fig. 1).

The two sides of *Darwinius masillae* are now for the first time studied simultaneously. The two sides are named Plate A (PMO 214.214) for the right side housed in the Natural History Museum in Oslo, and Plate B (WDC-MG-210) for the less complete left side housed in the Wyoming Dinosaur Center. Plate A and Plate B have been micro-CT scanned at the Senckenberg Forschungsinstitut Frankfurt, each slice with the thickness of 37.8 μm. Combining the two series of scans reveals the complete dentition of the specimen. Here we present the complete dentition of *Darwinius* in 3D for the first time (Fig. 2).

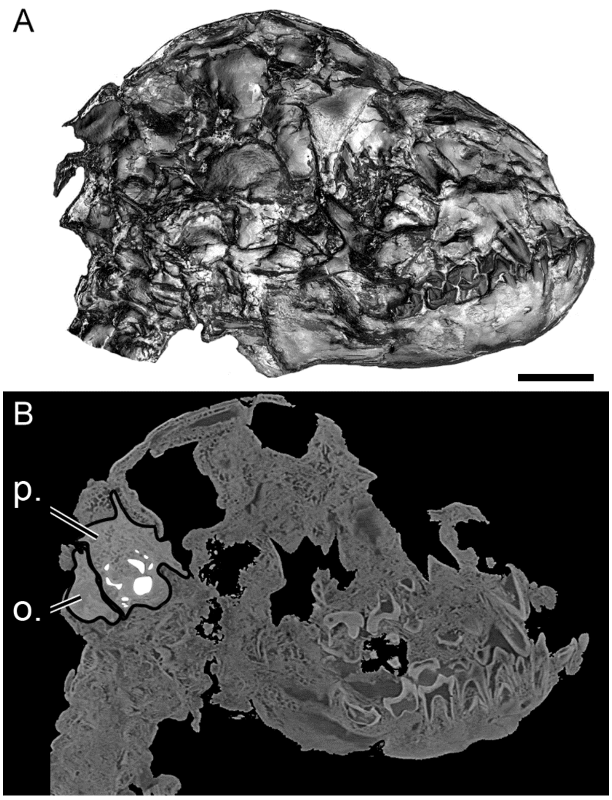

Figure 1. Skull of *Darwinius masillae* Plate A (PMO 214.214). **A.** Photograph. **B.** CT section no. 77 showing part of the inner ear in white, p.= petrosal; o.= occipital, Scale bar 8.5mm.

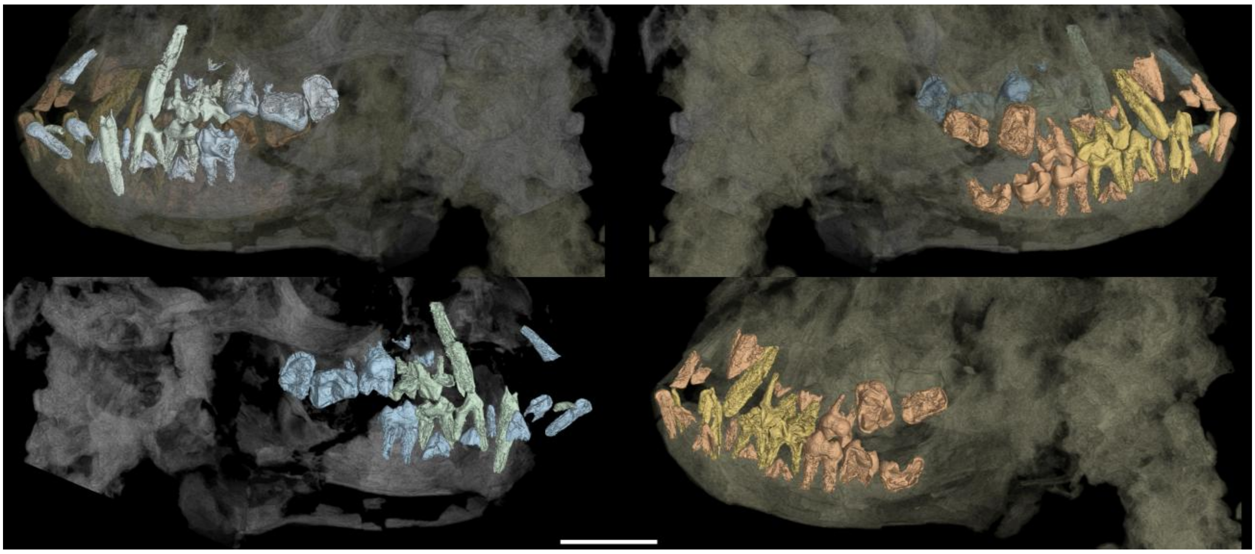

Figure 2. Left dentition (upper and lower left) and right dentition (upper and lower right) of *Darwinius masillae* from combined 3D micro-CT data sets of Plate A and Plate B. Scale bar 10.0 mm.

FLEAGLE, J.G. (2010). The many worlds of Ida. Perspectives in Biology and Medicine 53 (4): 605-612.

FRANZEN, J.L., GINGERICH, P.D., HABERSETZER, J., HURUM, J.H., KOENIGSWALD, W.V., SMITH, B.H. (2009). Complete primate skeleton from the middle Eocene of Messel in Germany: Morphology and paleobiology. PLoS ONE 4 (5): 1-27, e5723.

GINGERICH, P.D., FRANZEN, J.L., HABERSETZER, J., HURUM J.D., SMITH, B.H. (2010). *Darwinius masillae* is a haplorhine – Reply to Williams *et al.* (2010). Journal of Human Evolution 59: 574-579.

A new late Paleocene micromammal fauna from Montchenot (Paris Basin)

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Fossil faunas from the Paris Basin provide the best window into the structure of tetrapod and particularly mammal faunas in Europe prior to the Paleocene/Eocene boundary. Late Paleocene mammals of the Paris Basin are known mainly from Cernay and Berru near Reims (Louis, 1996). A new Thanetian mammal fauna is described here from the marls accessible in the abandoned quarry "Les Monts-Martin" at Montchenot near Reims (Marne), a deposit previously known for its well-preserved freshwater mollusk fauna (Laurain and Henry, 1968). The occurrence of mammals and other vertebrates in the Marnes de Montchenot has been announced by Laurain and Meyer (1986), but no detailed analysis of this fauna has up to now been published.

The study of the Montchenot mammal fauna is based on collections previously made by amateurs and on the results of excavations carried out by the Laboratoire d'Evolution des Primates (EPHE). Fossil mammal specimens occur in grayish marls rich in algal concretions, especially in their upper levels. 320 kg of sediment was screen-washed in 2009, yielding about 40 identifiable mammal teeth, which complement approximately 90 identifiable mammal specimens available from older collections. Further increase of the sample size is expected from sorting of the residue obtained by the screen-washing of 670 kg of matrix in 2010. Identifiable mammal specimens are almost exclusively isolated teeth, but a maxillary with P^3-M^3 of the louisinine "condylarth" *Louisina* demonstrates the site's potential for delivering more complete fossil remains. Small-sized mammals are dominating the assemblage, and none of the largest-sized species known from the Thanetian of the Paris Basin have been recovered up to now.

Multituberculates form an abundant and diversified part of the Montchenot assemblage, with at least four species of *Neoplagiaulax* identified thus far. Insectivore-like eutherians are also well represented, especially the erinaceomorph lipotyphlans, which include the highly common *Adapisorex* and the rarer *Adunator*. Of particular interest are several specimens of an insectivore first described as *Aboletylestes?* sp. on the basis of a single upper molar from the Lentille de Berru (Russell *et al.*, 1966). The Berru specimen was subsequently assigned to *Nosella europaea* (López-Martínez and Peláez-Campomanes, 1999), a species of uncertain affinities based on material from the Thanetian of the Tremp Formation in the Spanish Pyrenees. The additional sample from Montchenot, which includes upper molars (Fig. 1) and tentatively associated lower molars, will allow for a better characterization of the species present in the Paris Basin, for evaluation of its identity with the Tremp species, and for investigation of its affinities.

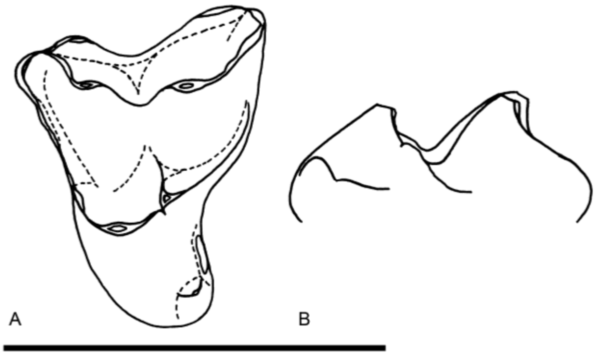

Figure 1. M^1 from Montchenot (MON DD 18) possibly referable to *Nosella europaea* Peláez-Campomanes, 1999. A. Occlusal view. B. Posterior view. Scale bar 3 mm.

The smallest insectivore-like forms from Montchenot belong to the Adapisoriculidae, a family recently brought into the focus of research because of their possible relationships with plesiadapiforms (Storch, 2008) or Euarchonta (Smith *et al.*, 2010). Preliminary results suggest that at least the adapisoriculid genera *Adapisoriculus* and *Afrodon* are present at Montchenot. Among definitive plesiadapiforms, *Plesiadapis* is common at Montchenot (approximately 10% of all specimens) but not as dominant as in the faunas of Cernay and Berru. In contrast, the tiny toliapinid plesiadapiform *Sarnacius* is surprisingly common at Montchenot, accounting for almost 5% of the currently known specimens. Additional collecting will show whether this unusual structure of the plesiadapiform component of the fauna can be confirmed for larger sample sizes.

As is typical of the European late Paleocene faunas, "condylarth" mammals are well represented at Montchenot. Small-sized forms belonging to the Louisininae are the most common and diverse "condylarths" in this assemblage. They include previously described species (*Dipavali petri*, *Louisina mirabilis)* as well as several probably new forms. The pleuraspidotheriid "condylarths" *Pleuraspidotherium* and *Orthaspidotherium*, which form a dominant part of the faunas of Cernay and Berru, are present but rare at Montchenot. This may be explained at least for the former genus by its relatively large size. Arctocyonids, most of which are likewise larger-sized, are documented by rare occurrences of *Arctocyonides*.

The fossil mammals recovered from the Marnes de Montchenot allow correlation with the European mammalian reference level MP6, confirming the Late Thanetian age previously determined on the basis of mollusks (Laurain and Henry, 1968) and charophytes (Riveline, 1976). The Montchenot assemblage differs from the faunas of Cernay and Berru in being dominated by small mammal species, with high abundance of multituberculates, small insectivores and louisinine "condylarths" and less common occurrence of *Plesiadapis* and pleuraspidotheriid "condylarths". In these respects it resembles the small collection of Thanetian mammals briefly described by Russell *et al.* (1966) from the Marnes de Rilly, about 3 km east of Montchenot, apparently a close stratigraphic correlative (Laurain and Meyer, 1986). Differences in faunal composition compared to the fluvial-deltaic Conglomérat de Cernay and the fluviatile deposits of Berru seem to result mainly from a different environmental setting and different preservation biases in a calm, yet not completely stagnant freshwater milieu (Laurain and Henry, 1968).

The mammal fauna from Montchenot thus provides the opportunity to better understand a hitherto rarely sampled habitat and to improve our knowledge of the small mammals existing in Europe before the large-scale faunal exchanges linked to the advent of the Eocene. Further study of the new fauna, based on increased sample sizes, may allow for its more detailed placement in the succession of fossil localities in the Paris Basin close to the Paleocene-Eocene boundary.

Laurain, M., Henry, P. (1968). Montchenot: Gisement accessible de la faune thanétienne du calcaire lacustre de Rilly. Annales de l'Université et de l'ARERS, Reims 6: 127–132.

Laurain, M., Meyer, R. (1986). Stratigraphie et paléogéographie de la base du Paléogène champenois. Géologie de la France 1986: 103–123.

López-Martínez, N., Peláez-Campomanes, P. (1999). New mammals from south-central Pyrenees (Tremp Formation, Spain) and their bearing on late Paleocene marine-continental correlations. Bulletin de la Société géologique de France 170: 681–696.

Louis, P. (1996). Recherches de mammifères paléogènes dans les départements de l'Aisne et de la Marne pendant la deuxième moitié du vingtième siècle. Palaeovertebrata 25: 83–113.

Riveline, J. (1976). Étude floristique des niveaux marneux de la carrière de Montchenot (Marne). Mise en évidence d'une nouvelle association de Characées d'âge thanétien. Comptes Rendus de l'Académie des Sciences de Paris, série D 283: 25–28.

Russell, D.E., Louis, P., Poirier, M. (1966). Gisements nouveaux de la faune cernaysienne (Mammifères paléocènes de France). Bulletin de la Société géologique de France, 7e sér. 7: 845-856.

Smith, T., Bast, E. de, Sigé, B. (2010). Euarchontan affinity of Paleocene Afro-European adapisoriculid mammals and their origin in the late Cretaceous Deccan Traps of India. Naturwissenschaften 97: 417–422.

Storch, G. (2008). Skeletal remains of a diminutive primate from the Paleocene of Germany. Naturwissenschaften 95: 927–930.

The taphonomic settings of the Eocene Messel Pit, Germany: Insights from the turtle fauna

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The Eocene (Lutetian) Messel pit near Darmstadt, Germany is notable for its extremely diverse assemblage of animals and plants that are preserved in a black oil shale. The site has yielded a large number of vertebrate fossils preserved as complete skeletons, often including soft tissue structures (e.g., Schaal *et al.*, 1988; Koenigswald and Storch, 1998). The exclusive presence of fresh water and terrestrial taxa reveals that the Messel oil shale was deposited under anoxic conditions at the bottom of a deep, tropical lake. There is little agreement, however, which mechanisms lead to the unusual accumulation of bats and birds relative to other fossil lake deposits. Some taphonomic models suggest that high levels of poisonous gases, such as carbon dioxide, were periodically emitted from the volcanic lake and thereby caused the death of the animals in the lake as well as numerous overflying birds and bats (e.g.; Richter and Storch, 1980; Franzen and Köster, 1994). A more recent competing hypothesis, by contrast, suggests that episodic algal blooms in the summer months poisoned the animals that lived in or drank from the surface waters of the lake (Koenigswald *et al.*, 2004).

Turtles represent a notable aspect of the Messel fauna. At least seven turtle taxa are currently recognized, including a trionychid (Karl, 1999), a carettochelyid (Keller and Schaal, 1988), a podocnemidid (Schleich, 1993), and four testudinoids (Hervet, 2004). The carettochelyid turtle *Allaeochelys crassesculpta* (Harrassowitz, 1922) is a particularly notable element, not only because it represents the only known occurrence of complete fossil carettochelyid skeletons worldwide, but also because a considerable portion of specimens (at least fourteen) are found in pairs (Fig. 1). Rietschel (1998) hypothesized that these pairs represent turtles that died during copulation. Koenigswald *et al.* (2004) agreed, but suggested that the prevalence of mating deaths indicate that surface waters were poisoned by cyanobacteria during the mating season of these animals, likely during the late spring to early summer.

Trionychians, the clade formed by Trionychidae and Carettochelyidae, generally lack osteological characteristics that allow distinguishing the sexes, including the concave plastron so typical of other turtles (Ernst and Barbour, 1989). We therefore see no possibility of morphologically confirming that the *A. crassesculpta* couples consist of female and male individuals. We nevertheless agree that accidental death while mating is the most plausible mechanism that would lead to the accumulation of so many couples. The extant taxon *Carettochelys insculpta* is nevertheless known to be highly territorial outside the mating season and it therefore appears at least plausible that these couples represent individuals that perished during territorial fights.

Trionychians are unique among extant freshwater turtles by having almost fully lost the reptilian scales that primitively cover the entire body and shell of other turtles (Ernst and Barbour, 1989). Among living trionychids the absence of scales has been shown to be coupled with the skin acting as a respiratory membrane that allows animals to absorb oxygen from the water and remain under water for extended time (e.g., Ultsch *et al.*, 1984; Bagatto and Henry, 1998). The selective advantage of this external respiratory membrane, however, has been shown to be a disadvantage under anoxic conditions, because poisons are absorbed as well (Reese *et al.*, 2003). Although the physiological properties of carettochelyid skin has not yet been studied, the gross similarity with trionychid skin, the sistergroup relationship to trionychids (Meylan, 1987), and exclusive presence of the extant *C. insculpta* in oxygenated rivers and lakes (Ernst and Barbour, 1989) allow us to speculate that carettochelyids also respire over the skin.

The reproductive behavior of fresh water turtles is poorly known (Ernst and Barbour, 1989), but some tendencies are nevertheless apparent: aquatic turtles universally mate in the water and the male universally mounts the female from the rear. Finally, once the male successfully mounts the female, the couple will often actively freeze in their position before separating. If mounting occurs in the open water, the mating couple may therefore sink to considerable depths. Although no data is available, we think it to be impossible for a dead couple to be transported in this embrace.

By comparison to their extant relatives (Ernst and Barbour, 1989), the carettochelyid *A. crassesculpta* is the only Messel turtle to have likely inhabited and mated in the open waters of the lake. The respiratory capability of their skin, however, predicts that surface waters were oxygenated and non-poisonous. Instead, it appears more plausible that the turtle courted and initiated copulation in surface waters, but perished while sinking into toxic subsurface layers.

In conclusion, we confirm that the surprising number of *A. crassesculpta* pairs found at Messel represent turtle pairs that perished while mating. The exclusive presence among turtles of *A. crassesculpta* pairs, however, is only a taphonomic bias, as these are the only turtles at Messel to likely have mated in

Figure 1. Ventral view of SMF ME 2449, two individuals of *Allaeochelys crassesculpta* recovered from the Eocene Messel pit near Darmstadt, Germany. The contact of both individuals in the caudal region is further evidence that this fossil may represent a couple that perished during copulation. The dorsally positioned larger individual likely represents the male who slipped of the highly domed carapace of the female just before or after death. © Senckenberg Forschungsinstitut und Naturmuseum Frankfurt.

the open water. The likely respiratory qualities of the skin of *A. crassesculpta* and the likely inability of these turtles to live in poisonous waters predicts that the turtle must have courted and mated in regular, oxygenated water, but perished while sinking to deeper, poisonous layers. Although the possibility remains that the surface waters at Messel were poisoned regularly by cyanobacterial blooms, the dead *A. crassesculpta* couples are more consistent with a stratified lake with poisonous deep waters.

Bagatto, B., Henry, R.P. (1999). Exercise and forced submergence in the pond slider (*T. scripta*) and softshell turtle (*A. ferox*): influence on bimodal gas exchange, diving behaviour and blood acid-base status. Journal of Experimental Biology 202: 267–278.

Ernst, C.H., Barbour, R.W. (1989). Turtles of the World. Smithsonian Institution Press, Washington DC.

Franzen, J.L., Köster, A. (1994). Die eozänen Tiere von Messel - ertrunken, erstickt oder vergiftet? Natur und Museum 124: 91–97.

Harrassowitz, H. (1922). Die Schildkrötengattung *Anosteira* von Messel bei Darmstadt und ihre stammesgeschichtliche Bedeutung. Abhandlungen der Hessischen Geologischen Landesanstalt zu Darmstadt 6: 137–238.

Hervet, S. (2004). Systématique du groupe «*Palaeochelys* sensu lato–*Mauremys*» (Chelonii, Testudinoidea) du Tertiaire d'Europe occidentale : principaux résultats. Annales de Paléontologie 90: 13–78.

Karl, H.-V. (1999). Die Zoogeographie der känozoischen Weichschildkröte *Trionyx triunguis* Forskal, 1775 (Testudines: Trionychidae). Joannea – Geologie und Paläontologie, 1: 27–60.

Keller, T., Schaal, S. (1988). Schildkröten – zu Lande und im Wasser. In: Schaal, S., Ziegler, W. (eds) Messel – Ein Schaufenster in die Geschichte der Erde und des Lebens. Kramer, Frankfurt am Main, pp. 101–106.

Koenigswald, W.v., Braun, A., Pfeiffer, T. (2004). Cyanobacteria and seasonal death: a new taphonomic model for the Eocene Messel lake Palaontologische Zeitschrift 78: 417–424.

Koenigswald, W.v., Storch, G. (eds) (1998). Messel, ein Pompeji der Palaontologie. Thorbecke, Sigmaringen.

Meylan, P.A. (1987). Phylogenetic relationships of soft-shelled turtles. Bulletin of the American Museum of Natural History 186: 1–101.

Reese, S.A., Jackson, D.C., Ultsch, G.R. (2003). Hibernation in freshwater turtles: softshell turtles (*Apalone spinifera*) are the most intolerant of anoxia among North American species. Journal of Comparative Physiology B 173: 263–268.

Richter, G., Storch, G. (1980). Beiträge zur Ernährungsbiologie eozäner Fledermause aus der Grube Messel. Natur und Museum 110: 353–367.

Rietschel, S. (1998). Schildkröten bei der Paarung? In: von Koenigswald, W., Storch, G. (eds) Messel, ein Pompeji der Palaontologie. Thorbecke, Sigmaringen, pp. 44–45.

Schaal, S., Ziegler, W. (eds) (1988). Messel – Ein Schaufenster in die Geschichte der Erde und des Lebens. Kramer, Frankfurt am Main.

Schleich, H.-H. (1993). New reptile material from the German Tertiary. 11. *Neochelys franzeni* n. sp., the first pleurodiran turtle from Messel. *Kaupia* 3: 15–21.

Ultsch, G.R., Herbert, C.V., Jackson, D.C. (1984). The comparative physiology of diving in North American freshwater turtles. I. Submergence tolerance, gas exchange and acid–base balance. Physiological Zoology 57: 620–631.

Fossil bugs (Insecta: Heteroptera) of Messel and the Green River Formation (USA) – Are there any connections?

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Analyses of Cenozoic diversity trends and of the historical biogeography of certain insect groups are still rare. On the one hand, this is probably because of the still limited data basis for fossil insects. On the other hand, comparisons of taxa of different fossil sites have to be handled with caution because of the incompleteness of the fossil record and influences of taphonomy on fossilization (Kidwell and Holland, 2002). Similarly, interrelationships between climate change and biogeographic diversity patterns are still under discussion (e.g., Wiens and Donoghue, 2004; Lomolino *et al*., 2006).

Biogeographic history plays a decisive role in forming large-scale diversity patterns. There are hypotheses which suggest that niche conservatism in the face of climate change is an important driving force in the distribution of taxa (Wiens and Donoghue, 2004). Species in clades that initially evolved in the warm climates of the early Cenozoic may have been heavily extirpated in the northern parts of their former distribution during the cooling in the Cenozoic (e.g., Eskov, 2002; Grimaldi and Engel, 2005).

The increasing availability of well-founded hypotheses on phylogenetic relationships among insects, in combination with reliable fossil records, makes it possible to illuminate biogeography and biogeographic history (e.g., Wiens and Donoghue, 2004). Including temporal information in biogeographic studies is crucial for elucidating connections between biogeographic patterns and their underlying causes. For example, only via inclusion of the timing of events it is possible to connect diversification processes with processes in the geological history and perhaps infer their causal explanations (Donoghue and Moore, 2003).

Fossils have been shown to be important in redefining biogeographic hypotheses for many insect groupsthat were believed to have restricted distributions when only extant taxa were considered (e.g., Eskov, 2002; Grimaldi and Engel, 2005).

In this study, heteropteran insects are taken as a showcase for illuminating differences and similarities of biodiversity between Eocene fossil sites. A focus will be the investigation of the Heteroptera mainly from the Eocene fossil sites Messel (Germany, 47 Ma (Mertz and Renne, 2005)) and from the Piceance Creek Basin, part of the Green River locality (USA, about 50 Ma (Smith *et al*., 2008)).

From both fossil sites a high number of well-preserved heteropteran fossils is available for study. About 1,400 heteropteran specimens from Messel are accessible via the collection of the Senckenberg Research Institute (Frankfurt am Main, Germany); from Green River there are several hundred fossil heteropterans available for investigation, which are stored at the National Museum of Natural History, Smithsonian Institution (Washington, USA). Heteroptera are the largest and most diverse group of hemimetabolous insects. Over 80 families with more than 42,000 species are described from all over the world (Schuh and Slater, 1995; Henry, 2009). Fossil bugs have not been studied extensively by paleoentomologists, and little is known about the Heteroptera from both localities.

Based on comparative systematic studies of heteropteran taxa from both sites, biogeographic questions will be addressed and will be put into a broader context of biogeographic history. For example, for assassin bugs (Reduviidae), the biodiversity in Messel and Green River will be compared. Based on already existent phylogenies, diversification processes and pathways of biogeography will be reconstructed. To supplement the study, heteropterans from other mostly Eocene fossil sites will be studied.

DONOGHUE, M.J., MOORE, B.R. (2003). Toward an integrative historical biogeography? Integrative and Comparative Biology 43: 261-270.

ESKOV, K.Y. (2002). Geographical history of insects. In: Rasnitsyn, A.P., Quicke, D.L.J. (eds) History of Insects. Kluwer Academic Publishers, Dordrecht, pp 427-435.

GRIMALDI, D.A., ENGEL, M.S. (2005). Evolution of the insects. Cambridge University Press, Cambridge. 755 pp.

HENRY, T. (2009). Biodiversity of Heteroptera. In: Foottit, R.G., Adler, P.H. (eds) Insect Biodiversity Science and Society. Wiley-Blackwell, Chichestter, pp 223-263.

KIDWELL, S.M., HOLLAND, S.M. (2002). The quality of the fossil record: Implications for evolutionary analyses. Annual Review of Ecology and Systematics 33: 561-588.

LOMOLINO, M.V., RIDDLE, B.R., BROWN, J.H. (2006). Biogeography. Sinauer Associates, Sunderland, Massachusetts. 845 pp.

MERTZ, D.F., RENNE, P.R. (2005). A numerical age for the Messel fossil deposit (UNESCO World Heritage Site) derived from 40Ar/39Ar dating on a basaltic rock fragment. Courier Forschungsinstitut Senckenberg 255: 67-75.

SCHUH, R.T., SLATER, J.A. (1995). True bugs of the world (Hemiptera: Heteroptera). Classification and Natural History. Cornell University Press. Ithaca, New York. 337 pp.

SMITH, M.E., CARROLL, A.R., SINGER, B.S. (2008). Synoptic reconstruction of a major ancient lake system: Eocene Green River Formation, western United States. Geological Society of America Bulletin 120: 54-84.

WIENS, J.J., DONOGHUE, M.J. (2004). Historical biogeography, ecology and species richness. Trends in Ecology and Evolution 19: 639-644.

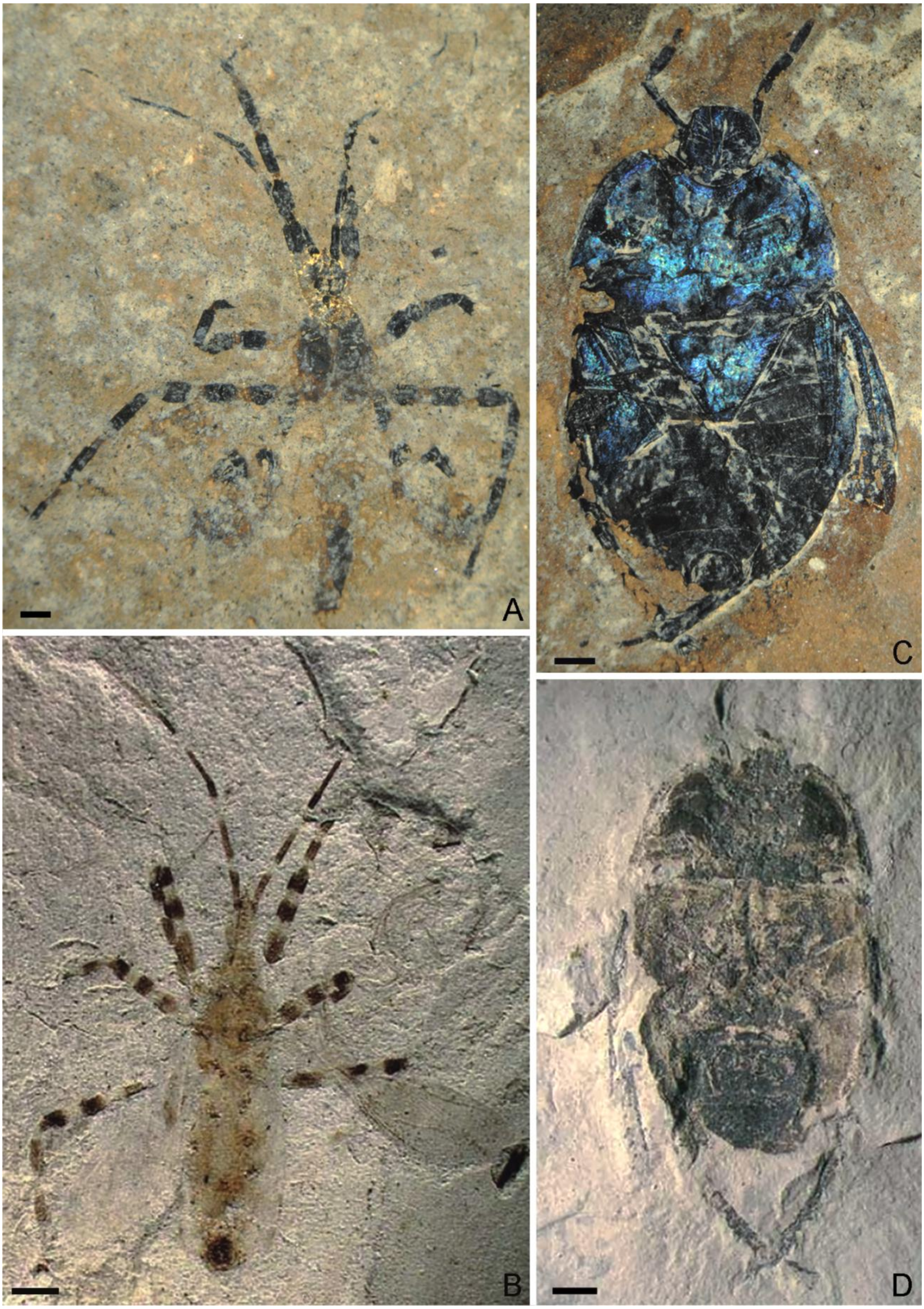

Figure 1. A) Assassin bug (Reduviidae) from Messel (FIS, coll.-nr. Mel7203). B) Assassin bug (Reduviidae) from Green River (SI, coll.-nr. He 169). C) Burrower bug (Cydnidae) from Messel (FIS, coll.-no. Mel4714). D) Burrower bug (Cydnidae) from Green River (SI, coll.-no. He 126). Photographs A + C: Kiel, B + D: Hamlin. Scale bars = 1mm.

Morphology and evolution of the distal phalanges in primates

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Flat nails and scutiform distal phalanges characterize the hands and feet of primates. However, these display a variety of forms and combinations: Lemuroidea and Lorisoidea have a distinct pedal grooming claw; *Daubentonia* has additional claws; *Tarsius* has two pedal grooming claws; Callithrichidae have claws on fingers and most toes. The adapoid primates *Darwinius* and *Europolemur* from Messel have been interpreted both to have and to lack a grooming claw (Koenigswald, 1979; Franzen, 1994; Franzen *et al.*, 2009).

A single two-state character, "*presence or absence of claws or grooming claws*," was used to represent claws in the cladistic analyses of Seiffert *et al.* (2009), Williams *et al.* (2010), and Gingerich *et al.* (2010). However, the distal phalanges in primates are quite diverse, and the claws or claw-like structures of primates may not be adequately represented by a single two-state character. In a detailed survey we provisionally distinguished 11 morphological types of distal phalanges in primates. Some are shown in Figs. 1–11. In the course of this survey, we realized that it is not sufficient to simply note the presence or absence of particular types of distal phalanges, their occurrence on specific fingers or toes having great significance as well. Many primate taxa have distal phalanges of different forms on different digits of the hands and feet. Thus in addition to characterizing the form of individual phalanges, the position and combination with other types of phalanges has to be recognized.

Positions and combinations are especially important when isolated distal phalanges of fossils are discussed (Godinot 1992; Bloch *et al.*, 2010) because their positions and combinations are unknowable. Very few skeletons of fossil primates are known that allow an unquestionable assignment of distal phalanges to specific fingers or toes. Messel in Germany is one of the few localities where such assignments are possible because the fossils are preserved in oil shale as partial or complete articulated skeletons.

To better understand *Europolemur* and *Darwinius*, we started a survey comparing the morphology of distal phalanges across primates. We included *Tupaia* as an outgroup. Zoological collections often have distal phalanges retained in skin preparations or, in articulated skeletons, partially hidden by ligaments. For this reason, it has been advantageous to use high-resolution virtual reconstructions from micro-CT scans.

Our preliminary results show some basic differences in different primates that will enable a more detailed characterization of their distal phalanges (DP), and also of their positions and combinations on various digits of the hands and feet. Here we denote distal phalanges of the manus as Mɪ, Mɪɪ, Mɪɪɪ, Mɪᴠ, and Mᴠ; and distal phalanges of the pes as Pɪ Pɪɪ, Pɪɪɪ, Pɪᴠ, and Pᴠ.

Scandentia, represented by *Tupaia* (Fig. 7), are characterized by laterally compressed claws with large tubercles for the insertion of the flexor tendon in all rays (Mɪ–Mᴠ and Pɪ–Pᴠ). The claws of *Tupaia*, in contrast to those of *Callithrix* (Fig. 11), have no lateral furrows (Le Gros Clark, 1936; Godinot, 1992).

Lemuroidea and Lorisoidea, represented by *Indri, Microcebus, Lemur* (Figs. 1, 2, 8), *Varieca* (Fig. 9), *Cheirogaleus* (Fig. 12), and others, have scutiform DPs on all digits of the hand. The shaft is well separated from the shield, which is pointed. Mɪ is of variable size but never prominent, in contrast to the enlarged and widened DP of Pɪ. The characteristic grooming claw, Pɪɪ, is elongated and slender. There is variability within Lemuroidea, but several characteristics were found that distinguish the grooming claws of lemurs, including *Daubentonia*, from claws of *Tupaia.* The remaining DPs (Pɪɪɪ–Pᴠ) are typically scutiform. The only lemur known to lack grooming claws is *Archaeolemur*, which has no grooming claw in the reconstruction of Jungers *et al.* (2005).

Tarsioidea, represented by *Tarsius* (Fig. 10, 13), has scutiform DPs on all fingers. The opposable Pɪ is scutiform, as are those of Pɪᴠ and Pᴠ. Pɪɪ and Pɪɪɪ are commonly classified as "grooming claws". However, they differ from lemuroid and lorisoid grooming claws not only in number and position, but also in their morphology. The grooming claws of *Tarsius* are short and have a triangular cross-section. A large attachment for the flexor tendon is present, well separated from the plantar side. Thus they are not a duplication of the lemuroid Pɪɪ but seemingly a similar but independent adaptation. The scutiform DPs of *Tarsius* are more similar to those of lemuroids and lorisoids than are the grooming claws.

Ceboidea, Cercopithecoidea, and Hominoidea have similar DPs on fingers and toes, and share the enlarged, widened, more or less scutiform DP of Pɪ. The pattern of the remaining digits does not show any differentiation of Pɪɪ or Pɪɪɪ. The morphology of these DPs seems to be basically different from that of lemuroids, lorisoids, and tarsioids. The DPs have a large articular facet, and the distal part is more columnar and rounded without being pointed (Fig. 4). Some genera show a tendency to develop some rugosity near the distal end (Fig. 5). This pattern was found, e.g., in *Cebus*, *Macaca*, *Mandrillus*, and *Pan*. Only a few genera developed properly scutiform DPs, best

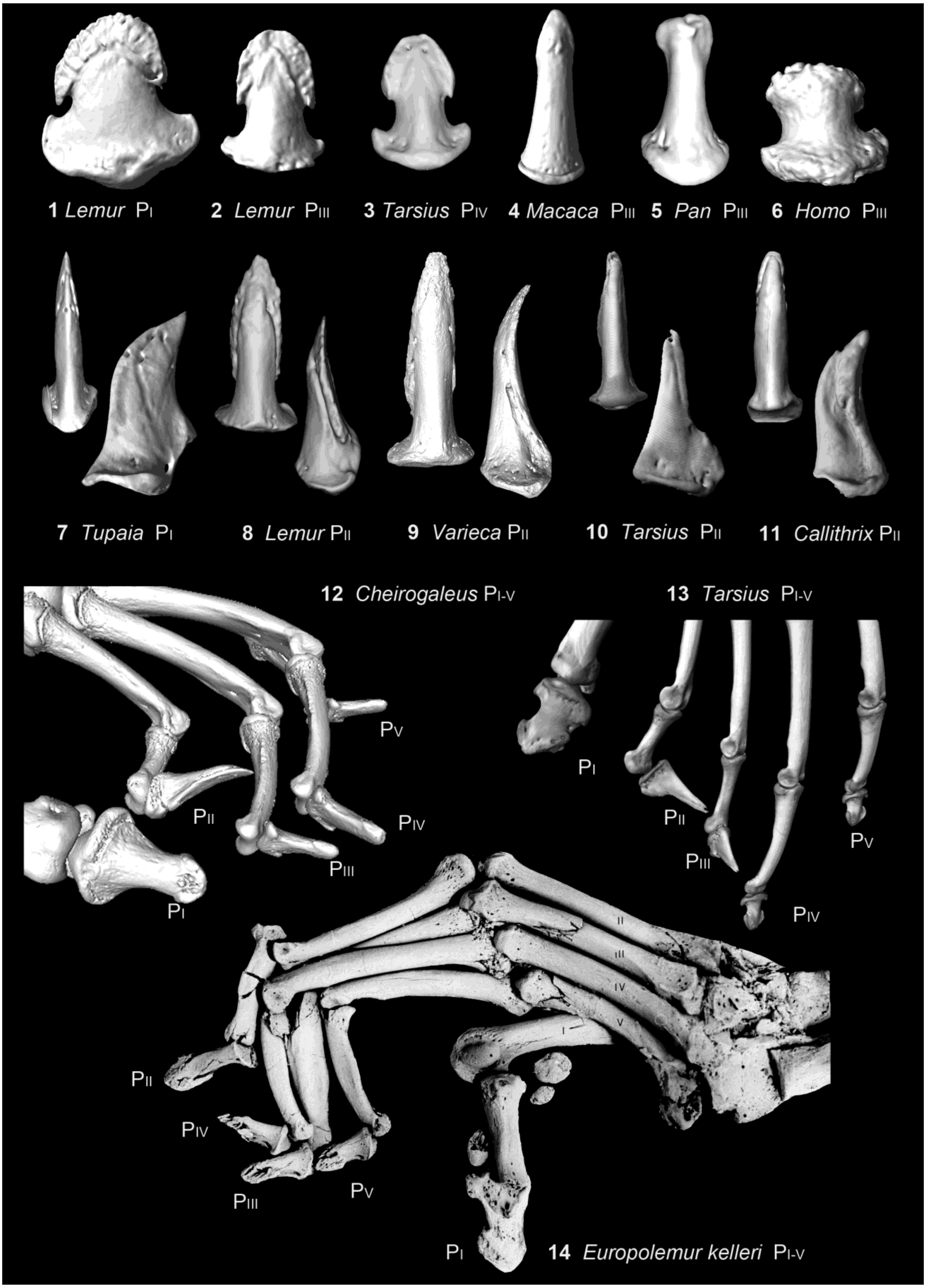

Figure 1-14. Morphological diversity of distal phalanges in the feet of primates and *Tupaia* in high-resolution images reconstructed from micro-CT scans (not to scale). 1-3: scutiform distal phalange (DP); 4: columnar DP; 5-6: columnar DP with terminal rugosity; 7: tupaioid claw (in dorsal and lateral aspect); 8-9: lemuroid grooming claw; 10: tarsioid grooming claw; 11: callithrichine claw; 12: lemuroid foot pattern; 13: tarsioid foot patter; 14: adapoid foot pattern (*Europolemur kelleri* HLMD Me 7430).

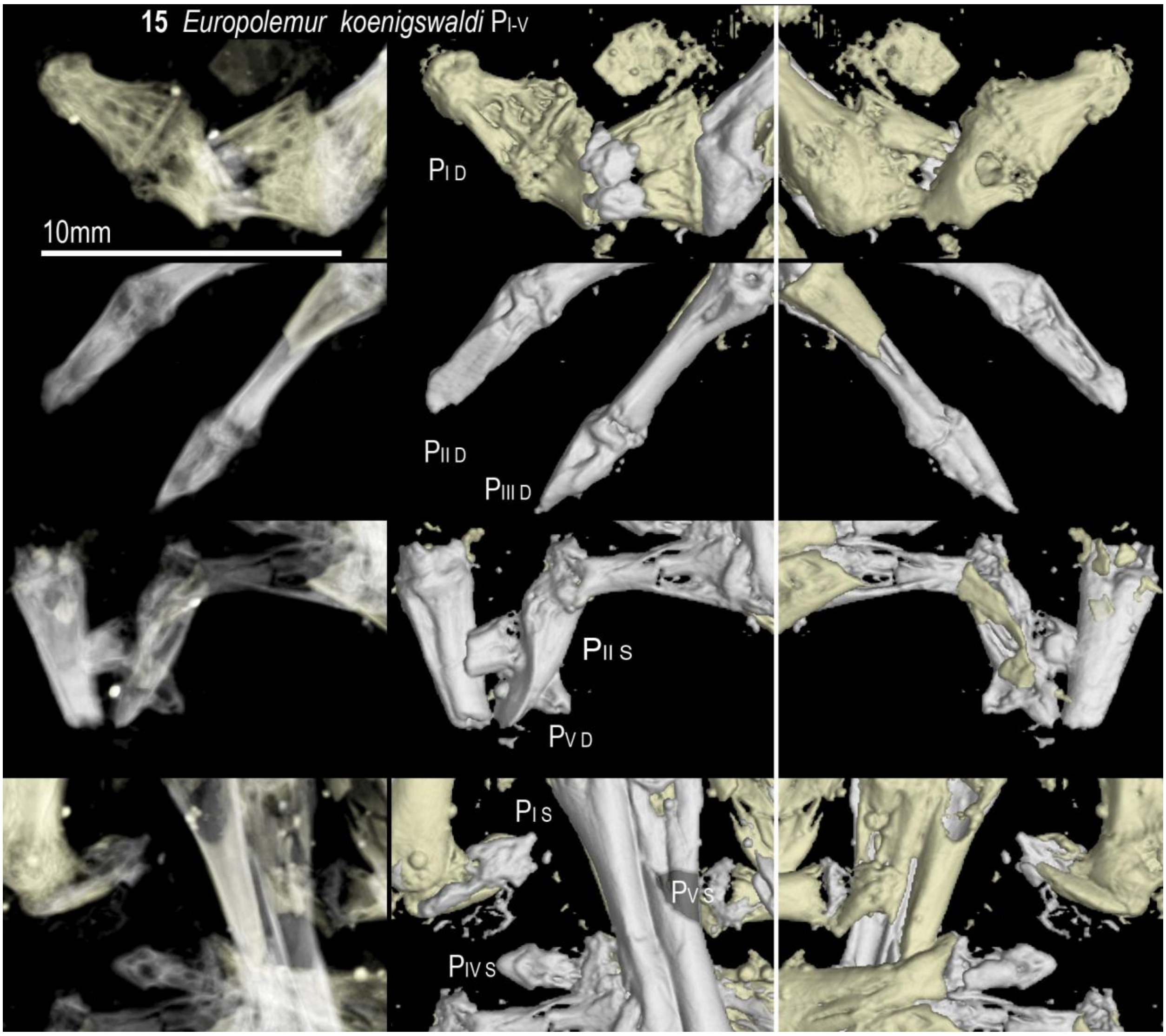

Figure 15. Adapoid foot pattern and distal phalanges of *Europolemur koenigswaldi* (SMNK-Me1125). Left and right foot are partially preserved on plate A (white color) and plate B (yellow-grey color). Micro-CT scans of both plates A and B are superimposed. Distal PI-PV are indicated with D for the right foot and S for the left foot. Frontal views (referring to plate A) are shown for X-rays in the left column, 3D surfaces in the middle column, and views from the back-side (referring to plate B) are shown in the right column.

seen in the hands of *Homo*. Most human pedal DPs (except PI) are better described as rugose than as scutiform (Fig. 6). *Callithrix* has a clawlike development of manual and pedal DPs. PI is scutiform as usual, but MI–MV and PII–PV are clawlike. These differ from claws of *Tupaia* in having a distinct lateral furrow (Godinot 1992).

Results of this preliminary survey of the DPs of extant primates enable the following comments on fossil proprimates and euprimates. *Plesiadapis* shows, as far as is known, claws without any differentiation of the various digits (Gingerich, 1976; Godinot and Beard, 1991; Boyer, 2009). *Carpolestes* has a widened, slightly scutiform PI, other DP as far as is known seem to be clawlike (Bloch and Boyer, 2002). Adapoidea: *Europolemur kelleri* has a scutiform PI; the PII has distinct similarities to a lemuroid grooming claw, e.g., the exclusive differentiation of the PII, the elongated PII with a distinct shaft, the low cross-section of the shield, the expanded lateral rims of the shield that extend to the plantar surface, and the flat and slightly concave plantar surface (Koenigswald, 1979). The remaining DPs (PIII–PV) are scutiform as in lemuroids (Fig. 14). Similar morphology is found in *Europolemur koenigswaldi* (Fig. 15). The DPs differ from lemuroid DPs in having a distinct grove or foramen in the lateral side of the shaft. This foramen is found in other isolated DPs attributed to *Notharctus tenebrosus* (Bloch *et al.*, 2010). In *Darwinius masillae* the DPs of the hand are scutiform (Franzen *et al.*, 2009). The PI is enlarged, the PII slightly elongated. In PIV and PV the scutiform outline can be recognized. However, it appears that parts of the DPs may have been brushed away during preparation and, in contrast to *Europolemur kelleri*, few anatomical details are discernable, especially on PII. The claimed absence of a grooming claw in *Darwinius* is a subject of ongoing interpretation.

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BLOCH J.I., BOYER D.M. (2002). Grasping primate origins. Science 298: 1606-1610.

BLOCH, J., RANDALL, Z., SILCOX, M., CHESTER, S., BOYER, D. (2010). Distal phalanges of Eocene North American notharctines (Mammalia, Primates): Implications for primate and anthropoid origins. Journal of Vertebrate Paleontology, SVP Program and Abstracts Book, 2010, 60A.

BOYER, D.M. (2009). New cranial and postcranial remains of late Paleocene Plesiadapidae (‘Plesiadapiformes’, Mammalia) from North America and Europe: Description and evolutionary implications. Ph.D. dissertation, Stony Brook University, Stony Brook, 569 pp.

FRANZEN J.L. (1994). The Messel primates and anthropoid origins. In: Fleagle J.G., Kay R.F. (eds) Anthropoid Origins. Plemum Press , New York. pp: 99-122.

FRANZEN, J.L., GINGERICH, P.D., HABERSETZER, J., HURUM, J.H., KOENIGSWALD, W.V., SMITH, B.H. (2009). Complete primate skeleton from the middle Eocene of Messel in Germany: Morphology and paleobiology. PLoS One 4 (e5723) 1-27.

GINGERICH, P.D. (1976). Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). University of Michigan Papers on Paleontology 15: 1-141.

GINGERICH, P.D., FRANZEN, J.L., HABERSETZER, J., HURUM J.D., SMITH, B.H. (2010). *Darwinius masillae* is a haplorhine – Reply to WILLIAMS *et al.* (2010). Journal of Human Evolution 59: 574-579. – doi:10.1016/j.jhevol.2010.07.013.

GODINOT, M. (1992). Early euprimate hands in evolutionary perspective. Journal of Human Evolution 22: 267-283.

GODINOT, M., BEARD K.C. (1991). Fossil primate hands: A review and an evolutionary inquiry emphasizing early forms. Human Evolution 6: 307-354.

JUNGERS, W.L., LEMELIN, P., GODFREY, L.R., WUNDERLICH, R.E., BURNEY, D.A., SIMONS, E.L., CHATRATH, P.S., JAMES, H.F., RANDRIA, G.F.N. (2005). The hands and feet of *Archaeolemur*: Metrical affinities and their functional significance. Journal of Human Evolution 49: 36-55.

KOENIGSWALD, W.V. (1979). Ein Lemurenrest aus dem eozänen Ölschiefer der Grube Messel bei Darmstadt. Paläontolgische Zeitschrift 53: 63-76.

LE GROS CLARK W.E. (1936). The problem of claws in primates. Proceedings of the Zoological Society of London 1936: 1-24.

SEIFFERT, E.R., PERRY, J.M.G., SIMONS, E.L., BOYER, D.M. (2009). Convergent evolution of anthropoid-like adaptations in Eocene adapiform primates. Nature 461: 1118 -1121.

WILLIAMS, B.A., KAY, R.A., KIRK, E.C., ROSS, C.W. (2010). *Darwinius masillae* is a strepsirrhine – Reply to FRANZEN *et al.* (2009). Journal of Human Evolution 59: 567-573 - doi:10.1016/j.jhevol.2010.01.003.

The Messel food web

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Although many paleoecological studies focus on species diversity and distribution, there are few opportunities to analyze species interactions in depth within the fossil record. We present highly and evenly resolved food-web data for the Messel Shale deposit. Our dataset includes species that occurred in the immediately surrounding paratropical forest and those that occupied the water column and substratum of a maar lake. Our data is notable for the detailed resolution of terrestrial plant–insect associations, representation of multiple habitats, the presence of terrestrial and aquatic feeding chains, and the elevated certainty for most of the interaction data, particularly between plants and their insect and vertebrate consumers. Using various techniques of network structure analysis, including the recently developed probabilistic niche model (Williams *et al.*, 2010), we assess the organization of this paleo-food web with comparisons to published, extant ecological networks.

The lacustrine deposit at Messel, near Darmstadt, in central Germany, is of earliest middle Eocene age, equivalent to the early Lutetian stage, and corresponding to an absolute radioisotopic age of 47 Ma based on an ^{40}Ar/^{39}Ar date from a basalt fragment (Mertz and Renne, 2005). The included strata consist of 190 m of oil shale and other fine-grained sedimentary rocks (Felder and Harms, 2004), occurring in an area of 0.7 km^2 (Schaal and Ziegler, 1992). The time represented by this deposit is moderately time averaged, representing 1 to 1.5 million yr, estimated from sedimentation rates of 0.1 to 0.15 mm/yr, resulting in an average rate of 0.14 mm/yr (Lenz *et al.*, 2010). These highly resolved, varved sedimentary strata contain annual, lightly hued spring/summer laminae and darkly hued fall/winter laminae over 600 kyr, straddling almost half of the total time represented and indicating a direct connection with greenhouse middle Eocene El Niño–Southern Oscillation climate dynamics (Lenz *et al.*, 2010).

In addition to the resolved temporal, stratigraphic and paleoclimatic settings, Messel represents perhaps the most favorable, deep-time candidate for a food-web reconstruction known in the fossil record, based on biological evidence. This is attributable to several factors. First, preservational details such as soft tissues, specific plant–insect associations, gut contents, identifiable constituents in dispersed coprolites, and anatomical detail of feeding structures, provide unusual precision for ascertaining trophic interactions. Second, ecological uniformitarianism supplies extant autecologic trophic inferences that would not normally be available in older deposits. Third, the taxa documented at Messel represent a trophically balanced spectrum of producers, herbivores, carnivores and decomposers ranging from bacteria to crocodylians. Fourth, there is a breadth of host resource use in the terrestrial environment that is unparalleled in the fossil record, including, in the case of insects, fine-tuned associations as varied as external foliage feeding, piercing-and-sucking, leaf mining, galling, seed predation, oviposition, and even predation and parasitoid interactions (e.g., Hughes *et al.*, 2011). Fifth, preserved Messel fossils are overwhelmingly autochthonous, and signify deposition of a highly local biota in a geologically narrow time period, an unusual circumstance for the fossil record. Sixth, the number of trophically distinct taxa included in the dataset is greater than in published food webs for extant ecosystems (Dunne *et al.*, 2004). Last, the interdisciplinary study of Messel, especially during the last 30 years by teams of specialist paleobiologists, have provided one of the best-documented examples in a fossil assemblage of co-occurring taxa that were once living and feeding in a contiguous environment.

A limited sample of 25 trophic associations at Messel is presented in Figure 1. Evidence for determination of these associations include gut contents, vertebrate dentition and insect mouthpart structure, dispersed coprolites, plant–insect interactions, feeding structures penetrating prey items (Labandeira, 2002), and other lines of inference such as isotopic geochemical relationships in the case of bacteria and other microorganisms. Documented associations include herbivory by vertebrates [Fig. 1(A): a,c; 1(B): a,c,d,h,i,k,l] and insects [Fig. 1(A): f–l,n], vertebrate carnivory [Fig. 1(A): d,j] and insectivory [Fig. 1(A): m; 1(B): b,e–g], and saprobic associations [Fig. 1(A): b,e]. Within insects, specific functional feeding groups include external foliage feeding [Fig. 1(A): k], leaf mining [Fig. 1(A): g,i,n], seed predation [Fig. 1(A): l], palynivory with or without pollination [Fig. 1(A): j,l], and oviposition [Fig. 1(A): f]—an association that uses plant resources analogous to that of herbivory. This breadth of evidence indicates that Messel is one of the trophically best-documented deposits in the fossil record.

The full Messel food web consists of 700 trophically unique taxa and 6446 links (Fig. 2). Fifty-four percent of the taxa are resolved to the genus or species level, and 82 percent to the family level or better. The taxa consist of 187 land plants, 326 invertebrates (overwhelmingly insects) and 143 vertebrates. The remaining 44 taxa are protists, fungi,

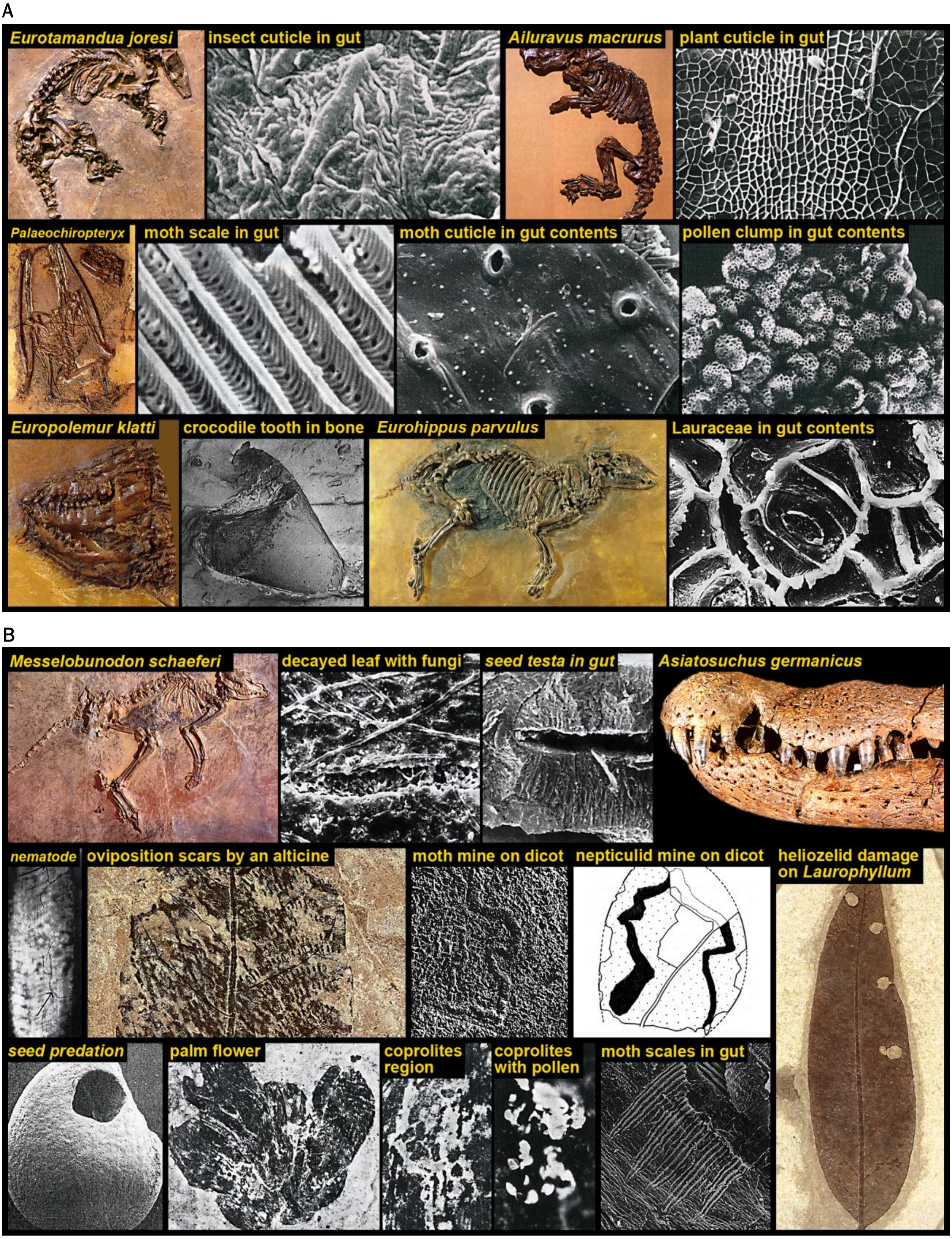

Figure 1. (A) Associations emphasizing plant–insect associations and vertebrate dentition. (B) Associations emphasizing vertebrate gut contents and dentition.

and prokaryotes. Seventy-seven percent of the links are rated as middle or of high certainty. The web can be split into a terrestrial web of 633 taxa and 5551 links, and an aquatic web with 94 taxa and 517 links. While levels of maximum generality are similar between the two habitats, in particular with a species in each habitat that feeds on ca. 30 percent of the taxa, there nevertheless is much greater trophic specialization in the terrestrial web, as reflected in its low connectance (0.014), compared to the aquatic

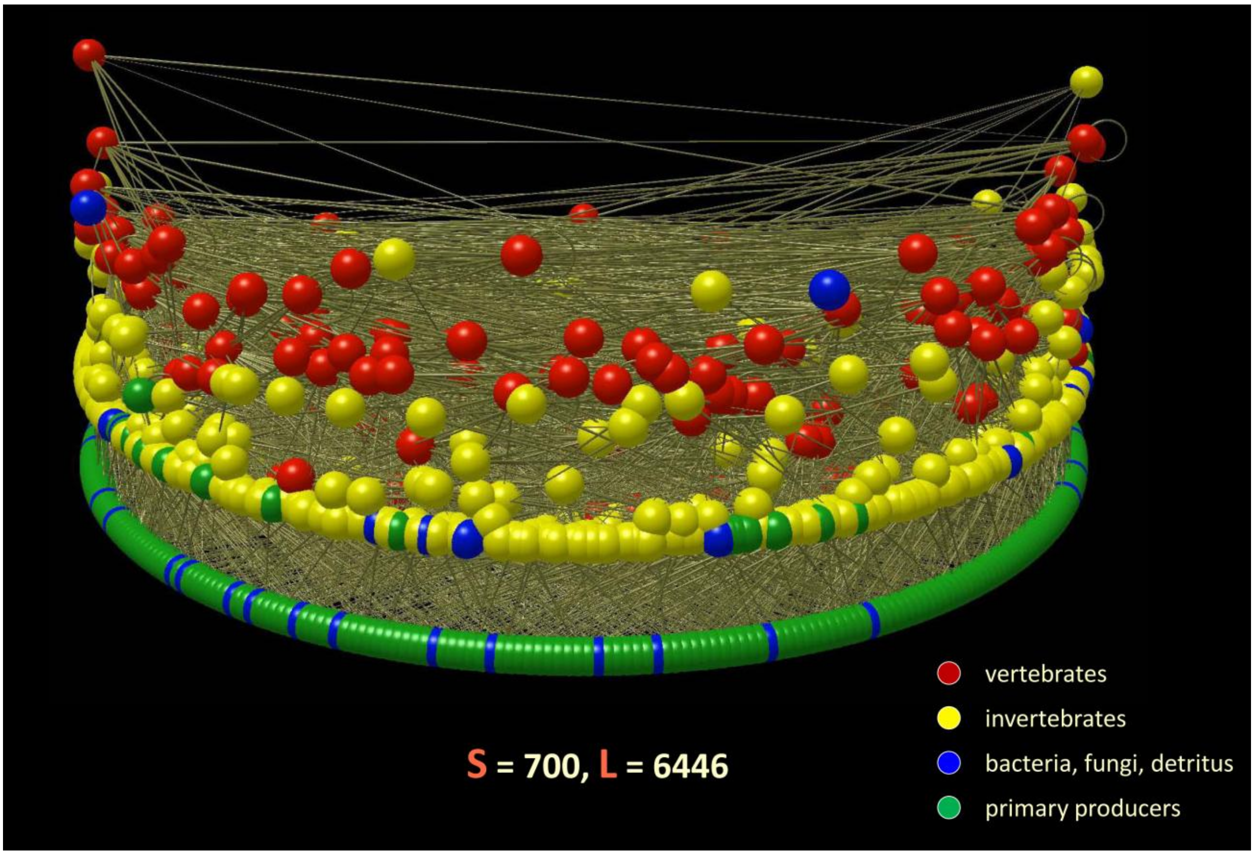

Figure 2. The entire Messel food web. Color scheme: green = primary producers, tan = fungi and other saprobes, blue = arthropods; red = vertebrates.

web (0.059). Probabilistic niche model (PNM) analysis (Williams *et al.*, 2010) indicates that the niche model structure of the aquatic web is within the range observed for extant webs, while the PNM performs poorly for the terrestrial web, even when it is strongly aggregated by trophic similarity. Adding a second niche dimension increases fit of the PNM for both webs. The results are very robust to the removal of low certainty links. Reasons for the poor PNM fit of the terrestrial web are considered, and potentially include factors such as its size, high resolution of specialized plant–insect associations, differences between extinct and extant ecosystems, and methodology.

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DUNNE, J.A., WILLIAMS, R.J., MARTINEZ, N.D. (2004). Network structure and robustness of marine food webs. Marine Ecology Progress Series 273: 291–302.

FELDER, M., HARMS, F-J. (2004). Lithologie und genetische Interpretation der vulkano-sedimentären Ablagerungen aus der Grube Messel an Hand der Forschungsbohrung Messel 2001 und weiterer Bohrungen. Courier Forschungsinstitut Senckenberg 252: 151–203.

GOTH, K. (1990). Der Messeler Ölshiefer—Ein Algenlaminit. Courier Forschungsinstitut Senckenberg 131: 1–143.

HUGHES, D., WAPPLER, T., LABANDEIRA, C.C. (2011). Ancient death-grip leaf scars reveal ant–fungal parasitism. Biology Letters 6: 67–70.

LABANDEIRA, C.C. (2002). The history of associations between plants and animals. In Herrera, C., Pellmyr, O. (eds) Plant–Animal Interactions: An Evolutionary Approach. Blackwell Science, Oxford, pp. 26–74, 248–261.

LENZ, O.K., WILDE, V., RIEGEL, W., HARMS.F-J. (2010). A 600 k.y. record of El Niño–Southern Oscillation (ENSO): Evidence for persisting telecommunications during the middle Eocene greenhouse climate of Central Europe. Geology 38: 627–630.

MERTZ, D.F., RENNE, P.R. (2005). A numerical age for the Messel fossil deposit (UNESCO World Heritage Site) derived from ^{40}Ar/^{39}Ar dating on a basaltic rock fragment. Courier Forschungsinstitut Senckenberg 255: 67–75.

SCHAAL, S., ZIEGLER, W. (1992). Messel: An Insight into the History of Life and of the Earth. Oxford University Press. 322pp.

WILLIAMS, R.J., ANANDANADESAN, A., PURVES, D. (2010). The probabilistic niche model reveals the niche structure and role of body size in a complex food web. PLoS ONE, 5(8): e12092.

The labyrinthine morphology of *Pronycticebus gaudryi* (Primates, Adapiformes)

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Morphological variation of the bony labyrinth across taxa reflects differences in locomotor behavior (Spoor and Zonneveld, 1998) and hearing performance (West, 1985). Recently, Lebrun *et al.* (2010*a*) showed that the morphology of the bony labyrinth of primates also conveys a phylogenetic signal: in strepsirhines, labyrinthine morphological variation is well-correlated with neutral genetic variation, and change in labyrinthine morphology is adequately described with a random walk model, i.e. random phenotypic dispersal in morphospace. Under this hypothesis, average shapes calculated for each node of a phylogenetic tree give an estimate of inner ear shapes of the respective last common ancestors (LCAs). Lebrun *et al.* (2010*a*) showed that the morphology of Eocene Adapinae is close to the inferred state of the ancestral toothcombed primate labyrinthine morphology, which supports the hypothesis that Adapiformes are the sister group of toothcombed primates. The recent description of a well-preserved Eocene primate, *Darwinius masillae* (Cercamoniinae, Notharctidae), has revived the debate on the phylogenetic relationships of Adapiformes and extant primates (Franzen *et al.*, 2009). Investigation of the morphological affinities between the labyrinthine morphology of another Cercamoniinae, *Pronycticebus gaudryi*, and extant primates and other Eocene primate taxa may thus also help to clarify the phylogenetic position of this extinct primate group.

MATERIALS AND METHODS

3D data of *Pronycticebus gaudryi* were obtained via high-resolution micro-CT on VISCOM AG equipment. The comparative dataset consists of 91 left inner ears of primates (Lebrun *et al.*, 2010*a*,*b*). Two adapine specimens had only their right inner ear preserved: in those cases, a virtual mirror image of their right labyrinth was produced and used for analysis. Labyrinthine shape was quantified with 22 landmarks, following the protocol used by Lebrun *et al.* (2010*a*). In order to take into account the possible confounding effect of size allometry on labyrinthine shape, size-corrected shapes were obtained as follows. Regression of Procrustes coordinates by the logarithm of centroid size were computed for Lorisiformes, Lemuriformes, Catarrhines, Platyrrhines, Adapiformes, Omomyiformes, and Tarsiiformes, yielding group-specific allometric shape vectors (ASVg). The ASVg represent directions in shape space which characterize group-specific allometric patterns of labyrinthine shape variation. A common allometric shape vector (ASVc), obtained as the mean of all the ASVg, provided a direction in shape space that minimizes potential divergence in labyrinthine allometric patterns across taxonomic groups. All labyrinths were then projected on ASVc, the residuals representing the size-independent component of labyrinthine shape. Size-independent shape variation was analyzed by principal components analysis (PCA) of shape using the interactive software package MORPHOTOOLS (Lebrun, 2008; Specht, 2007; Specht *et al*., 2007).

RESULTS AND DISCUSSION

In *Pronycticebus*, Adapinae and Microchoerinae, the posterior semi-circular canal assumes a high position relative to the lateral canal (see Fig. 1), resulting in partial fusion of the two canals. Furthermore, the semi-circular canals are round, and the posterior canal is relatively smaller than the lateral and superior ones. We propose that shared Adapiformes/Omomyidae features represent symplesiomorphies of primate labyrinthine morphology. Microchoerinae and *Tarsius* exhibit similar cochlear morphology and orientation. The labyrinth of *Pronycticebus* is closest in morphology to that of Microchoerinae, Adapinae and Lepilemuridae, and differs considerably from that of anthropoids. Anthropoid labyrinths are extended in an anteromedial to posterolateral direction, whereas the labyrinths of prosimians tend to be compressed in this direction. The lateral canal of anthropoids is extended along an anteromedial to posterolateral direction, while that of prosimians shows extension in the anterolateral to posteromedial direction. The cochlea of strepsirhines tends to point more ventrally than that of anthropoids.

CONCLUSION

No synapomorphy was found between the labyrinths of *Pronycticebus* and modern anthropoids. On the contrary, *Pronycticebus* is closer in labyrinthine shape to extant strepsirhines, which supports the hypothesis that Cercamoniinae and other Adapiformes are the sister group of toothcombed primates. Investigation of the morphological affinities between *Pronycticebus gaudryi* and the sole other Cercamoniinae for which a cranium is known, *Darwinius masillae*, will help to clarify the phylogeny of Adapiformes. Also, our results call for further comparative analyses, including of the inner ear of notharctine Adapiformes for which the cranium is preserved, such as *Notharctus* and *Smilodectes* and of fossil anthropoids.

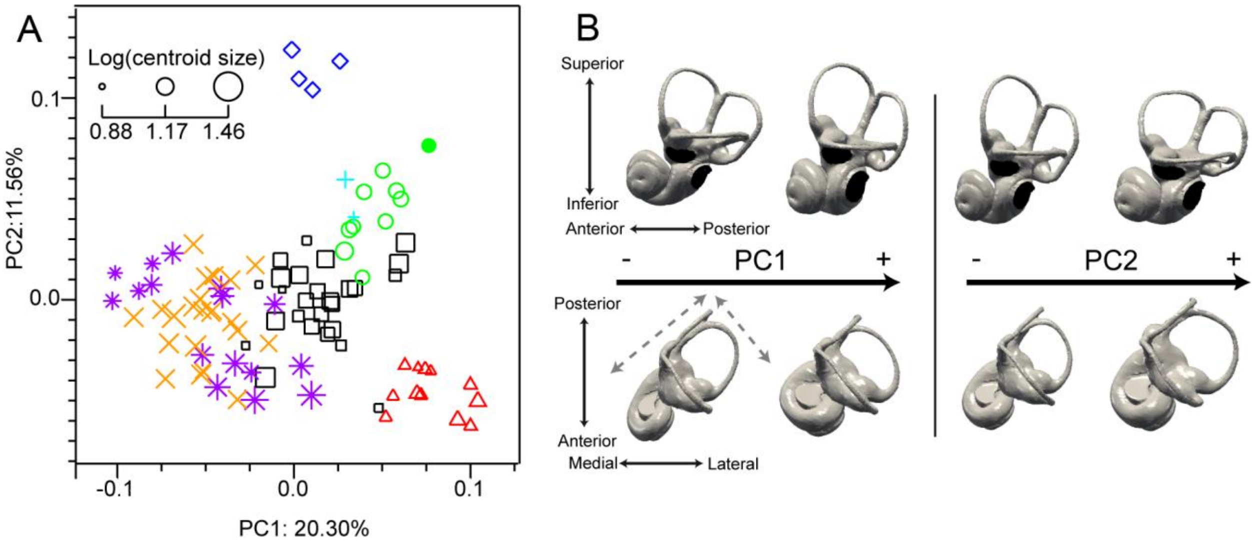

Figure 1. Principal Components Analysis (PCA) of labyrinthine size-corrected shape variation. (A) Graphing the first two components of shape space, PC1 and PC2, shows differences in labyrinthine morphology across anthropoids, extant strepsirhines, Eocene primates and *Tarsius*. For the strepsirhines, Triangles: Lorisiformes; Squares: Lemuriformes; Open circles: Adapinae; Filled circle: *Pronycticebus*. For the haplorhines, Stars: Platyrrhines; X: Catarrhines; Diamonds: *Tarsius*; +: Microchoerinae (B) Patterns of labyrinthine shape variation associated with PC1 and PC2, respectively. Grey arrows: anteromedial-to-posterolateral and anterolateral-to-posteromedial directions.

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FRANZEN, J.L., GINGERICH, P.D., HABERSETZER, J., HURUM, J.H., KOENIGSWALD, W.V., SMITH, B.H. (2009). Complete primate skeleton from the Middle Eocene of Messel in Germany: Morphology and paleobiology. PLos ONE 4: e5723.

LEBRUN, R. (2008). Evolution and Development of the Strepsirrhine Primate Skull. Ph.D. Thesis in Paleontology: Université Montpellier II, University Zürich Irchel.

LEBRUN, R., PONCE DE LEÓN, M.S., TAFFOREAU, P., ZOLLIKOFER, C.P.E. (2010*a*). Deep evolutionary roots of strepsirrhine primate labyrinthine morphology. Journal of Anatomy 216: 368-380.

LEBRUN, R., PONCE DE LEÓN, M.S., ZOLLIKOFER, C.P.E. (2010*b*). Does anthropoid labyrinthine morphology reflect phylogeny or locomotion? American Journal of Physical Anthropology Supplement 50: 152-153.

SPECHT, M. (2007). Spherical Surface Parameterization and Its Application to Geometric Morphometric Analysis of the Braincase. Ph.D. Dissertation. Zürich: University of Zürich Irchel.

SPECHT, M., LEBRUN, R., ZOLLIKOFER C.P.E. (2007). Visualizing shape transformation between chimpanzee and human braincases. Visual Computer 23: 743-751.

SPOOR, C., ZONNEVELD, F. (1998). Comparative review of the human bony labyrinth. American Journal of Physical Anthropology Supplement 27: 211-251.

WEST, C. D. (1985). The relationship of the spiral turns of the cochlea and the length of the basilar membrane to the range of audible frequencies in ground dwelling mammals. Journal of the Acoustical Society of America 77: 1091-1100.

Eocene vegetation of New Zealand and Australia: High latitude “tropics” in the Southern Hemisphere

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Sites such as Messel and Eckfeld provide amazing windows through which to study both plant and animal life in the Northern Hemisphere during the Eocene. However, middle to late Eocene sites in New Zealand and Australia are beginning to reveal new perspectives on Southern Hemisphere high-latitude tropical and subtropical forests. Using fossil evidence from lake and river sediments as well as extensive coal deposits representing Eocene swamps, our poster will present new palaeobotanical and climate data from selected Eocene sites in New Zealand and SE Australia. Although few animal fossils are known from these deposits, there are abundant ferns, epiphyllous fungi, conifers, monocots including palms, Lauraceae, *Nothofagus*, and taxa belonging to a range of other lineages now found in tropical to subtropical rainforests (Fig. 1A).

The Eocene was a period of global warmth, but there was cooling and ongoing floristic change in Australasia (as elsewhere) following the initial Eocene thermal maximum (IETM) ~55 Ma (Pocknall, 1989, 1990; Lee *et al.*, 2001). Nevertheless, during the mid- to late Eocene there were floras of a tropical to subtropical nature at palaeolatitudes of ~50°S associated with high temperatures, rainfall and humidity, as well as compressed temperature, photoperiod and sun angle extremes (Hill, 1994).

Despite being close to the Antarctic Circle (~66°S), early Eocene (~50 Ma) assemblages from western Tasmania indicate very warm climates. This flora was uniquely diverse, with complex forests containing plants such as the equatorial mangrove palm *Nypa*, extinct, toothed Lauraceae (Carpenter *et al.*, 2007), monocots (Conran *et al.*, 2009), abundant southern conifers, and even a refugial seed fern that survived the K/T boundary mass extinction (McLoughlin *et al.*, 2008). Many mid-Eocene (~45–40 Ma) largely Lauraceae- and Myrtaceae-dominated rainforest floras are known from Australia, including Anglesea in Victoria (Christophel *et al.*, 1987), Maslin Bay (Christophel and Blackburn, 1978) and Golden Grove (Christophel and Greenwood, 1987; Conran and Christophel, 1998), both near Adelaide, South Australia, Nelly Creek near Lake Eyre (Christophel *et al.*, 1992), Nerriga in New South Wales (Hill, 1982, 1986) and Hasties in Tasmania (Pole, 1992). Although many of these were structurally and floristically similar to the modern Wet Tropics of northern Queensland (15–20°S), there were clear floristic differences between them, indicating spatial and temporal heterogeneity, including evidence for the development of seasonally dry, smaller-leaved and more sclerophyllous vegetation in Central Australia and cooler, conifer-dominated moist forest vegetation in Tasmania.

Numerous Eocene sites are known from New Zealand, but most have been studied only palynologically (e.g., Pocknall, 1990) or have not yet been published. Late Eocene sites in southern New Zealand at a paleolatitude of ~50ºS indicate a continued high

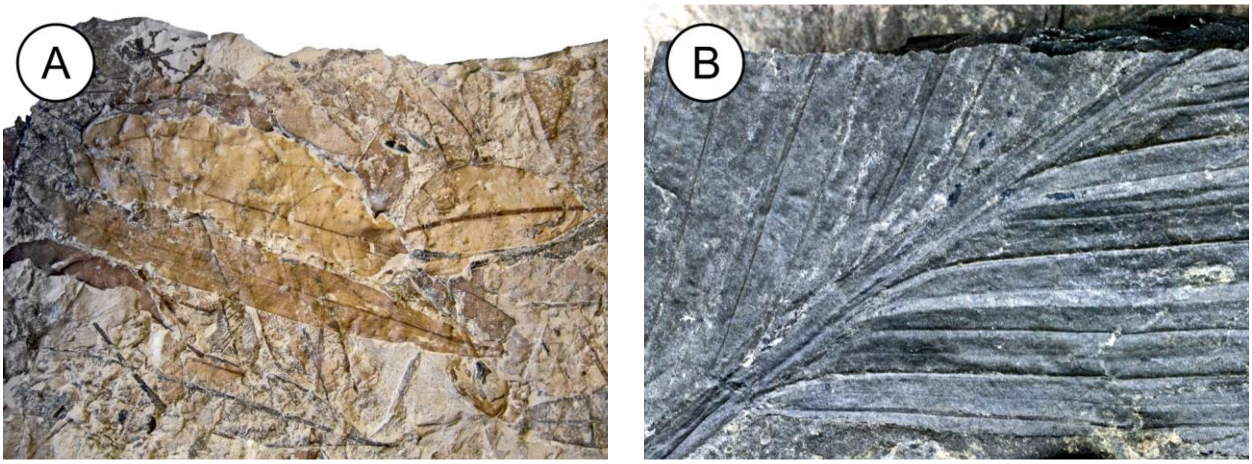

Figure 1. Examples of fossil plants from Eocene Australasia. A: Middle Eocene leaf block from Golden Grove (South Australia) with several Lauraceae and Myrtaceae leaf taxa, as well as the arborescent monocot *Paracordyline aureonemoralis*. B. Part of a recently discovered unnamed 1.2-m-long late Eocene palm frond from Pikopiko (New Zealand).

diversity (Pocknall, 1989, 1990). At Pikopiko, a petrified *in situ* forest includes leaf beds containing diverse fern macrofossils, suggesting that ferns dominated the understorey in the Eocene just as they do in modern New Zealand rainforests (Cieraad and Lee, 2006). The macrofossils are dominated by Lauraceae and Myrtaceae leaves, but there are also palms (Fig. 1B), including a *Calamus*-like rattan (Hartwich *et al*., 2010). Fossil pollen includes Casuarinaceae, Sapindaceae (tribe Cupanieae) and Euphorbiaceae (*Austrobuxus*), together with several Proteaceae and *Nothofagus* (*Fuscospora* and *Brassospora*) pollen types. Abundant associated fossil epiphyllous fungi including *Asterina, Entopeltacites, Callimothallus, Meliolinites, Quillonia*, and *Trichopeltinites* further support the evidence for high rainfall and a warm, humid climate.

When incorporated with palaeoclimatic data from the Northern Hemisphere, these Australasian sites show that floras of a much warmer and more humid nature persisted at high palaeolatitudes well into the late Eocene. They provide further pieces of the puzzle that is the world in the Eocene, albeit one for which further study of Southern Hemisphere floras and the effects of significant climate change is still required.

Carpenter, R.J., Jordan, G.J., Hill, R.S. (2007). A toothed Lauraceae leaf from the Early Eocene of Tasmania, Australia. International Journal of Plant Sciences 168: 1191-1198.

Christophel, D.C., Blackburn, D.T. (1978). Tertiary megafossil flora of Maslin Bay, South Australia: A preliminary report. Alcheringa 2: 311-319.

Christophel, D.C., Greenwood, D.R. (1987). A megafossil flora from the Eocene of Golden Grove, South Australia. Transactions of the Royal Society of South Australia 111: 155-162.

Christophel, D.C., Harris, W.K., Syber, A.K. (1987). The Eocene flora of the Anglesea locality, Victoria. Alcheringa 11: 303-323.

Christophel, D.C., Scriven, L.J., Greenwood, D.R. (1992). An Eocene megafossil flora from Nelly Creek, South Australia. Transactions of the Royal Society of South Australia 116: 65-76.

Cieraad, E., Lee, D.E. (2006). The New Zealand fossil record of ferns for the past 85 million years. New Zealand Journal of Botany 44: 143-170.

Conran, J.G., Carpenter, R.J., Jordan, G.J. (2009). Early Eocene *Ripogonum* (Liliales: Ripogonaceae) leaf macrofossils from southern Australia. Australian Systematic Botany 22: 219-228.

Conran, J.G., Christophel, D.C. (1998). *Paracordyline aureonemoralis* (Lomandraceae): An Eocene monocotyledon from South Australia. Alcheringa 22: 351-359.

Hartwich, S.J., Conran, J.G., Bannister, J.M., Lindqvist, J.K., Lee, D.E. (2010). Calamoid fossil palm leaves and fruits (Arecaceae: Calamoideae) from Late Eocene Southland, New Zealand. Australian Systematic Botany 23: 131-140.

Hill, R.S. (1982). The Eocene megafossil flora of Nerriga, New South Wales, Australia. Palaeontographica B 181: 44-77.

Hill, R.S. (1986). Lauraceous leaves from the Eocene of Nerriga, New South Wales. Alcheringa 10: 327-351.

Hill, R.S. (1994) History of the Australian Vegetation: Cretaceous to Recent. Cambridge University Press, Cambridge. 433 pp.

Lee, D.E., Lee, W.G., Mortimer, N. (2001). Where and why have all the flowers gone? Depletion and turnover in the New Zealand Cenozoic angiosperm flora in relation to palaeogeography and climate. Australian Journal of Botany 49: 341-356.

Mcloughlin, S., Carpenter, R.J., Jordan, G.J., Hill, R.S. (2008). Seed ferns survived the end-Cretaceous mass extinction in Tasmania. American Journal of Botany 95: 465-471.

Pocknall, D.T. (1989). Late Eocene to Early Miocene vegetation and climate history of New Zealand. Journal of the Royal Society of New Zealand 19: 1-18.

Pocknall, D.T. (1990). Palynological evidence for the early to middle Eocene vegetation and climate history of New Zealand. Review of Palaeobotany and Palynology 65: 57-69.

Pole, M.S. (1992). Eocene vegetation from Hasties, northeastern Tasmania. Australian Systematic Botany 5: 431-475.

Lake Messel, an extraordinary archive for the middle Eocene greenhouse climate

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The Palaeogene was the most recent greenhouse period on Earth. High-resolution palynological studies and varve analyses of the early Middle Eocene maar lake sediments of Messel now provide an insight into the climate dynamics during the Palaeogene greenhouse period far beyond well-known short-term hyperthermal "events" such as the Paleocene-Eocene Thermal Maximum (PETM) and the Middle Eocene Climatic Optimum (MECO) which were superimposed on the general trend of the climate. Numerous climate-related palaeobotanical studies on the Paleocene and the Eocene have focused on the above-mentioned events, but less is known about the interaction of climate and vegetation in the Palaeogene greenhouse phase between the hyperthermal events. The continuous core "Messel 2001" from the center of the maar basin, which includes a complete reference section of the middle Eocene lake deposits (Lower and Middle Messel Formation), recently provided a unique high-resolution climate archive for a timespan of less than one million years within the Eocene greenhouse period in Central Europe. The character of the annually laminated sediments of the Middle Messel Formation allowed studies at an unprecedented resolution with regard to Palaeogene times.

The initial phase of Lake Messel as represented by the Lower Messel Formation is characterized by alternating breccias, tuffs, layers of sand and clay and the beginning of oil shale deposition together with a palynological record showing the progressive recolonization of a completely disturbed habitat (Lenz *et al.*, 2007*a*). The classical "Messel oil shale" of the Middle Messel Formation is known for its continuous succession of finely laminated bituminous claystones, representing long-term stable meromictic conditions (Fig. 1). They show a very fine light and dark lamination, which was caused by seasonal algal blooms of the coccal green alga *Tetraedron minimum* that were superimposed on the terrigenous background sedimentation as represented by the dark layers. An average sedimentation rate of 0.14 mm/yr has been calculated from the annual lamination, but there are short-term fluctuations in varve thickness between 0.1 mm/yr and 0.15 mm/yr, which can be attributed to an "Eocene ENSO" (Lenz *et al.*, 2010*a*). Today ENSO is one of the most important factors in global climate dynamics. Low frequency ENSO-like modulations have also been observed in the geological record, but for the Eocene, only climate modelling has until now suggested that ENSO in Central Europe was robust during the Eocene hothouse ca. 35–55 Ma (Huber and Caballero, 2003).

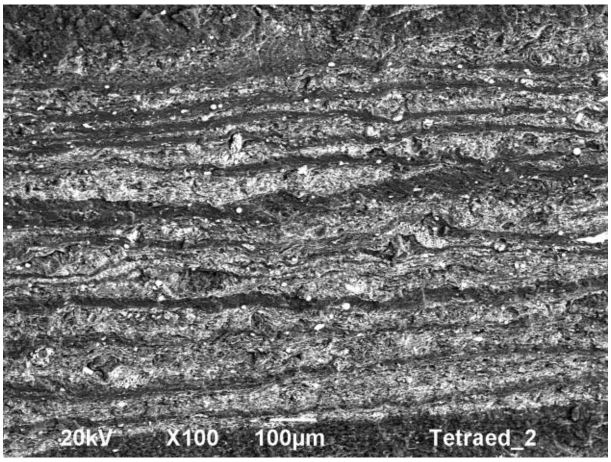

Figure 1. Cross-section of a typical laminated Messel oil shale. SEM image of the Messel oil shale, showing alternating light and dark layers. Light-coloured layers are composed of *Tetraedron minimum* remains, whereas dark layers are dominated by backround sedimentation.

Fluctuations are significant in the quasi-biennial (2.1–2.5 yr) and low-frequency band (2.8–3.5 yr, 4.9–5.6 yr), thus showing that algal growth as well as the background sedimentation were controlled by ENSO effects at least over a time interval of 600 kyr. This confirms the existence of the previously postulated robust Eocene ENSO. Significant signals of quasi-decadal (10–12 yr), interdecadal (17–22 yr) and multidecadal fluctuations (~52 yr, ~82 yr) show the enduring influence of more or less cyclic instabilities which are comparable to modern ENSO-instabilities such as the Pacific Decadal Oscillation (PDO).

High-resolution palynological analysis of the oil shale of the Middle Messel Formation in the core, which represents a time interval of about 640 kyr, now provides unique insight into the dynamics of a paratropical climax vegetation during the middle Eocene greenhouse climate. Pollen and spores show that the vegetation surrounding Lake Messel did not change substantially in qualitative composition, but a change from a humid climate with relatively high water levels in the lake to significantly less humid conditions and lower water levels may be reflected by changes in the quantitative composition of the assemblage towards the top of the section (Lenz *et al.*, 2010*b*). A shift in the algal community from the freshwater dinoflagellate cyst *Messelodinium thielepfeifferae* to a dominance of *Botryococcus* in the uppermost part of the core can be interpreted as a response to related changes in acidity and nutrient availability within the lake (Lenz *et al.*, 2007*b*).

In addition to long-term changes in vegetation and phytoplankton, short-term fluctuations in the frequency of individual taxa and certain clusters of taxa are recognizable. Accepting an annual lamination, time series analyses of palynological data suggest that pollen assemblages reflect periodicities within the range of eccentricity (~100 kyr), obliquity (40–25 kyr), long precession (22–25 kyr) and short precession (16–19 kyr). This implies that orbital control of climate change was sufficient to impose quantitative changes in the composition of the terrestrial vegetation in the area, though no taxonomic turnover occurred (Lenz *et al.*, 2010*b*). Ongoing studies of inorganic parameters will hopefully reveal information on the underlying climatic factors such as temperature, precipitation and humidity.

According to the cyclicity of the palynological data and with the availability of the astronomical solutions of Laskar *et al.* (2004) and Varadi *et al.* (2003), it is now possible to implement an astronomical tuning to the 640 kyr record of the Middle Messel Formation. When tuning the pollen data to the La2004 Earth's orbital solution, the age of the Middle Messel Formation can be astronomically fixed between 46.6 and 47.3 Ma.

HUBER, M., CABALLERO, R. (2003). Eocene El Niño: Evidence for robust tropical dynamics in the "Hothouse". Science 299: 877–881.

LASKAR, J., ROBUTEL, P., JOUTEL, P., GASTINEAU, M., CORREIA, A.C.M., LEVRARD, B. (2004). A long-term numerical solution for the insolation quantities of the earth. Astronomy & Astrophysics 428: 261–285.

LENZ, O.K., WILDE, V., RIEGEL, W. (2007*a*). Recolonization of a Middle Eocene volcanic site: Quantitative palynology of the initial phase of the maar lake of Messel (Germany). Review of Palaeobotany and Palynology 145: 217–242.

LENZ, O.K., WILDE, V., RIEGEL, W. (2007*b*). Distribution and paleoecologic significance of the freshwater dinoflagellate cyst *Messelodinium thielepfeifferae* gen. et sp. nov. from the Middle Eocene of Lake Messel, Germany. Palynology 31: 119–134.

LENZ, O.K., WILDE, V., RIEGEL, W., HARMS, F.J. (2010*a*). A 600 k.y. record of El Niño-Southern Oscillation (ENSO): Evidence for persisting teleconnections during the Middle Eocene greenhouse climate of Central Europe. Geology 38 (7): 627–630.

LENZ, O.K., WILDE, V., RIEGEL, W. (2010*b*). Short-term fluctuations in vegetation and phytoplankton during the Middle Eocene greenhouse climate: A 640 kyr record from the Messel oil shale (Germany). International Journal of Earth Sciences, DOI 10.1007/s00531-010-0609-z.

VARADI, F., RUNNEGAR, B., GHIL, M. (2003). Successive refinements in long-term integrations of planetary orbits. Astrophysical Journal 592: 620–630.

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Maar-diatreme volcanism and its relevance for the Messel volcano

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INTRODUCTION

In 1980 a few drill holes in the Messel pit penetrated the lake beds and entered underlying indurated tephra beds. In 2001 the Messel research drill hole penetrated 200 m into these tephra beds. It was thus realized that the famous Messel lake beds were occupying the crater of a maar-diatreme volcano. A similar discovery was made in the fossiliferous Eocene Eckfeld lake beds. And worldwide many continental fossil sites are maar crater deposits, mostly lake sediments. For understanding the particulars of the palaeoenvironment of the Messel site and thus of the Messel volcano, knowledge of the volcanology of this type of volcano is required.

Maar-diatreme volcanoes are characterized by distinct features (Fig. 1):

1. The Maar Crater

In 1819-1820 Johann Steininger realized that the round lakes in the Eifel, which the local people called a “Maar,” occupied volcanic craters surrounded by volcanic ash. Consequently he applied this name for the lakes to the volcanic crater and its ejecta. The term *maar* was soon introduced into the international literature, making the Eifel the classic maar region of the world. Similar to the larger calderas, maars are craters cut into the pre-eruptive country rocks. In case of large maars, the crater may measure up to a few km from crest to crest of the surrounding tephra ring, and up to several hundred m in depth.

2. The Maar Tephra Ring

Surrounding the maar crater on the pre-eruptive surface, the maar tephra ring could have a thickness at its crest from less than 10 m up to c. 100 m and a diameter up to several km. The ring is composed of hundreds or even thousands of mostly ash and lapilli beds. The thickness of these beds varies between 1 mm and 20 cm. They are the result of a number of similar individual eruptions. Thus it is not a single very powerful eruption that formed the maar crater and its tephra ring, as frequently assumed. The tephra consists of juvenile and country-rock clasts, with the latter forming up to 80–90% by vol. The tephra beds were deposited by radially flowing, ground-hugging eruption clouds called *base surges*. Outside the tephra ring, ash falls from eruptions clouds make up a thin ash deposit.

3. The Diatreme

Daubrée (1891, 1893) introduced the term *diatreme* for pipe-shaped volcanic structures like those of the kimberlite pipes or the feeder structures of the Eifel and Auvergne maars. Below maar craters, the diatreme extends as an inverted cone down to a depth of c. 2–2.5 km. Its upper diameter corresponds with the floor of the maar crater. The diatreme fill consists of the same tephra types occurring in the tephra ring, as well as subsided blocks of country rocks and usually some intrusive magmatic bodies (dykes, sills, plugs).

4. The Root Zone

The tip of the diatreme is surrounded and underlain for up to several 100 m by the irregularly shaped so-called root zone. It contains breccias of country rocks, formed in situ in individual explosion chambers, and intrusive bodies.

5. The Feeder Dyke

The root zone extends into the dyke that had cut through the crust and that near the surface fed magma into the maar-diatreme volcano. Such dykes are usually between 0.3 and 1–2 m thick.

EMPLACEMENT PROCESSES OF THE MAAR-DIATREME VOLCANO

Today, the main model in respect to the formation of maar-diatreme volcanoes assumes many explosive magma-groundwater interactions. When the hot magma rises in a dyke and meets in near-surface environments sufficient groundwater, ultrafast heat transfer from the magma into the water causes phreatomagmatic (thermohydraulic) explosions, i.e., the collapse of vapour films between the two media leads to expansion of water and fragmentation of the surrounding melt. This thermohydraulic explosion emits shock waves which fragment surrounding country rock. Evaporation of the water drives the eruption of superheated water vapour, steam, and juvenile and country rock clasts, as well as water droplets and some juvenile gases. Repeated explosions and eruptions cause a mass deficiency in the explosion chambers. The collapse of these chambers forms a sink hole, the diatreme. If the collapse propagates upwards, the surface also collapses and generates a maar crater. The longer these explosions and eruptions continue, the larger and deeper the diatreme and the maar crater grow and the thicker the tephra ring gets. Large maar-diatreme volcanoes may be active for up to ten years.

POST-PHREATOMAGMATIC PROCESSES

Phreatomagmatic eruptions end when there is a lack either of groundwater or magma to continue this activity. When only magma is still available, it intrudes the root zone and diatreme, and when reaching the maar crater it may form a scoria cone (as in c. 130 small West Eifel maars) or a lava lake (as in the Hegau volcanic field: e.g., Hohenstoffeln, Hohenhewen, and Höwenegg main craters). If magma is no longer rising, then groundwater and surface water enter the crater and form a crater lake, as

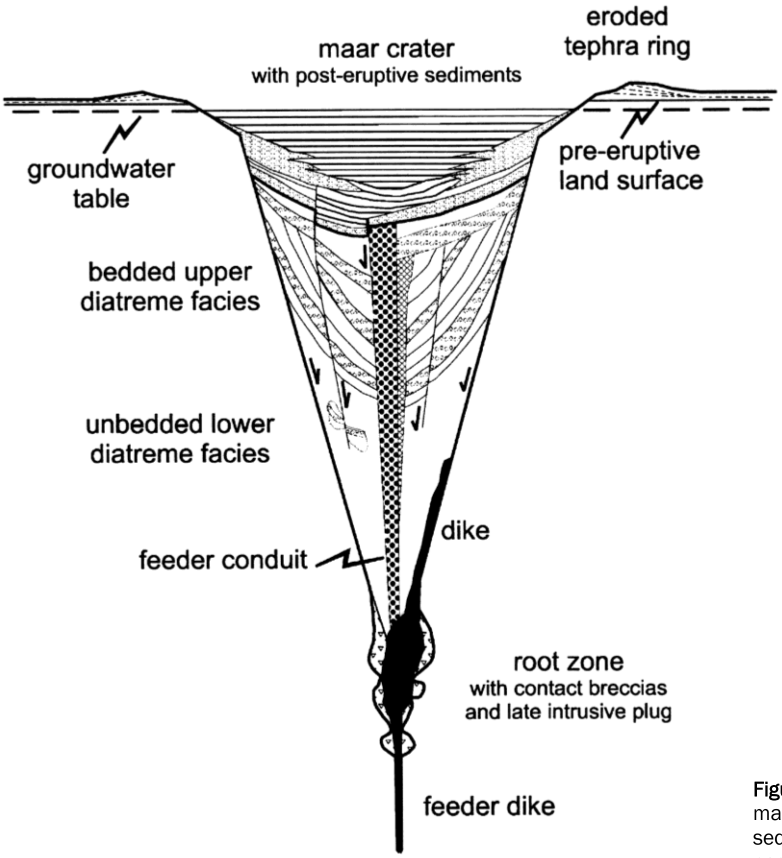

Figure. 1. Schematic maar-diatreme volcano showing main volcanological features and post-eruptive crater sediments, as well as results of post-eruptive compaction-related subsidence within diatreme walls.

happened in many maars, and as happened at Messel. Characteristic lacustrine sediments are C_{org}-rich pelites, carbonates, debrites and turbidites, as well as fan-delta and scree deposits. The lacustrine sediments may be several hundred m thick in large maar craters, e.g., at Messel, and formed over several hundred thousand or even up to one million years. Via fan deltas or peat deposits, as occur in West Eifel maars, purely subaerial sediment deposition may start.

Post-eruptive compaction and subsidence

During this post-eruptive filling of the maar crater and concurrent erosion of the tephra ring, there is still activity going on underneath in the diatreme fill. The tephra in the diatreme gets water-saturated rather fast. Simultaneously, the diagenetic processes of compaction, alteration and cementation start. Compaction begins rather fast (as it did in the Ukinrek East Maar after it erupted in 1977) and then continues at a decreasing rate for up to tens of millions of years, as, e.g., at the Oligocene maar-diatreme Kleinsaubernitz in Saxony. During compaction of the diatreme fill, the overlying crater lake sediments – deposited in a rather horizontal position – subside too and reach positions inside the diatreme wall. The diatreme wall acts as a ring-fault that propagates through the lake and overlying sediments. As a consequence of the cone-shaped diatreme, these subsiding sediments display a bowl-shaped structure and lateral folds, as do, e.g., the Messel crater lake deposits.

Messel: two diatremes?

Since the maximum diameter of the Messel diatreme is c. 1000 m, the depth of the diatreme may roughly be calculated: assuming the diatreme wall dips at about 80°, then the depth would be c. 2800 m; if 82°, the depth would be c. 3400 m. According to most maximum depths worked out and recorded for diatremes (2–2.5 km), these Messel diatreme depths – with the root zone not even taken into account – seem to be too large. Therefore, we suggest that the Messel structure is formed by two separate diatremes that may have coalesced into one joint elongate maar crater.

Lorenz, V., Kurzlaukis, S. (2007). Root zone processes in the phreatomagmatic pipe emplacement model and consequences for the evolution of maar-diatreme volcanoes. Journal of Volcanology and Geothermal Research 150: 4-32.

Lorenz, V., Zimanowski, B. (2008). Volcanology of the West Eifel Maars and its relevance to the understanding of kimberlite pipes. 9th International Kimberlite Conference field trips, 7.-10. & 16.-18. August 2008.

Pirrung, M., Büchel, G., Lorenz V., Treutler, H.-C. (2008). Posteruptive development of the Ukinrek East Maar since its eruption in 1977 A.D. in the periglacial area of south-west Alaska. Sedimentology 55 (2): 305-334, doi: 10.1111/j.1365 3091.2007.00900.x.

Suhr, P. Goth, K., Lorenz, V., Suhr, S. (2006). Long lasting subsidence and deformation in and above maar-diatreme volcanoes – A never ending story. Zeitschrift der Deutschen Gesellschaft für Geowissenschaften 157 (3): 491-511.

White, J.D.L., Ross, P.-S. (2011). Maar-diatreme volcanoes: A review. Journal of Volcanology and Geothermal Research 201: 1-29.

The Eocene Eckfeld Maar in the Tertiary Hocheifel Volcanic Field, Germany: 25 years of research – an overview

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After 25 years of continuous fieldwork and research we present a short account of the present state of knowledge on the Eckfeld Maar (Fig. 1), the oldest among more than 400 eruption sites in what is known as the Tertiary Hocheifel Volcanic Field. In between, more than 250 papers and books have been published that deal with or refer to results of our excavation programme. This talk will not attempt to include all of the information available, such as the geology and sedimentology of the Eckfeld Maar itself, the morphological development of its surroundings since Eocene times, or its highly diverse and excellently preserved assemblage of fossils. We will merely provide a brief overview and restrict ourselves to some of the most important results.

The Eckfeld Maar is a unique complement to other Middle Eocene lagerstaetten and allows another detailed insight into the Eocene greenhouse ecosystem in the centre of Europe. The fossil record – although taphonomically biased – comprises a broad spectrum of biota that lived in the meromictic lake or in the dense forest surrounding the crater. There are biomarkers and lithified bacteria, algae, a diversity of tracheophytes, numerous insects, a few mollusks, and a wide range of vertebrates. Highlights include a great number of flowers with pollen in situ, a worldwide unique fossil louse with remnants of its last meal, and a pregnant mare of the proto-horse *Propalaeotherium voigti* whose fetus is preserved with its placenta. Another important fact is that up to

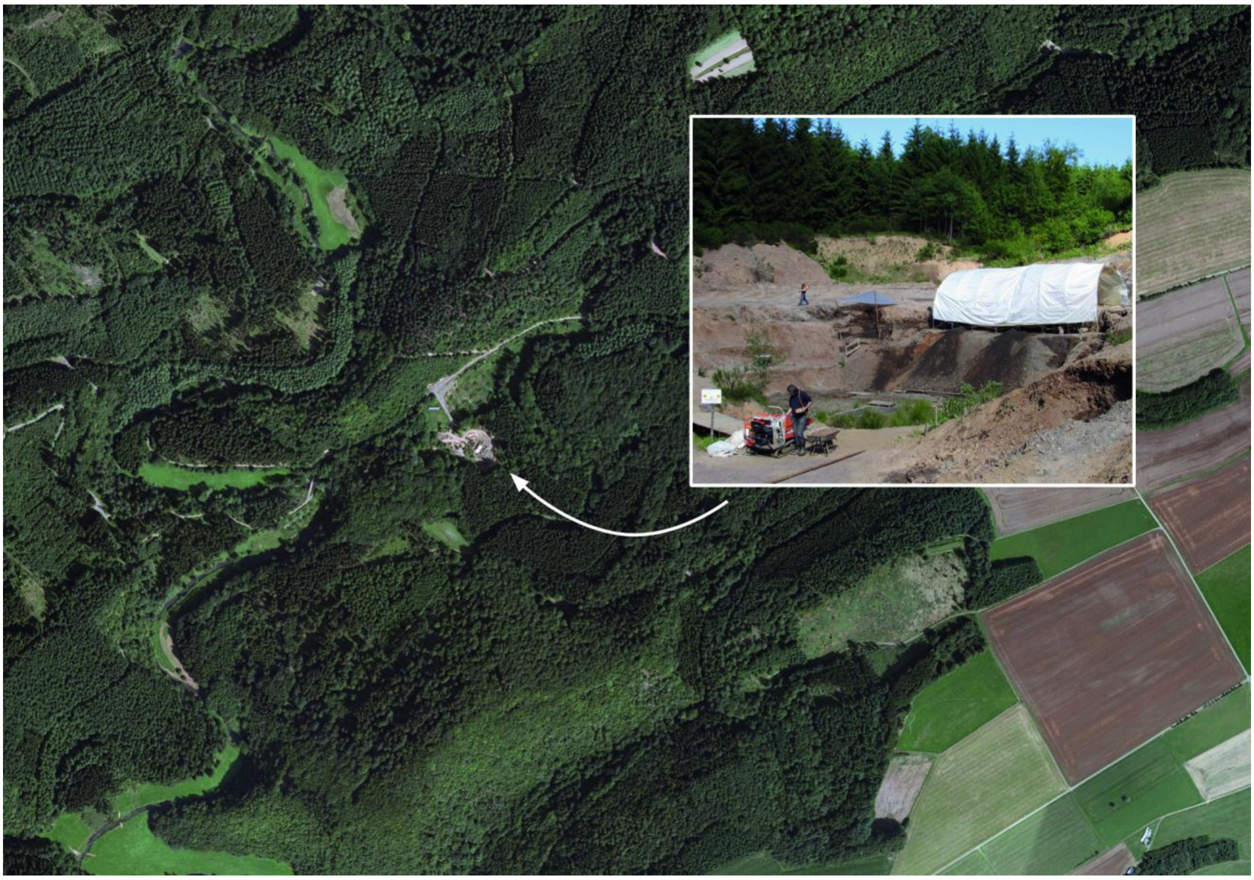

Figure 1. Today the Eckfeld Maar is hardly recognizable owing to intensive erosion during the Rhenish Uplift and the dense forest which is covering this part of the Eifel. The inset photo gives an idea of how our excavation site looks like.

now four species of primates have been found, among them the oldest representatives of the Adapidae thus far (Franzen, in press).

Biochronologically the flora and fauna of the Eckfeld Maar represents the late Geiseltalium of the European Land Mammal Ages (ELMA), which corresponds to the middle part of the Lutetian of the global geochronological time scale. The mammals clearly indicate reference level Mammal Paleogene (MP) 13. The Eckfeld Maar was the first European mammal site which could also be dated radiometrically by using $^{40}Ar^{39}Ar$, thus providing the first calibration for the continental Paleogene of Europe. Eckfeld and its biota are approximately 44 million years old. In contrast, Messel represents MP 11 and has provided a radiometric age of approximately 47 million years.

Correlating geochemical and sedimentological information with field data about the vertical distribution of fossils has provided insight into the development of the lake over the time period represented by 3 m of sediments exposed at the excavation site and corresponding to a time span of approximately 6000 years. Numerous individual data suggest that the lake's water level changed considerably over this time span. At times of lower water levels the basin was isolated, and in between these periods higher water levels led to a connection with the regional drainage system at least by an outlet. These changes most probably reflect changes in the climate, especially with respect to humidity and precipitation. This dynamic model for a rather early stage of the maar lake of Eckfeld also aids in understanding taphonomic processes in meromictic (maar) lakes in general. At the time of Eckfeld, mean temperatures had already decreased by approximately 2–3 °C compared to the time of Messel. Together, both lagerstaetten allow not only for a calibration of the terrestrial biochronological time scale in Europe, but also for the possibility of deciphering the rate of changes in biodiversity, coevolutionary processes, and even whole ecosystems in this part of Europe. Furthermore, Eckfeld has proved to be of outstanding importance in the reconstruction of geological and geodynamical processes within the Eifel in general.

Franzen, J.L. (in press). Neue Säugetierfunde aus der mitteleozänen Fossillagerstätte Eckfeld (Eifel, Deutschland). Mainzer Naturwissenschaftliches Archiv 49.

The following recently published papers provide comprehensive bibliographies of papers we are here referring to. Another list of publications can be found under the address http://www.eckfelder-maar.de/.

Frankenhäuser, H., Franzen, J.L., Kaulfuß, U., Koziol, M., Löhnertz, W., Lutz, H., Mertz, D.F., Mingram, J., Wappler, T., Wilde, V. (2009). Das Eckfelder Maar in der Vulkaneifel – Fenster in einen küstenfernen Lebensraum vor 44 Millionen Jahren. Mainzer Naturwissenschaftliches Archiv 47 (Festschrift): 263-324.

Lutz, H., Kaulfuß, U., Wappler, T., Löhnertz, W., Wilde, V., Mertz, D., Mingram, J., Franzen, J., Frankenhäuser, H., Koziol, M. (2010). Eckfeld Maar: Window into an Eocene Terrestrial Habitat in Central Europe. Acta Geologica Sinica (English Edition) 84 (4): 984-1009.

Paleogene primates from the Iberian Peninsula: Past, present and future

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The Paleogene records the first occurrence of primates and the great radiation of prosimians, as well as the apparition of first anthropoids. Especially during the Eocene, primates underwent a very important radiation with the appearance of two different groups, Omomyiformes and Adapiformes. In the Iberian Peninsula, Paleogene continental deposits are well represented in several basins (Fig. 1), constituting one of the most complete primate fossil records from Europe (Table 1).

The first works on Paleogene primates from Spain were developed at the Institut de Paleontologia de Sabadell (now Institut Català de Paleontologia Miquel Crusafont) during the 1960s by Dr. M. Crusafont and his team. They discovered several fossil sites containing prosimian remains (mainly isolated teeth) such as Sant Cugat de Gavadons, Sossís, and Les Saleres (Crusafont, 1965, 1967; Crusafont and Golpe-Posse, 1974), and they defined several new genera and species (*Agerinia roselli*, *Arisella capellae*, *Pivetonia isabenae*, *Pseudoloris reguanti*).

Later, in the 1990s, further studies carried out by the researchers of this institution led to the discovery of more Paleogene primate sites, such as Sant Jaume de Frontanyà, where three different primates were identified and preliminarily described by Moyà-Solà and Köhler (1993). The erection of the species *Pseudoloris godinoti* from the site of Fonollosa represents the only microchoerid which survived the climatic crisis of the Eocene-Oligocene boundary (Köhler and Moyà-Solà, 1999). In this decade, some Eocene primate remains were also reported from other localities, such as Santa Clara and Caenes (Moyà-Solà and Köhler, 1992).

A third phase in the study of Paleogene prosimians has started during the last few years, with this line of investigation being taken up again by studying in detail the material from the old collections and by prospecting new areas. This phase is providing very interesting results. For example, the analysis of the fossil primates from Mazaterón has led to the definition of a new genus and species of Cercamoniinae, *Mazateronodon endemicus*, which has helped to clarify the phylogeny of the tribe Anchomomyini (Marigó *et al.*, 2010), and a new, still unnamed, species of *Pseudoloris* (Minwer-Barakat *et al.*, in preparation). The discovery of these two taxa, clearly different from the representatives of their groups found in the Pyrenean basins and the rest of Europe, reinforces the endemic character of the faunas from the Western Iberian Bioprovince (Badiola *et al.*, 2009). Secondly, the detailed study of the material from the above-mentioned site of Sant Jaume de Frontanyà has also allowed the definition of two new species. One, the omomyid *Pseudoloris pyrenaicus*, represents the most complete sample of the genus recovered from the Iberian Peninsula, and permits the proposal of an anagenetic lineage which evolved in the middle-late Eocene in Europe (Minwer-Barakat *et al.*, 2010). The other, the adapiform *Anchomomys frontanyensis*, has allowed the confirmation of the existence of a new lineage of this genus in the Iberian Peninsula different from that of the rest of Europe, as well as a reconsideration of the phylogenetic relationships of the tribe Anchomomyini with asiadapines, extant lemuriforms and lorisiforms (Marigó *et al.*, 2011).

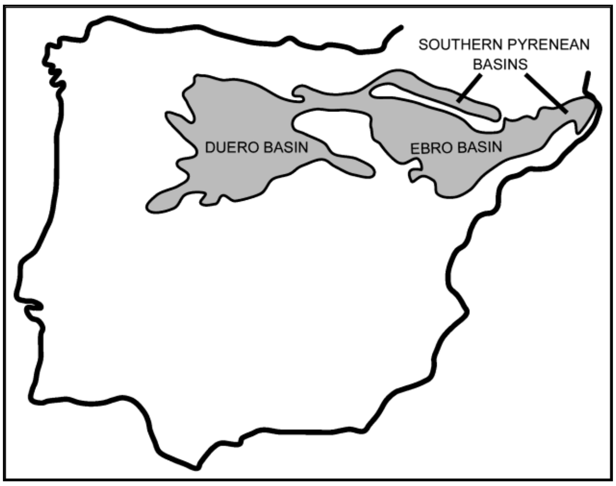

Figure 1. Spanish Paleogene basins with primate remains. Modified from Badiola *et al.*, 2009.

Currently we are studying material from Sossís, including new rich samples of microchoerids, as well as the remains of an adapiform, probably belonging to a new *Anchomomys* species, and new remains of a still not determined microchoerine from Zambrana, probably *Microchoerus* or *Necrolemur*.

The Paleogene primate record of the Iberian Peninsula is thus essential in helping solve some of the most debated questions regarding the evolution of the group during this time interval, such as the relationship between Adapiformes and extant Strepsirrhines, one of the most controversial topics in recent years (Gingerich *et al.*, 2010; Godinot, 2006; Seiffert *et al.*, 2010; Williams *et al.*, 2010). Another topic that has generated great interest is the drastic diminution in the number of primate species in the Northern Hemisphere coinciding with the Eocene-Oligocene boundary. The record of the Iberian Peninsula, from which the only microchoerine that survived this limit has been identified, can be crucial to our understanding of the climatic factors involved in such decrease of diversity.

BASIN	MP	LOCALITY	TAXA
Ebro	21-22	Fonollosa 13, Santpedor 2	*Pseudoloris godinoti*
	10-11	Ulldemolins I, Montblanc, Coll de l'Illa	Anchomomyini indet.
	10	La Coma	*Agerinia* sp. & *Cantius* sp.
Duero	15-16	Caenes	*Microadapis* sp.
		Mazaterón	*Mazateronodon endemicus, Pseudoloris* nov. sp. & Adapidae indet.
	13-14	Santa Clara	*Anchomomys* cf. *pygmaeus*
Southern Pyrenean	19	Sant Cugat de Gavadons	*Pseudoloris reguanti, Necrolemur* sp. & *Microchoerus ornatus*
	17	Roc de Santa	*Leptadapis magnus* & *Necrolemur antiquus*
		Sossís	*Adapis* cf. *parisiensis, Pseudoloris parvulus, Microchoerus erinaceus* & *Anchomomys* nov. sp.
	15	Pontils 38	Omomyidae nov. gen. et sp.
		Sant Jaume de Frontanyà-1	*Anchomomys* sp. & *Necrolemur* sp.
	14	Sant Jaume de Frontanyà-2	*Necrolemur* sp.
		Sant Jaume de Frontanyà-3	*Anchomomys frontanyensis, Adapis* sp. & *Pseudoloris pyrenaicus*
		Capella	*Leptadapis priscus, Arisella capellae* & *Pseudoloris isabenae*
	11/12	Casa Ramon	*Pseudoloris* sp.
	10	Les Saleres, Güell I, Castigaleu, Escarlà, Les Badies, Can Picantón	*Agerinia roselli*
		Mont de Roda	Prosimii indet.

Table 1. List of primate taxa of Paleogene localities from the Iberian Peninsula (updated from Antunes *et al.*, 1997).

To sum up, the Iberian Paleogene record of primates is especially abundant, diverse and well preserved in several key moments of the evolution of the group: the Eocene, when prosimians underwent a huge radiation and the first anthropoids appeared, and the Eocene-Oligocene boundary, when primate diversity decreased dramatically as a result of climatic changes.The key geographic position of the Iberian Peninsula will play an important role in interpreting different phylogenetic relationships in conjunction with paleobiogeographic information. However, the knowledge of the evolutionary history of the group is still far from clear. It is thus highly important to continue work at the previously known fossil sites as well as to prospect unstudied sections to find new fossiliferous levels that will increase the amount of exceptional material already available in our institution.

Antunes, M.T., Casanovas, M.L., Cuesta, M.A., Checa, Ll., Santafé, J.V., Agustí, J. (1997). Eocene mammals from Iberian Peninsula. Actes du Congrès Biochrom'97, Mémoires et Travaux de l'Ecole pratique des Hautes Etudes, Institut de Montpellier 21: 337-352.

Badiola, A., Checa, L., Cuesta, M.A., Quer, R., Hooker, J.J., Astibia, H. (2009). The role of new Iberian finds in understanding European Eocene mammalian paleobiogeography. Geologica Acta 7(nº1-2): 243-258.

Crusafont, M. (1965). Los Mamíferos, y en especial los Primates del Eoceno prepirenaico. Notas y Comunicaciones del Instituto Geológico y Minero de España 78: 159-166.

Crusafont, M. (1967). Sur quelques prosimiens de l'Eocène de la zone préaxiale pyrénaïque et un essai provisoire de reclassification. Colloques Internationaux de Centre National de la Recherche Scientifique 163: 611-632.

Crusafont, M., Golpe-Posse, J.M. (1974). Primates fósiles de España. Miscellanea Alcobé: 29-44.

Gingerich, P.D., Franzen, J.L., Habersetzer, J., Hurum J.D., Smith, B.H. (2010). *Darwinius masillae* is a haplorhine. Reply to Williams *et al.*, 2010. Journal of Human Evolution 59: 574-579.

Godinot, M. (2006). Lemuriform origins as viewed from the fossil record. Folia Primatologica 77: 446-464.

Köhler, M., Moyà-Solà, S. (1999). A finding of Oligocene primates on the European continent. Proceedings of the National Academy of Sciences USA 96(25): 14664-14667.

Marigó, J., Minwer-Barakat, R., Moyà-Solà, S. (2010). New Anchomomyini (Adapoidea, Primates) from the Mazaterón Middle Eocene locality (Almazán Basin, Soria, Spain). Journal of Human Evolution 58: 353-361.

Marigó, J., Minwer-Barakat, R., Moyà-Solà, S. (2011). New *Anchomomys* (Adapoidea, Primates) from the Robiacian (Middle Eocene) of northeastern Spain. Taxonomic and evolutionary implications. Journal of Human Evolution 60: 665-672.

Minwer-Barakat, R., Marigó, J., Moyà-Solà, S. (2010). A new species of *Pseudoloris* (Omomyidae, Primates) from the middle Eocene of Sant Jaume de Frontanyà (Eastern Pyrenees, Spain). American Journal of Physical Anthropology 143: 92-99.

Moyà-Solà, S., Köhler, M. (1992). Los primates del paleógeno de Castilla y León: una introducción. Vertebrados fósiles de Castilla y León. Museo de Salamanca: 121-125.

Moyà-Solà, S., Köhler, M. (1993). Middle Bartonian Locality with *Anchomomys* (Adapidae, Primates) in the Spanish Pyrenees: Preliminary Report. Folia Primatologica. 60: 158-163.

Seiffert, E.R., Simons, E.L., Boyer, D.M., Perry, J.M.G., Ryan, T.M., Sallam, H.M. (2010). A fossil primate of uncertain affinities from the earliest late Eocene of Egypt. Proceedings of the National Academy of Sciences USA 107(21): 9712-9717.

Williams, B.A., Kay, R.A., Kirk, E.C., Ross, C.W. (2010). *Darwinius masillae* is a strepsirrhine. Reply to Franzen *et al.*, 2009. Journal of Human Evolution 59: 567-573.

Talar morphology of azibiids, strepsirhine-related primates from the Eocene of Algeria

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Over the past decades, the Afrocentric model for anthropoid primate origins has relied upon the >45-Myr-old fossil *Algeripithecus minutus* from Algeria (Gour Lazib, Hammada du Dra), which was widely acknowledged to be one of the oldest known anthropoids (Godinot and Mahboubi, 1992, 1994; Beard, 2002; Seiffert *et al.*, 2005). However, very recent discoveries of more nearly complete fossils of *Algeripithecus*, as well as of *Azibius trerki*, another primate of uncertain affinity (formerly; Sudre, 1975) from the same rock unit of Algeria, strongly suggest that these two primates are closely related and, in any case, phylogenetically remote from the clade Anthropoidea. *Algeripithecus* and *Azibius* make up the family Azibiidae and represent the earliest offshoots of an Afro-Arabian strepsirhine clade that embraces extant toothcombed primates (lemurs, lorises and galagos) and their fossil relatives (Tabuce *et al.*, 2009). This new fossil-based interpretation strongly challenges the role of Africa as the ancestral homeland for anthropoids, yet, at the same time, reveals an ancient African origin for crown strepsirhines. Beyond these highly critical phylogenetic implications, these fossils have also highlighted some aspects of the paleobiology of these ancient African primates. The new paleontological evidence assembled has indeed revealed that azibiids were highly dentally specialized (e.g., high-crowned posterior premolars forming a blade-like structure, and pronounced bunodonty of molars with a large hypocone), appearing somewhat as an aberrant group of stem strepsirhines having strong dietary specializations. In addition, cranial remains (fragments of maxillary-bearing teeth) referred to *Azibius trerki* have also provided anatomical evidence suggesting nocturnality in this taxon. However, information regarding the locomotor behaviour of these primates has so far remained elusive because of a lack of primate postcranial evidence in the Gour Lazib fossil record.

Our continuing long-standing field efforts in the primate-bearing localities of the Gour Lazib area have finally led to the recovery of postcranial remains of primates. Two ankle bones of distinct size (the small UM/HGL50-466, and the large UM/HGL50-467) have been sorted after acid treatment of the indurated sediments of the HGL-50 layer located on the Glib Zegdou outlier. The HGL-50 locality is famous for having yielded several dental remains of primates, including *Algeripithecus minutus*, *Azibius trerki*, and a new species of cf. *Azibius*. The last is documented by isolated upper and lower teeth (unpublished material), which are about three times larger than their counterparts in *A. trerki*. The two new primate tali from HGL-50 are reasonably well preserved, lacking any apparent post-mortem distortion. However, the numerous local breaks and the exposure of the trabecular bone structure in several talar regions (cortical bone eroded) indicate that these tali were damaged during deposition and/or fossilization processes.

Despite the clear difference in size between UM/HGL50-466 and UM/HGL50-467, these two tarsal elements are virtually comparable in terms of structure. In overall proportions, both tali are markedly narrow relative to their length, and moderately tall in medial or lateral view. The length of their talar neck plus head is about half of total talar length, and clearly longer than the length of the trochlea. Their necks are only very slightly deflected medially (17–18°) relative to the anteroposterior axis of the trochlea, a condition which strongly contrasts with the very medially angled talar neck observed in practically all extinct and extant anthropoid primates. The overall proportions and the low degree of neck deviation of these two new tali are generally observed in certain modern strepsirhine families, particularly in the Cheirogaleidae (e.g., *Allocebus*, *Microcebus*). Modern tarsiids (i.e., *Tarsius*) exhibit also a weak neck deviation, but differ in overall proportions. In anterior view, the heads appear ovoid in shape, being wider than high, with their long axis oriented mediolaterally relative to the dorsal plane of the trochlea. On UM/HGL50-467, the trochlea is only moderately grooved, displaying rounded and symmetrical medial and lateral trochlear rims. On this talus, the medial trochlear rim extends slightly farther distally onto the talar neck compared with the distal end of the lateral rim, a condition not found in UM/HGL50-466. Proximally, the two tali bear a prominent trochlear shelf, which is characteristic of most extant strepsirhines and Paleogene adapiforms, but also, to a lesser extent, of omomyids, omomyiforms and eosimiids anthropoids. A set of talar features has proven to be useful in reconstructing higher-level primate phylogeny (e.g., Gebo, 1988; Beard *et al.*, 1988; Dagosto and Gebo, 1994). Interestingly, UM/HGL50-466 and UM/HGL50-467 display a suite of derived morphological characteristics which are otherwise found only in strepsirhine primates. These features include a lateral position on the posterior trochlea of the groove for the *flexor hallucis longus* muscle, the lateral talofibular facet sloping gently laterally over its entire extent, and a dorsoplantarly large and deep medial talo-tibial facet ("full" condition *sensu* Gebo, 1988). Such talar conditions differ radically from alternative and divergent talar conditions found in all extinct and extant anthropoids. Based on regressions of talar dimensions against body mass in living primates, UM/HGL50-466 and UM/HGL50-467 belonged to two distinct taxa having body masses ranging from about 130–200 g and 630–920 g, respectively (estimated from all-strepsirhine bivariate regression equations based on several linear talar dimensions (MTRW, TL and HT) provided by Dagosto and Terranova (1992)). Based on first lower molar areas of *Azibius trerki* and cf. *Azibius* sp. from HGL-50, the body masses of these two primates are estimated at 115–125 g and 650–860 g, respectively (from the all-primate and prosimian least-squares bivariate regressions presented by Conroy (1987)). Therefore, given the overlap between molar and talus body mass estimates, and given the degree of phylogenetic congruence (i.e., strepsirhine affinities) between the cranio-dental morphology of the two species of *Azibius* and the talar morphology described here, the referral of UM/HGL50-466 and UM/HGL50-467 to *Azibius trerki* and cf. *Azibius* sp., respectively, seems to be the most appropriate taxonomic option here.

Despite the cortical bone alteration, which limits the description of the joint facets (notably regarding the navicular facet of the talar heads), UM/HGL50-466 and UM/HGL50-467 exhibit a suite of osteological features that reflect functional attributes related to locomotor behaviour. Both tali display a relatively tall talar body and moderately long and nearly straight talar neck, and show a moderately grooved trochlea, which is only slightly wedge shaped. In addition, they bear a well-developed posterior trochlear shelf, a structure which acts as a bony stop in extreme plantarflexion at the talocrural joint during a leap (Gebo, 1988). All these talar features indicate that both *Azibius* species were probably engaged in a form of quadrupedalism with some degree of proficiency in leaping. These conditions contrast markedly with that observed on tali of frequent climbers, which show specialized features promoting much greater mobility (e.g., talar body dorsoventrally flat, short and medially deflected talar neck, and strongly wedged trochlear surface). However, the characteristics of the trochlea in *Azibius*' tali (only slightly grooved (quite flattened), rounded rims, slightly wedged shaped), suggest orderly movements but with some degree of mobility at the talocrural joint, thereby indicating that these species were also proficient climbers. To summarize, the functional attribute depicted on the UM/HGL50-466 and UM/HGL50-467 tali imply intermediate joint mechanics compared with more extreme morphologies associated with highly specialized leaping and climbing. These functionally intermediate features indicate a greater emphasis on arboreal quadrupedalism for *Azibius*, with some abilities to leap and climb.

Beard, K.C. (2002). Basal anthropoids. In: Hartwig, W.C. (ed) The Primate Fossil Record. Cambridge University Press, Cambridge, pp 133-149.

Beard, K.C., Dagosto, M., Gebo, D.L., Godinot, M. (1988). Interrelationships among primate higher taxa. Nature 331: 712-714.

Conroy, G.C. (1987). Problems of body-weight estimation in fossil primates. International Journal of Primatology 8: 115-137.

Dagosto, M., Gebo, D.L. (1994). Postcranial anatomy and the origin of the Anthropoidea. In: Fleagle, J.G., Kay, R.F. (eds) Anthropoid Origins. Plenum Press, New York, pp 567-593.

Dagosto, M., Terranova, C.J. (1992). Estimating the body size of Eocene primates: A comparison of results from dental and postcranial variables. International Journal of Primatology 13: 307-344.

Gebo, D.L. (1988). Foot morphology and locomotor adaptation in Eocene primates. Folia Primatologica 50: 3-41.

Godinot, M., Mahboubi, M. (1992). Earliest known simian primate found in Algeria. Nature 357: 324-326.

Godinot, M., Mahboubi, M. (1994). Les petits primates simiiformes de Glib Zegdou (Éocène inférieur à moyen d'Algérie). Comptes Rendus de l'Académie des Sciences, Paris 319: 357-364.

Seiffert, E.R., Simons, E.L., Clyde, W.C., Rossie, J.B., Attia, Y., Bown, T.M., Chatrath, P., Mathison, M.E. (2005). Basal anthropoids from Egypt and the antiquity of Africa's higher primate radiation. Science 310: 300-304.

Sudre, J. (1975). Un prosimien du Paléogène ancien du Sahara nord occidental : *Azibius trerki* n. g. n. sp. Comptes rendus de l'Académie des Sciences, Paris 280: 1539-1542.

Tabuce, R., Marivaux, L., Lebrun, R., Adaci, M., Bensalah, M., Fabre, P.-H., Fara, E., Gomes Rodrigues, H., Hautier, L., Jaeger, J.-J., Lazzari, V., Mebrouk, F., Peigné, S., Sudre, J., Tafforeau, P., Valentin, X., Mahboubi, M. (2009). Anthropoid *vs.* strepsirhine status of the African Eocene primates *Algeripithecus* and *Azibius*: Cranio-dental evidence. Proceedings of the Royal Society of London 276: 4087-4094.

Paleoclimate of early Eocene highland floras of British Columbia, Canada, with focus on Falkland and Quilchena

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The Okanagan Highlands (OH) fossil floras of Western North America are now known to date mostly to the Ypresian (early Eocene). These fossil sites are rich in both insect (Archibald and Mathewes, 2000) and plant remains, offering multiple paleoclimate proxies and information about the character of the forest communities that surrounded the Eocene lakes (Greenwood *et al.*, 2005; Smith *et al.*, 2009). Volcanic ashes interbedding the fossiliferous shales at Quilchena (Villeneuve and Mathewes, 2005) and Falkland are dated radiometrically at 51.5 ± 0.4 Ma and 50.61 ± 0.16 Ma, respectively, which places

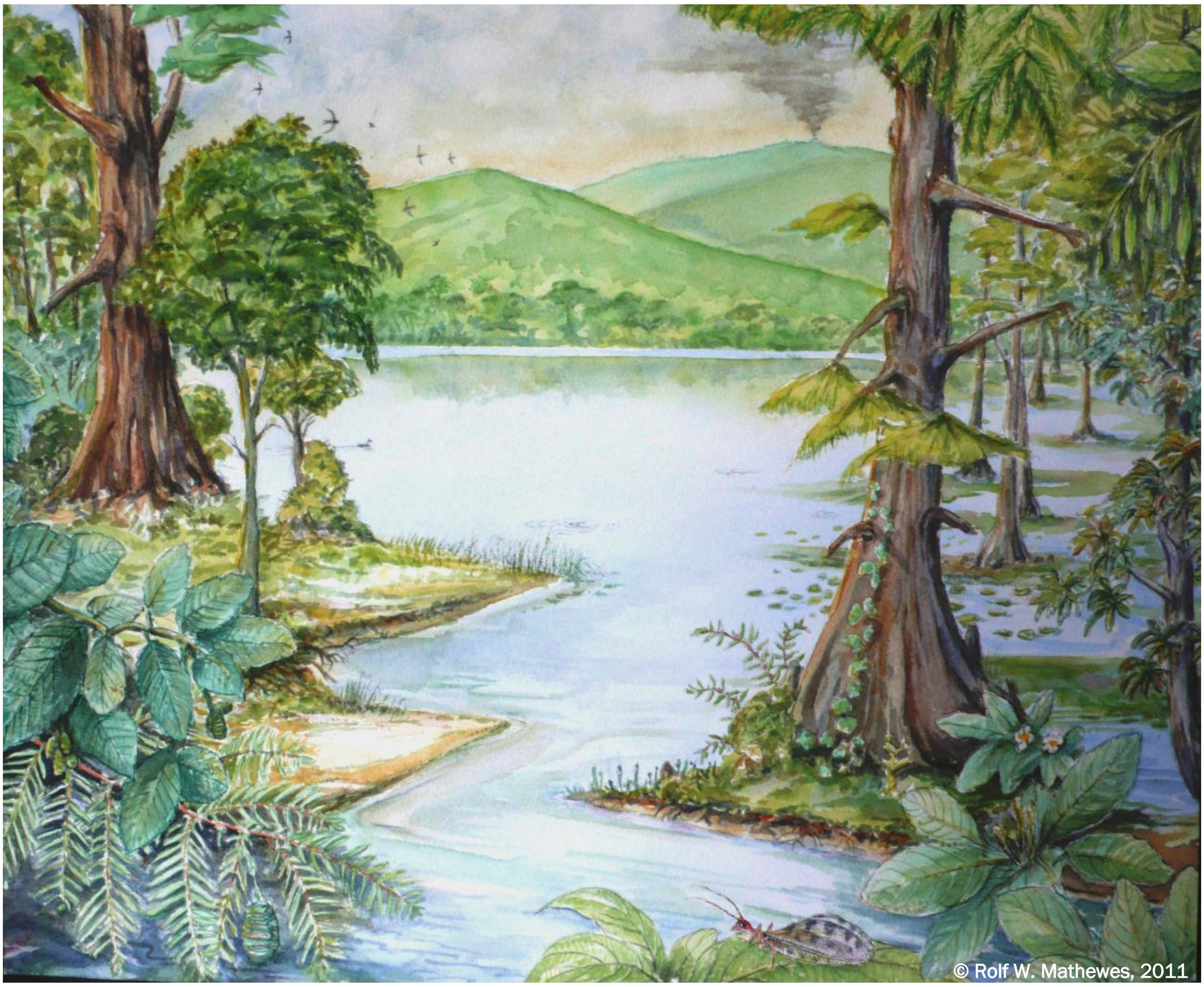
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Figure 1. "Early Eocene summer at palaeolake Quilchena, 51.5 million years ago. View from a shoreline swamp showing common macrofossil sources at an inlet stream. On the right, a large swamp cypress (*Taxodium*) tree with *Decodon* shoots at the left base. Theaceae (cf *Ternstroemites* or *Gordonia*) foliage on the far and lower right, with a fruiting branch of *Fraxinus* at upper right. The shallow waters around the *Taxodium* (or occasional *Glyptostrobus*) in the background support floating mats of *Azolla* and algae, interspersed with leaves of Nymphaeaceae. At left, a branch of *Alnus parvifolia* with cones hangs over a fertile shoot of *Metasequoia*. Beside the large *Metasequoia* at left, other angiosperm trees and shrubs are indicated, representing a diversity of taxa. The monocots at the middle water's edge are not grasses, but an unknown graminoid.

Animal fossils include insects, here indicated by a rare giant lacewing (Neuroptera) with patterned wings. March flies (Bibionidae) are the commonest insect fossils, and likely provided food for the swallow-like swifts (upper left), whose presence was recently confirmed at this site. Two taxa of fishes are common at Quilchena, large predatory bowfins (*Amia*) based on scales, and complete juvenile suckers (*Amyzon*) who likely inhabited the shallow edges of the lake. Two rings indicating feeding fish are hinted at in the middle of the painting. Abundant "pellets" containing small fish remains have been interpreted by Mark Wilson as regurgitated by piscivorous birds. A flight feather fossil led me to include a distant bird at left center, whose identification is still a mystery. The physical environment suggests a shallow and fluctuating water level, and a distant volcanic eruption is consistent with a time of active volcanism and tectonic activity during the Early Eocene."

these two floras at the middle and end of the Early Eocene Climatic Optimum (EECO), a significant hyperthermal episode 2–3 million years in duration associated with atmospheric carbon dioxide levels ($p\mathrm{CO_2}$) twice Holocene values (i.e., $p\mathrm{CO_2}$> 800ppm). Both leaf-physiognomic analysis of dicot leaves and bioclimatic reconstructions using a nearest living relative (NLR) approach have determined that the paleoclimate of Quilchena was both the warmest and wettest of the OH sites, with Falkland showing a secular decline in both temperature and $p\mathrm{CO_2}$ up-section (Smith *et al.*, 2010), consistent with its stratigraphic position at the waning phase of the EECO. The majority of the OH floras are interpreted as having little temperature seasonality. While other fossil floras from this upland region, including Falkland, are classified as microthermal (MAT < 13° C), Quilchena is warmer and falls within the meso-thermal category (~15° C), consistent with its stratigraphic position at the middle of the EECO. The presence of thermophilic taxa used in the NLR climatic analysis of Quilchena is confirmed by reproductive organs of taxa such as *Glyptostrobus*, *Taxodium*, *Pseudolarix*, *Sequoia*, *Keteleeria*, *Eucommia*, and *Dipteronia*. Rarefaction analyses of plant diversity at these sites corroborates recent analysis of insect diversity at the McAbee OH site (Archibald *et al.*, 2010), showing tropical-style diversity for both Falkland and Quilchena (Fig. 1). High diversity at these sites is not, however, associated with tropical-character temperature regimes, but rather a novel combination of moderate temperatures and mild winters. As chronologies of other localities become better constrained, it is hoped that a time series of climate and vegetational changes will be developed that will assess the impact of the changes surrounding the warmest interval (‘hyperthermal’) of the Cenozoic. A comparison of Quilchena and Falkland with other OH floras such as Republic, Princeton, McAbee, Thomas Ranch, and Driftwood Creek constitutes an opportunity to better understand the long-term consequences of climate warming and cooling on ecosystems.

The fossil lake at Quilchena also exhibits some similarities to the Messel Lake, based on evidence for shallow water, anoxic events with fish kills, and recent evidence for the presence of swifts as part of the local avifauna.

Archibald, S.B., Bossert, W.H., Greenwood, D.R., Farrell, B.D. (2010). Seasonality, the latitudinal gradient of diversity, and Eocene insects. Paleobiology 36 (3): 374-398.

Archibald, S.B., Mathewes, R.W. (2000). Early Eocene insects from Quilchena, British Columbia and their paleoclimatic implications. Canadian Journal of Zoology 78: 1-24.

Greenwood, D.R., Archibald, S.B., Mathewes, R.W., Moss, P.T. (2005). Fossil biotas from the Okanagan Highlands, southern British Columbia and northeastern Washington State: Climates and ecosystems across an Eocene landscape. Canadian Journal of Earth Sciences 42: 167–185.

Smith, R.Y., Basinger, J.F., Greenwood, D.R. (2009). Depositional setting, fossil flora, and paleoenvironment of the early Eocene Falkland site, Okanagan Highlands, British Columbia. Canadian Journal of Earth Sciences 46 (11): 811-822.

Smith, R.Y., Greenwood, D.R., Basinger, J.F. (2010). Estimating paleoatmospheric pCO2 during the Early Eocene Climatic Optimum from stomatal frequency of Ginkgo, Okanagan Highlands, British Columbia, Canada. Palaeogeography, Palaeoclimatology, Palaeoecology 293: 120–131.

Villeneuve, M., Mathewes, R.W. (2005). An Early Eocene age for the Quilchena fossil locality, southern British Columbia. Geological Survey of Canada, Current Research 2005-A4, 7pp.

Up to the top – Plant diversification on the Tibetan Plateau

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Trying to understand the processes generating high biodiversity levels has always been a challenge for scientists. Geophysical as well as climatic changes may increase rates of speciation and/or strongly affect dispersal in plants. Such changes occurred during the course of the emergence of the Qinghai Tibetan Plateau (QTP).

The QTP, also known as the “Roof of the World”, is the highest and largest plateau in the world, with an average elevation of more than 4000 m above sea level and covering a region of 2.3 million km² (Herzschuh *et al.*, 2009). The uplift of the QTP was the consequence of the collision of the Indian subcontinent with Eurasia during the early Eocene, about 55–50 million years ago (mya) (Tapponnier *et al.*, 2001; Royden *et al.*, 2008). The uplift of the QTP was uneven and first affected its southern margin: during the late Eocene (c. 35 mya) isotopic evidence shows that the Plateau might have already reached 4000 m (Mulch and Chamberlain, 2006; Rowley and Currie, 2006). The rising of the Plateau progressed northwards through the Eocene, and the QTP was nearly totally uplifted during the mid-Miocene (Mulch and Chamberlain, 2006).

Generally, the earth’s climate is affected significantly by the presence of mountains and plateaus (Kutzbach *et al.*, 1993). In our study system, the uplift of the QTP had a great impact on regional and worldwide climates by playing a fundamental role in the establishment of the Asian monsoon system (Manabe and Terpstra, 1974; Wu and Zhang, 1998). Its onset is dated back to 22–8 mya (Guo *et al.*, 2002; Zhisheng *et al.*, 2001). Such drastic geophysical and climatic changes caused habitat diversification and could consequently have triggered a burst of speciation in the neighbouring regions of the QTP. Yet the influence of the uplift of the QTP on the evolution of various taxa is under-studied. The QTP and the neighbouring regions of the Himalayas and southeast China harbour a remarkable species richness and abundance of endemics. The Plateau itself contains about 4385 plant species of 1174 genera in 189 families, and an estimated 25% of those species are considered endemic (Chen *et al.*, 2005).

In the scope of our project, we are going to use plant genera of the families Ericaceae (*Agapetes*, *Vaccinium*) and Rhamnaceae (*Rhamnus)* as model systems for the investigation of the role of the uplift of the QTP on plant diversification and biogeographic history. These three genera were chosen because of their good representation in the region in terms of species numbers. In the case of *Rhamnus*, fossils reveal that this genus was present in the Tibetan region before the uplift occurred (Mehrotra *et al.*, 2005). The distribution of these genera is also interesting because it will allow us to compare the biogeographic history of both temperate (*Rhamnus*) and tropical (*Agapetes*) groups in relation to the uplift of the QTP. In this study, phylogenetic reconstructions based on several nuclear and plastid molecular markers and on a significantly large taxonomic sampling of the three genera will be associated with biogeographical analyses to (1) identify the role of the uplift of the Tibetan Plateau for plant diversification during the Eocene and Miocene, (2) unravel migration/dispersal routes by which this region was colonized, (3) estimate the relative contribution of the Tibetan Plateau to the worldwide subalpine and montane plant diversity, and (4) investigate how temperate and tropical genera differ in their biogeographical history.

CHEN, S., XIA, T., CHEN, S., ZHOU, Y. (2005). RAPD profiling in detecting genetic variation in endemic *Coelonema* (Brassicaceae) of Qinghai-Tibet Plateau of China. Biochemical Genetic 43: 189-201.

GUO, Z.T., RUDDIMAN, W.F., HAO, Q.Z., WU, H.B., QIAO, Y.S., ZHU, R.X., PENG, S.Z., WEI, J.J., YUAN, B.Y., LIU, T.S. (2002). Onset of Asian desertification by 22 Myr ago inferred from loess deposits in China. Nature 416: 159-163.

HERZSCHUH, U., BIRKS, H.J.B., NI, J., ZHAO, Y., LIU, H., LIU, X., GROSSE, G. (2009). Holocene land-cover changes on the Tibetan Plateau. The Holocene 2009: 1-14.

KUTZBACH, J.E., PRELL, W.L., RUDDIMAN, W.F. (1993). Sensitivity of Eurasian climate to surface uplift of the Tibetan Plateau. Journal of Geology 101: 177-190.

MANABE, S., TERPSTRA, T.B. (1974). The effects of mountains on the general circulation of the atmosphere as identified by numerical experiments. Journal of the Atmospheric Sciences 31: 3-42.

MEHROTRA, R.C., LIU, X.Q., LI, C.S., WANG, Y.F., CHAUHAN, M.S. (2005). Comparison of the Tertiary flora of southwest China and northeast India and its significance in the antiquity of the modern Himalayan flora. Review of Palaeobotany and Palynology 135: 145-163.

MULCH, A., CHAMBERLAIN, C.P. (2006). The rise and growth of Tibet. Nature 439: 670-671.

ROWLEY, D.B., CURRIE, B.S. (2006). Palaeo-altimetry of the late Eocene to Miocene Lunpola basin, central Tibet. Nature 439: 677-681.

ROYDEN, L.H., BURCHFIEL, B.C., VAN DER HILST, R.D. (2008). The geological evolution of the Tibetan Plateau. Science 321: 1054-1058.

TAPPONNIER, P., XU, Z.Q., ROGER, F., MEYER, B., ARNAUD, N., WITTLINGER, G., YANG, J.S. (2001). Oblique stepwise rise and growth of the Tibet Plateau. Science 294: 1671-1677.

WU, G.X., ZHANG, Y.S. (1998). Tibetan Plateau forcing and the timing of the monsoon onset over South Asian and the South China Sea. Monthly Weather Review 126: 913-927.

ZHISENG, A., KUTZBACH, J.E., PRELL, W.L., PORTER, S.C. (2001). Evolution of Asian monsoons and phased uplift of the Himalaya–Tibetan plateau since Late Miocene times. Nature 411: 62-66.

The original colours of 47 million-year-old fossil moths from Grube Messel revealed by fossilised biophotonic nanostructures

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Structural colours are generated by scattering of light by periodic variations in tissue nanostructure (Prum *et al.*, 2006). They are widespread among animals (Vukusic and Sambles, 2003) and have been studied most extensively in butterflies and moths (Lepidoptera), which exhibit the widest diversity of photonic nanostructures, resultant colours and visual effects of any extant organism (Ingram and Parker, 2008). The evolution of structural coloration in lepidopterans, however, is poorly understood (Wilts *et al.*, 2009). Existing hypotheses based on phylogenetic and/or structural data (Tilley and Eliot, 2002; Wickham *et al.*, 2006) are controversial (Prum *et al.*, 2006; Ingram and Parker, 2008) and do not incorporate data from fossils. This stymies attempts to reconstruct the evolution of lepidopteran communication strategies and of photonic nanostructures in nature.

Here we report the preservation of structurally coloured scales in fossil lepidopterans and reconstruct the original colours of their wings. Specimens of two different ditrysian moths from the ~47 million-year-old Grube Messel oil shales (Germany) exhibit bright, non-iridescent metallic hues. The preserved colours are generated by a multilayer reflector comprising a stack of perforated laminae in the scale lumen; differently coloured scales differ in ultrastructure. The original colours were altered during fossilisation but are reconstructed based upon preserved ultrastructural detail. The dorsal surface of the forewings was a yellow-green colour that probably served as a dual-purpose defensive signal, i.e. aposematic during feeding and cryptic at rest. This visual signal was enhanced by reduction of iridescence (change in hue with viewing angle), achieved via two separate optical mechanisms – extensive perforation and concave distortion – of the multilayer reflector.

Our findings have significant wider implications. These lepidopteran fossils from Messel provide the first unequivocal evidence for the function of structural colour in the fossil record and for aposematism in fossil insects. Further, they demonstrate that plastic scale developmental processes and the use of complex optical mechanisms for interspecific signalling had evolved in lepidopterans by the mid-Eocene. Most importantly, the discovery of structurally coloured scales in these fossil lepidopterans confirms the potential for similar discoveries for other lepidopteran taxa and demonstrates the feasibility of reconstructing the colour of other lepidopteran fossils, even those that lack obvious colouration. This will lead to deeper understanding of the evolution of structural colours, of communication strategies, and of scale developmental processes in this group.

INGRAM, A.L., PARKER, A.R. (2008). A review of the diversity and evolution of photonic structures in butterflies, incorporating the work of John Huxley (The Natural History Museum, London from 1961 to 1990). Philosophical Transactions of the Royal Society B 363: 2465-2480.

PRUM, R.O., QUINN, T., TORRES, R.H. (2006). Anatomically diverse butterfly scales all produce structural colours by coherent scattering. Journal of Experimental Biology 209: 748-765.

TILLEY, R.J.D., ELIOT, J.N. (2002). Scale microstructure and its phylogenetic implications in lycaenid butterflies (Lepidoptera, Lycaenidae). Transactions of the Lepidopteran Society of Japan 53:153-180.

VUKUSIC, P., SAMBLES, J.R. (2003). Photonic structures in biology. Nature 424: 852-855.

WICKHAM, S., LARGE, M.C.J., POLADIAN, L., JERMIIN, L.S. (2006). Exaggeration and suppression of iridescence: The evolution of two-dimensional butterfly structural colours. Journal of the Royal Society Interface 3: 99-109.

WILTS, B.D., LEERTOUER, H.L., STAVENGA, D.G. (2009). Imaging scatterometry and microspectrophotometry of lycaenid butterfly wing scales with perforated multilayers. Journal of the Royal Society Interface 6: S185-S192.

Re-interpretation of the genus *Parabunodon* (Ypresian, Turkey): Implications for the evolution and distribution of pleuraspidotheriid mammals

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Parabunodon anatolicum Ducrocq and Sen, 1991, based on a single palate preserving P^4–M^3, was found by a miner in the Eski Çeltek coal mine, northern Anatolia, Turkey. This taxon was then referred to a “haplobunodontid” (=choeropotamid) artiodactyl on the basis of close resemblance with western European choeropotamids, such as “*Anthracobunodon*” (=*Amphirhagatherium*) from the middle Eocene of Geiseltal, and *Massilabune* from the Messel Pit. The age of the Eski Çeltek locality is somewhat controversial. Blumenthal (1937), who formally defined the Çeltek Formation, considered it early Eocene, based on the early Lutetian age of the benthic foraminifera of the overlying Armutlu Formation. Akgün (2002) studied the palynomorphs of these formations and proposed a middle-?late Eocene age for both units. Koç and Türkmen (2002) found a thin marine horizon above the mammal-bearing lignite seam with planktonic foraminifera of Ypresian age, while the overlying marine Armutlu Formation yielded rich benthic and planktonic foraminiferal assemblages dated to the early Lutetian. According to these results, the Eski Çeltek mammal locality, which also yielded remains of the embrithopod *Palaeoamasia kansui* Ozansoy, 1966, is most likely late Ypresian in age and not Lutetian as previously thought.

Other early Paleogene mammals have been reported from the red beds of the Uzunçarşıdere Formation exposed on the margin of the Haymana Basin near Ankara (Kappelman *et al.*, 1996; Maas *et al.*, 1998, 2001), and an early middle Eocene age was advocated for this mammal assemblage based mostly on the apparent lack of unconformity between this formation and the overlying marine Lutetian Orhaniye Formation. The fossil fauna includes marsupials, embrithopods, and the genus *Hilalia*, documented by dental and postcranial material, and representing four species of various sizes. First described as a “condylarth” *incertae sedis*, the taxonomic affinities of *Hilalia* have long remained somewhat problematic, raising more issues (e.g., phylogenetic and biogeographic) than offering responses. Recently, Ladevèze *et al.* (2010) investigated the phylogenetic relationships of western European pleuraspidotheriids among “condylarths”, and recognized affinities of *Hilalia* with *Pleuraspidotherium* and *Orthaspidotherium* from the late Paleocene of Western Europe. Although several symplesiomorphic resemblances shared by pleuraspidotheriids and artiodactyls were tentatively discussed, no unambiguous synapomorphy linking these two taxa could be identified based on the available material.

Here, we revisit the relationships of *Parabunodon anatolicum* in the light of these recent studies. *Parabunodon anatolicum* is characterized by buno-lopho-selenodont cheek teeth, with a W-shaped ectoloph linked to a strong mesostyle (closer to metacone), low and poorly crested paraloph and metaloph, inflated paraconule close to the protocone, well-developed labial and mesial cingula, presence of a cingulum between the pseudohypocone and protocone (entocingulum), absence of postprotocrista, M^3 smaller than M^2 with a posterior lobe transversely reduced, and submolariform P^4 with a small metacone fused to paracone. Most of these features are shared with *Hilalia* (although the latter has much more developed crests), suggesting close affinities between *Parabunodon* and *Hilalia*. Some of these dental features are diagnostic of the Pleuraspidotheriidae (e.g., M^{1-3} with pseudohypocone), or listed as synapomorphies of the Pleuraspidotheriid clade (e.g., P^4 with small but distinct metacone fused to paracone; Ladevèze *et al.* 2010: fig. 11A). *Parabunodon* is, however, clearly distinct from *Hilalia* and other pleuraspidotheriids. Beyond its large size (roughly equal to the largest species of *Hilalia: H. robusta*), the most obvious derived character of *Parabunodon* is the marked bunodonty of its upper molars. This is illustrated by the lower cusps, lower and inflated lophs that are obviously less sharp and less functional as illustrated by the absence of anterior shearing facet. Other derived features include reduced cingula in the upper molars (e.g., entocingulum not connected to the precingulum) and in premolars (no ectocingulum and precingulum on P^4), reduced parastyle and metastyle, an inflated (neomorphic) “metaconule” that is shifted mesially with respect to the pseudohypocone, and the transversely extended M^2. Most of these traits are probably autapomorphic in *Parabunodon*. *Parabunodon* and *Hilalia* have a paracone slightly larger than the metacone, in contrast to *Orthaspidotherium* and *Pleuraspidotherium*, the only two monospecific genera formerly included within the Pleuraspidotheriidae. Other dental features shared by *Hilalia* and *Parabunodon* are the mesio-distally compressed protocone and the transverse development of M^2. *Pleuraspidotherium* is distinguished by several probably autapomorphic traits (molarized P^4 showing full metacone, paracone and paraconule), advanced selenodonty, elongated muzzle, and reduced anterior premolar dentition. *Orthaspidotherium* is distinguished by several primitive features (triangular occlusal molar outline, small pseudohypocone, etc.) with respect to other pleuraspidotheres.

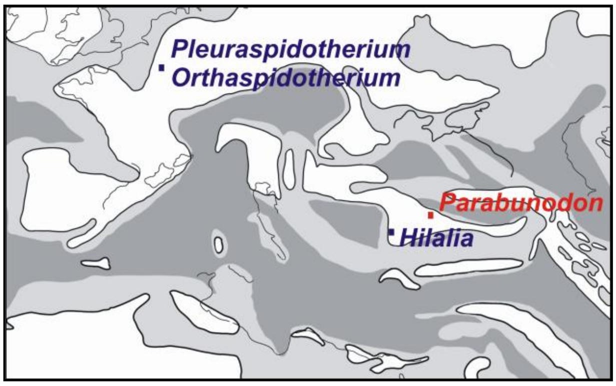

Figure 1. Geographic distribution of pleuraspidotheriid "condylarths" during the late Paleocene and early Eocene (map modified from Barrier and Vrielynck, 2008).

The inclusion of *Hilalia* within pleuraspidotheriid "condylarths", together with former biostratigraphic data (e.g., Kazanci and Gökten, 1986) and preliminary field data, clearly suggest a late Paleocene age for the fossil-bearing beds of the Uzunçarşıdere Formation, which is also supported by the absence of modern ungulates (perissodactyls and artiodactyls) and rodents in the fauna. *Parabunodon* is the only post-PETM pleuraspidotheriid known at this point. The taxonomic revision of *Parabunodon* has important implications for the temporal and geographic distribution of pleuraspidotheriid "condylarths" (Fig. 1). Long thought to be a typically western European and Paleocene group of primitive ungulates, pleuraspidotheriids now extend their geographic distribution to western Asia, suggesting land connection between Anatolia and the Paris Basin during the late Paleocene. However, the fauna from Eski Çeltek remains clearly distinctive from western European early Eocene fauna. *Parabunodon*, which is the most recent Pleuraspidotheriidae, might be a relictual taxon from the European Paleocene fauna that survived in Anatolia.

The Anatolian Plateau of Turkey lay at the crossroads between Afro-Arabia, Asia, and Europe during the late Mesozoic and early Paleogene. Although this area figures prominently for better understanding the early evolution and dispersals of many groups of extinct and modern mammal orders, its early Paleogene vertebrate fossil record remains very scarce. Further paleontological data from that area should shed new light on the dispersal history and early evolution of several groups of modern mammals around the Paleocene-Eocene Thermal Maximum (PETM).

Akgün, F. (2002). Stratigraphic and paleoenvironmental significance of Eocene palynomorphs of the Corum-Amasya area in the Central Anatolia, Turkey. Acta Palaeontologica Sinica 41: 576-591.

Barrier, E., Vrielynck, B. (2008). Palaeotectonic maps of the Middle East. Tectono–sedimentary–palinspastic maps from Late Norian to Pliocene. CGMW/CCGM, Paris, 14 maps.

Blumenthal, M.M. (1937). Amasya vilayetine tabi Çeltek'teki linyitli arazinin jeolojik tesekkülati hakkinda rapor. Maden Tetkik ve Arama Enstitüsü, Report No 157, 7p. (unpublished).

Ducrocq, S., Sen, S. (1991). A new Haplobunodontidae (Mammalia, Artiodactyla) from the Eocene of Turkey. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte H.1: 12-20.

Koç, C., Türkmen, I. (2002). Suluova (Amasya) kuzeyindeki kömürlü Eosen çökellerinin sedimantolojik özellikleri. Yerbilimleri 26: 101-117.

Kappelman, J.W., Maas M.C., Sen, S., Alpagut, B. Fortelius M., Lunkka, J.-P. (1996). A new early Tertiary mammalian fauna from Turkey and its paleobiogeographic significance. Journal of Vertebrate Paleontology 16: 592-595.

Kazanci, N., Gökten, E. (1986). Sedimentary characteristics of terrestrial Paleocene deposits in northern Ankara Region, Turkey. Communications of the Faculty of Sciences, University of Ankara, Serie C 4: 153-163.

Ladevèze, S., Missiaen P., Smith T. (2010). First Skull of *Orthaspidotherium edwardsi* (Mammalia, "Condylarthra") from the Late Paleocene of Berru (France) and phylogenetic affinities of the enigmatic European family Pleuraspidotheriidae. Journal of Vertebrate Paleontology 30: 1559-1578.

Maas, M.C., Thewissen, J.G.M., Kappelman, J.W. (1998). *Hypsamasia seni* (Mammalia: Embrithopoda) and other mammals from the Eocene Kartal Formation of Turkey. In: Beard, K.C., Dawson, M.R. (eds) Dawn of the Age of Mammals in Asia. Bulletin of Carnegie Museum of Natural History, Pittsburgh, pp 286-297.

Maas, M.C., Thewissen, J.G.M., Sen, S., Kazanci N., Kappelman, J.W. (2001). Enigmatic new ungulates from the early middle Eocene of Central Anatolia, Turkey. Journal of Vertebrate Paleontology 21: 578-590.

Ozansoy, F. (1966). Türkiye Senozoik Çaglarinda fossil insan formu problemi ve biostratigrafik dayanaklari. Ankara Univ. D.T.C.F. Yayinlari 172: 1-104.

Palaeoichthyology versus Geology? An interdisciplinary palaeoecological approach

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Stumm wie ein Fisch ("as silent as a fish") – this is a common figure of speech in German, even when it is known that some extant species are quite able to make sounds in different ways. Nor are fossil fishes mute witnesses concerning the past. As at least temporary residents of their former environments, they provide us with comprehensive information and tools for the reconstruction of their ancient habitats.

Eight nominal species of Messel fishes are known so far: *Atractosteus messelensis* Grande, 2010, *Masillosteus kelleri* Micklich and Klappert, 2001, *Cyclurus kehreri* (Andreae, 1893), *Thaumaturus intermedius* Weitzel, 1933, *Anguilla ignota* Micklich, 1985, *Amphiperca multiformis* Weitzel, 1933, *Palaeoperca proxima* Micklich, 1978, and *Rhenanoperca minuta* Gaudant and Micklich, 1990. General aspects as well as peculiarities of this fish fauna will be presented and discussed with special respect to the palaeoenvironmental framework.

GENERAL COMPOSITION OF THE ICHTHYOFAUNA

At Messel, "survival artists" dominated, especially the gars and the bowfins. Their living relatives are capable of surviving unfavourable environmental conditions, such as periods of low oxygen during heat waves. In some excavation areas these two types of fish make up three-fourths of all fish finds; however, there also are other excavation areas and profile sections that are dominated by other forms. But also the rarities among the Messel fish fauna may indicate special environmental conditions. There is only one record of the freshwater eel *Anguilla ignota.* Extant eels (*Anguilla anguilla* LINNAEUS, 1758) are catadromous fishes, which enter fresh waters as early juveniles and return to the sea to breed when fully grown. They furthermore also seem to substantiate the existence of occasional deleterious conditions. Mature individuals are environmentally sensitive: they leave as soon as unpleasant conditions occur in their home waters, and likewise do not enter areas without the appropriate water quality. Also the short-snouted gar (*Masillosteus kelleri*), represented by only a few specimens, could have been forced into rarity by unfavourable environmental conditions, such as a scarcity of appropriate forage items. Interestingly, these gars are more frequent in the close-by Prinz von Hessen fossil site, which may represent a different type of *Lagerstätte* with other palaeoenvironmental conditions.

COMPOSITION OF THE RESPECTIVE POPULATIONS

A few exceptions aside, all Messel fish taxa are represented by both small and larger specimens. These were considered as juveniles and adults in the past. Comparative investigations of length-frequency distributions as well as of annular growth cessation marks ("annuli") on the scales with those of extant reference species clearly show that the majority of the Messel specimens were immature juveniles, or may represent "baby" populations (*Rhenanoperca minuta).* Even somewhat larger specimens probably were not yet fully grown. However, some rare disarticulated remains also exist which seem to have come from almost fully grown adults that had already reached sexual maturity. As an exception, the percoid *Palaeoperca proxima* is represented mainly by individuals of a rather restricted size range. Here, the mean peaks of the length-frequency distribution, as well as the presumed age of these individuals, are close to the ones of certain extant percoids, which start their spawning migrations at that particular size and age.

INTRASPECIFIC VARIATION

With eight nominal genera and species, the Lake Messel fish fauna is taxonomically less diverse than some other almost contemporary freshwater fish associations, e.g., the one of the Green River Shales in Wyoming, USA. However, in morphological details, most of the taxa clearly exceed the degree of intraspecific variation known from closely related extant or fossil forms. Within most species, there are individuals that markedly differ from all other specimens in the development of certain skeletal features. Only a few of these deviations may be due to well-known phenomena, such as artifacts of fossilization, preservation and/or preparation, and time-averaging. Others are more likely to be due to a recent, ongoing, or near-future lineage divergence resulting from sympatric or allopatric speciation. Unfortunately, most of these peculiar character states cannot be investigated in the majority of the specimens, since analysis depends on a special bedding position or state of preservation.

VERTICAL AND HORIZONTAL DISTRIBUTION PATTERNS

Long-term, short-term, and also local differences and modifications in the composition of the respective fish associations are to be stated. There is a complete lack of fish in certain profile sections, whereas an alternation of layers in which only one or two species exist with those in which a more heterogeneous fish fauna is found is observed in others. Sometimes an apparently sudden appearance of other, new species is to be noticed. In addition, there are some striking differences in the general composition of the fish associations of different excavation sites within Messel Pit. Some species are very abundant and/or almost exclusively occur in certain excavation areas and stratigraphical sections, whilst others are distinctively rarer or are completely lacking. In addition, amongst those species which are widespread in various oil shale sections (e.g., *Cyclurus kehreri*, *Atractosteus messelensis*), the average sizes of the individuals may also differ for different excavation areas.

FOOD INTAKE

An indication of limited food availability for Messel fishes may be the fact that, in spite of the often outstanding preservation, prey remains can only rarely be found in their jaws or digestive tracts. This is in strong contrast to specimens from contemporaneous fossil sites, which often are found with prey items in situ. Curiously, if Messel fishes show direct evidence for their diet at all, the primitive teleost *Thaumaturus intermedius* seems to be the only one in which this matches the oral jaw morphology. By contrast, specimens of the other species show prey items that do not correspond to their general morphological traits, and/or indicate prey species that are comparatively rare in the Messel fossil record otherwise. *Masillosteus kelleri*, *Cyclurus kehreri* and *Rhenanoperca minuta*, for example, must be expected to have been “graters” or “crackers”, which were specialized in some kind of “hard-shelled” prey. Paradoxically, such kind of forage (e.g., freshwater shrimps and snails) is comparatively rare, especially in those layers most of the respective “predators” come from. Moreover, *Rhenanoperca minuta* and, to some minor extent, *Cyclurus kehreri* obviously preferred smaller individuals of their own species. The latter species, together with *Atractosteus messelensis*, at least occasionally also hunted *Palaeoperca proxima*, a generally rather uncommon percoid, which mainly occurs in particular excavation areas and oil shale layers.

PATHOLOGICAL PHENOMENA

In many specimens of almost all Messel fish taxa there are structures indicating that the animal survived adverse environmental conditions or disease. Sometimes there are knotty thickenings on fin rays which indicate healed fractures. Roundish perforations on scales probably resulted from ectoparasite infestations. Other irregularities in scale surfaces show that an individual survived an avitaminosis by marginal material resorption. A very peculiar phenomenon is the extraordinarily high percentage of regenerated scales. This is significantly above the degree of scale regeneration found in related modern species or in species with lifestyles likely similar to those at Messel. Looking at the amount of scale regeneration within the different body regions, for most Messel fishes, as well as their extant reference species, it generally can be stated that there is a higher degree of regeneration in the lower half of the body and that there is a more or less continuous increase from the anterior to the posteriormost parts of the body flank. This may indicate that the scale loss resulted from a similar phenomenon in both species, although the Messel forms were apparently more strongly affected than the recent ones.

CONCLUSION

Most of the peculiarities discussed herein probably result from a combination of various causes: local factors, which could be due to the relative positions of the excavation areas and thus the regions that they may have represented within the ancient lake basin, as well as general developmental traits within the lake’s history. They may have been triggered by a selective “input” of fishes into the lake, which also changed over more extended periods of time, e.g., depending on the intensity of occasional periods of high water or floodings. Such an input is in some contrast to the previous model ideas of the Messel maar lake. These are based mainly on geologic information and assume an almost complete isolation by crater walls.

MICKLICH, N. (2002). The fish fauna of Messel Pit: A nursery school? Courier Forschungsinstitut Senckenberg 237: 97-127.

MICKLICH, N. (2007). Coincidences or necessities? In: Gruber, G., Micklich, N. (eds) Messel – Treasures of the Eocene. Book to the exhibition “Messel on Tour”, Hessisches Landesmuseum Darmstadt, pp 38-48.

MICKLICH, N., KLAPPERT, G. (2004). Character variation in some Messel fishes. In: Arratia, G., Tintori, A. (eds) Mesozoic Fishes 3 – Systematics, Palaeoenvironments and Biodiversity. Friedrich Pfeil Verlag, München, pp 137-163.

Mammalian carnivores from Messel and a comparison of non-volant predator guilds from the middle Eocene of Europe and North America

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The Messel non-volant predator guild consists of species from at least four mammalian orders: Carnivora (*Messelogale*, *Paroodectes*), Hyaenodontida (*Lesmesodon*), Pantolesta (*Buxolestes*), and Prot-eutheria (*Leptictidium*). Furthermore, the paroxyclaenid *Kopidodon* is ecomorphologically equivalent to some modern omnivorous arborial Carnivora such as *Potos*, *Arctictis* and *Ailurus* (Morlo *et al*., 2010) and might thus be added to this guild. While the locomotor pattern of the Carnivora can be interpreted as arboreal, hyaenodontids and *Leptictidium* are scansorial or terrestrial. The two species of *Buxolestes* are ecomorphologically similar to recent otters and badgers, respectively.

For the proviverrid hyaenodontid *Lesmesodon edingeri*, three as yet undescribed specimens exist, one of which has the hitherto unknown M_3 preserved. As this M_3 was still erupting, the specimen is interpreted as a sub-adult and thus represents the first non-juvenile carnivore from Messel. The new specimens allow a better understanding of the relationships of *Lesmesodon* to other proviverrids (such as *Proviverra* and *Leonhardtina*) as well as to other Hyaenodontida. Our analysis corroborates the view that Proviverridae are an isolated, very plesiomorphic family within the order and may be interpreted as sister-taxon to all other Hyaenodontida.

The second new specimen (Fig. 1) is a partial, strongly distorted skeleton which presumably represents the vomitus of a snake. Such an interpretation has been suggested for a similarly preserved specimen of a Messel bird (Mayr, 2000). The most probable predator is *Palaeopython*, the largest boid from Messel. Snakes occasionally regurgitate fresh prey if they are disturbed during digestion. This juvenile *Lesmesodon* was not only probably snake prey, but also itself a predator: it shows stomach contents consisting of yet unidentified tetrapod bones. This verifies that individuals of *L. edingeri* with a tooth configuration of dP_3, dP_4, M_1, and erupting M_2 already consumed food and thus represent an ontogenetic stage after weaning.

The third new specimen displays the same tooth configuration and represents the hitherto best-preserved postcranial remains of *L. edingeri*.

All new specimens together thus enable analyses of various ontogenetic traits within the species and their relationships to one another, e.g., development of long bone growth vs. tooth eruption stages.

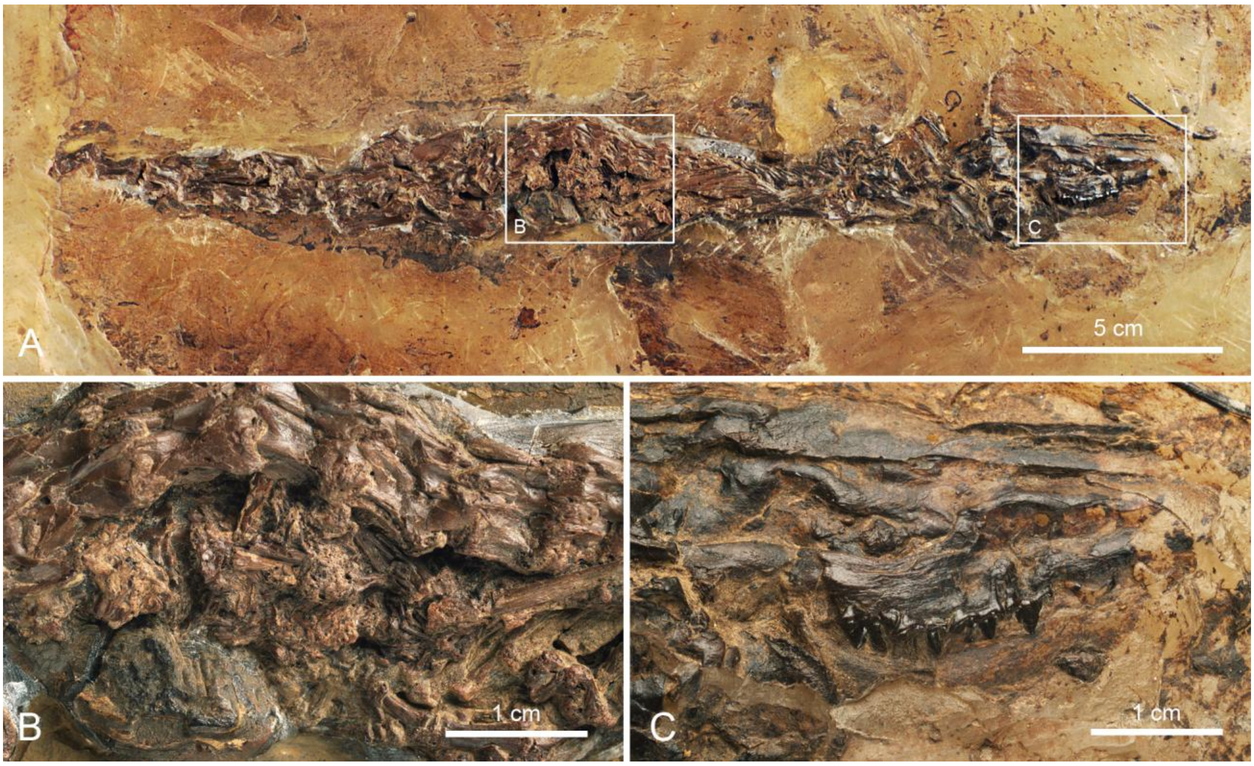

Figure 1. New specimen of *L. edingeri*, A: Overview of distorted skeleton, which is interpreted as a snake vomitus; B: Stomach content consisting of tetrapod bone fragments; C: Labial view of right upper dentition with dP^2 as imprint, dP^3, dP^4, M^1 and M^2 (still erupting). Presence of stomach content verifies that M^2-eruption occurred after weaning.

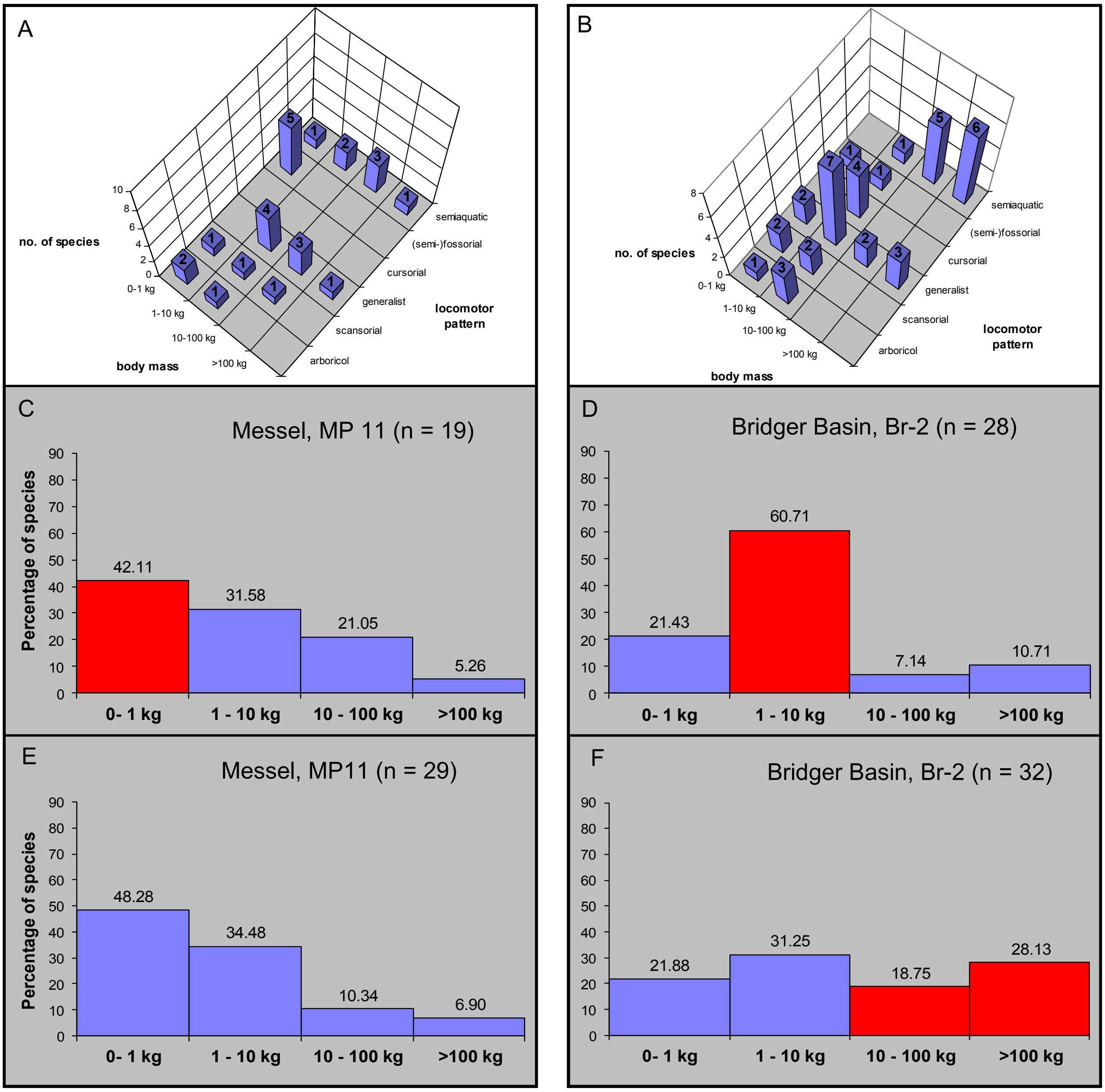

Figure 2. Ecomorphology of non-volant predators from Messel (MP 11) and Bridger Basin (Br-2). A-B: Guild structures of non-volant tetrapod predators from Messel and Bridger, C-D: Distribution of body mass among the non-volant tetrapod predators from Messel and Bridger. E-F: Distribution of body mass classes among the reptiles of Messel and Br-2. The higher mean body masses among the NA predators results from higher mean body masses of the Br-2 reptiles.

The guild of mammalian carnivores of Messel is strongly affected by the presence of large non-mammalian predators such as the bird *Diatryma*, terrestrial crocodyles (e.g., *Pristichampsus*), and a couple of middle-sized snakes.

Within the complete predator guild, mammals thus play a role as small predators with body masses <10 kg (Fig. 2a, c). This separates Messel from contemporary predator guilds of North America (Fig. 2b, d) where additionally large to very large mammalian predators occurred (Morlo *et al.,* 2010). Even more obvious is the presence of larger reptiles in Bridgerian zone 2 (Br–2), which may reflect higher paleotemperatures within the continental climate of North America (see, e.g., Hutchison (1982) or Head (2009) for discussion on paleotemperature and reptilian body size).

Head, J.J., Bloch, J.I., Hastings, Bourque, J.R., Cadena, E.A. Herrera, F.A., Polly, P.D., Jaramillo, C.A. (2009). Giant boid snake from the Palaeocene neotropics reveals hotter past equatorial temperatures. Nature 457: 715-717.

Hutchison, J.H. (1982). Turtle, crocodilian, and champsosaur diversity changes in the Cenozoic of the north-central region of western United States. Palaeogeography, Palaeoclimatology, Palaeoecology 37 (2-4): 149-164.

Mayr, G. (2000). Die Vögel der Grube Messel – Ein Einblick in die Vogelwelt Mitteleuropas von 49 Millionen Jahren. Natur und Museum 130 (11): 365-378.

Morlo, M., Gunnell, G.F., Nagel, D. (2010). Chapter 10 - Ecomorphological analysis of carnivore guilds in the Eocene through Miocene of Laurasia. In: Goswami A., Friscia, A. (eds) New Contributions to the Natural History of Carnivora. Cambridge University Press, pp 269-310.

Climate, plant (and animal) diversification at the time of Messel and beyond: A phylogeneticist's perspective

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To what extent were Cenozoic organismic diversification and environmental changes linked? What were the evolutionary impacts of the overall cooling trend, increasing seasonality, increasing aridity, and short-term cooling and warming events? Presently about two million species are known to science, most probably representing only a small fraction (c. 10%) of the "real" biodiversity (Hawksworth and Kalin-Arroyo, 1995). Both in space and within the phylogenetic "tree of life", species diversity is not homogeneously distributed. Concerning global terrestrial spatial distribution patterns of diversity, a latitudinal gradient with higher diversity in low latitudes can be observed (Ricklefs, 2004; Jablonski *et al.*, 2006). In addition, biodiversity hotspots do exist in various regions of the world (Myers *et al.*, 2000; Mutke *et al.*, 2005; Barthlott *et al.*, 2005). Similarly, within the phylogenetic tree of life, taxonomic diversity varies considerably, as can be seen by the very different number of species in different groups of organisms, e.g. insects versus plants or chordates (Hawksworth and Kalin-Arroyo, 1995). These modern biodiversity patterns are largely the result of the Cenozoic diversification that occurred after the mass extinction event at the K/T boundary, about 65 Ma ago, which in the marine realm extinguished about 76% of all species. The Cenozoic diversification was accompanied by profound palaeogeographic reorganization of the globe and by complex changes in climate (Rhode and Muller, 2005). Bringing together expertise in model systems covering a wide range of systematic groups and major habitats, phylogeneticists have recently become increasingly interested in general questions with particular focus on hypotheses linking evolutionary diversification and environmental change (e.g. Rull, 2008; Antonelli *et al.*, 2009; Cody *et al.*, 2010; Hoorn *et al.*, 2010; Richardson *et al.*, accepted). In the past two decades, molecular phylogenetics has advanced at an astonishing pace, and new methods and applications are being developed at an ever increasing rate (e.g. Swofford, 2002; Ronquist and Huelsenbeck, 2003; Stamatakis, 2006; Kubatko *et al.*, 2009; Larget, 2010).

Phylogenetic and related tools have not only improved our understanding of plant and animal phylogenetic relationships and trait evolution (for plants e.g. Stevens, 2001 onwards; Judd *et al.*, 2007; APG III, 2009; Soltis *et al.*, 2010), but have also allowed challenges to previous more-intuitive assumptions about biogeographic history and underlying causes for current global distribution patterns (e.g. Muellner *et al.* 2006, 2008, 2010; Richardson *et al.*, accepted; compare also reviews in Lomolino *et al.*, 2010).

The importance of molecular phylogenetics to biogeography and the general study of plant and animal diversification has grown rapidly during the past two decades. The reasons are manifold: there is an increasing availability of high-quality phylogenetic trees (enabling formerly postulated relationships between taxa to be accepted or rejected), as well as an increasing sophistication of phylogenetically based analyses employed to e.g. assess the relative influence of vicariance versus dispersal events in biogeographic history, dispersal routes and dispersal directions, and the influence of climate and sea level changes (e.g. Ronquist, 1997, 2002; Ree and Smith, 2008; Nylander *et al.*, 2008; Sanmartín *et al.*, 2008; Morrone, 2009). Additionally, while fossils have always been used in the reconstruction of lineage histories, they are now widely applied in setting temporal constraints on phylogenetic trees to derive estimates of times of lineage divergence (Renner, 2005; Rutschmann, 2006). Dated phylogenetic trees also have the potential to contribute to geological and climatological studies by providing temporal information on e.g. island emergence and the development of different climatic zones (Richardson *et al.*, accepted). Collaborations between systematists, palaeobiologists, palaeoclimatologists and geologists will ultimately provide a clearer picture of both the biotic and abiotic history of a region under investigation. In my talk, I will provide a brief overview about past and recent developments in the field and highlight some example studies.

ANTONELLI, A., NYLANDER, J.A.A., PERSSON, C., SANMARTÍN, I. (2009). Tracing the impact of the Andean uplift on Neotropical plant evolution. Proceedings of the National Academy of Sciences of the USA 106: 9749-9754.

APG [= ANGIOSPERM PHYLOGENY GROUP] III. (2009). An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Botanical Journal of the Linnean Society 161: 105-121.

BARTHLOTT, W., MUTKE, J., RAFIQPOOR, M. D., KIER, G., KREFT, H. (2005). Global centres of vascular plant diversity. Nova Acta Leopoldina 342: 61-83.

CODY, S., RICHARDSON, J.E., RULL, V., ELLIS, C., PENNINGTON, R.T. (2010). The Great American Biotic Interchange revisited. Ecography 33: 1-7

HAWKSWORTH, D.L., KALIN-ARROYO, M.T. (1995). Magnitude and distribution of biodiversity. In: Heywood, V.H. (ed) Global Biodiversity Assessment. Cambridge University Press, Cambridge, pp 107-191.

HOORN, C., WESSELINGH, F.P., STEEGE, H. TER, BERMUDEZ, M.A., MORA, A., SEVINK, J., SANMARTÍN, I., SANCHEZ-MESEGUER, A., ANDERSON, C.L., FIGUEIREDO, J., JARAMILLO, C., RIFF, D., NEGRI, F.R., HOOGHIEMSTRA, H., LUNDBERG, J., STADLER, T., SARKINEN, T., ANTONELLI, A. (2010). Amazonia through time: Andean uplift, climate change, landscape evolution and biodiversity. *Science* 330: 927-931.

JABLONSKI, D., ROY, K., VALENTINE, J.W. (2006). Out of the tropics: Evolutionary dynamics of the latitudinal diversity gradient. Science 314: 102-106.

JUDD, W.S., CAMPBELL, C.S., KELLOGG, E.A., STEVENS, P.F., DONOGHUE, M.J. (2007). Plant Systematics: A Phylogenetic Approach. 3rd Edition. Sinauer Associates, Sunderland, Massachusetts. 620pp.

KUBATKO, L.S., CARSTENS, B.C., KNOWLES, L.L. (2009). STEM: Species tree estimation using maximum likelihood for gene trees under coalescence. Bioinformatics 25: 971–973.

LARGET, B.R., KOTHA, S.K., DEWEY, C.N., ANÉ, C. (2010). BUCKy: Gene tree/species tree reconciliation with Bayesian concordance analysis. Bioinformatics 26: 2910-2911.

LOMOLINO, M.V., RIDDLE, B.R., WHITTAKER, R.J., BROWN, J.H. (2010). Biogeography. 4th Edition. Sinauer Associates, Sunderland, Massachusetts. 878pp.

MORRONE, J.J. (2009). Evolutionary biogeography: An integrative approach with case studies. Columbia University Press, New York. 304pp.

MUELLNER, A.N., PANNELL, C.M., COLEMAN, A., CHASE, M.W. (2008). The origin and evolution of Indomalesian, Australasian and Pacific island biotas: Insights from Aglaieae (Meliaceae, Sapindales). Journal of Biogeography 35: 1769-1789.

MUELLNER, A.N., PENNINGTON, T.D., KOECKE, A. V., RENNER, S.S. (2010). Biogeography of *Cedrela* (Meliaceae, Sapindales) in Central and South America. American Journal of Botany 97: 511-518.

MUELLNER, A.N., SAVOLAINEN, V., SAMUEL, R., CHASE, M.W. (2006). The mahogany family "out-of-Africa": Divergence time estimation, global biogeographic patterns inferred from plastid *rbcL* DNA sequences, extant and fossil distribution of diversity. Molecular Phylogenetics and Evolution 40: 236-250.

MUTKE, J., KIER, G., KRUPNICK, G., BARTHLOTT, W. (2005). Terrestrial plant diversity. In: Krupnick, G., Kress, J. (eds) Plant Conservation: A Natural History Approach. University of Chicago Press, Chicago, pp 15-25.

MYERS, N., MITTERMEIR, R.A., MITTERMEIR, C.G., DA FONSECA, G.A.B., KENT, J. (2000). Biodiversity hotspots for conservation priorities. Nature 403: 853-858.

NYLANDER, J.A.A., OLSSON, U., ALSTRÖM, P., SANMARTÍN, I. (2008). Accounting for phylogenetic uncertainty in biogeography: A Bayesian approach to dispersal–vicariance analysis of the thrushes (Aves: *Turdus*). Systematic Biology 57: 257-268.

REE, R.H., SMITH, S.A. (2008). Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. Systematic Biology 57: 4-14.

RENNER, S.S. (2005). Relaxed molecular clocks for dating historical plant dispersal events. Trends in Plant Science 10: 550-558.

RICHARDSON, J.E., COSTION, C.M., MUELLNER, A.N. (ACCEPTED) The Malesian Floristic Interchange: Plant migration patterns across Wallace's Line. In: Gower, D., Johnson, K., Richardson, J.E., Rosen, B., Rüber, L., Williams, S. (eds) Biotic Evolution and Environmental Change in Southeast Asia. Cambridge University Press, Cambridge.

RICKLEFS, R.E. (2004). A comprehensive framework for global patterns in biodiversity. Ecology Letters 7: 1-15.

ROHDE, R.A., MULLER, R.A. *(*2005*)*. Cycles in fossil diversity*.* Nature 434*:* 209-210*.*

RONQUIST, F. (1997). Dispersal-vicariance analysis: A new approach to the quantification of historical biogeography. Systematic Biology 46: 195-203.

RONQUIST, F. (2002). Parsimony analysis of coevolving species associations. In: Page, R.D.M. (ed) Cospeciation. Chicago University Press, Chicago, pp 22-64.

RONQUIST, F., HUELSENBECK, J.P. (2003). MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572-1574.

RULL, V. (2008). Speciation timing and neotropical biodiversity: The Tertiary-Quaternary debate in the light of molecular phylogenetic evidence. Molecular Ecology 17: 2722-2729.

RUTSCHMANN, F. (2006). Molecular dating of phylogenetic trees: A brief review of current methods that estimate divergence times. Diversity and Distributions 12: 35-48.

SANMARTÍN, I., VAN DER MARK, P., RONQUIST, F. (2008). Inferring dispersal: A Bayesian approach to phylogeny-based island biogeography, with special reference to the Canary Islands. Journal of Biogeography 35: 428-449.

SOLTIS, D.E., MOORE, M.J., GORDON BURLEIGH, J., BELL, C.D., SOLTIS, P.S. (2010). Assembling the Angiosperm Tree of Life: Progress and Future Prospects. Annals of the Missouri Botanical Garden 97: 514-526.

STAMATAKIS, A. (2006). RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22: 2688-2690.

STEVENS, P.F. (2001 ONWARDS). Angiosperm Phylogeny Website. Version 9, June 2008 [and updates]. http://www.mobot.org/MOBOT/research/APweb/.

SWOFFORD, D.L. (2002). PAUP*: Phylogenetic analysis using parsimony (*and other methods), v4. Sinauer Associates, Sunderland, Massachusetts.

A new Eocene squamate from Messel and the origin of Amphisbaenia

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Recent molecular investigations have dramatically challenged the traditional view of squamate phylogeny. Among the many changes in paradigm, the hypothesis of a monophyly of amphisbaenians and lacertids figures among the most prominent, as it has significant implications for the proposed relationship between amphisbaenians and snakes, as well as other limbless squamates. However, until recently there was no morphological or fossil support for an amphisbaenian-lacertid grouping, questioning the validity of this new hypothesis. A new genus and species of Eocene lizard from the famous Messel locality, consisting of a completely articulated specimen of which only a few parts of the tail are missing, now sheds new light on this issue. The taxon is characterized by a spatulate snout with a modified premaxilla and maxilla, notably small and anteriorly positioned orbits, the lack of a tympanic crest, a low tooth count, and reduced manus and pes. Also, it shows several features otherwise found only in amphisbaenians, such as the shape of the frontal suture and the morphology of the subolfactory processes. In a phylogenetic analysis including both morphological and molecular characters as well as extant and fossil taxa, the taxon is grouped as a sister taxon to amphisbaenians within a lacertid-amphisbaenian clade, providing for the first time morphological support for a sister-group relationship between amphisbaenian and lacertid lizards. Snakes, on the other hand, group with anguimorphs and marine squamates. Morphometric analysis of body shape and ecology among squamates places the taxon in cryptic or opportunistically burrowing habitats, and its distinctive anatomy indicates that head-first burrowing evolved prior to body elongation in Amphisbaenia.

The new taxon seemingly is a remnant of a non-crown-group, amphisbaenian-like squamate lineage that occurred together with crown lacertids and amphisbaenians, which both are known from contemporaneous and even older Paleogene strata. Interestingly, many currently known lizards from Messel seem to be related to either Mesozoic squamate lineages or represent stemgroup taxa outside of the crown, suggesting that Europe may have acted as refuge for ancient squamate lineages during the Paleogene. Our study also emphasizes that fossils are crucial for testing hypotheses of phylogenetic relationships, because extant taxa often reveal only a relatively restricted picture of their evolutionary history.

Phylogeny of the primates and their relatives: An analysis based on a large data matrix

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The phylogenetic relationships between primates and other euarchontans, namely plesiadapiforms, dermopterans and scandentians, have long been the subject of contention (Gunnell, 1989; Beard, 1990; Kay *et al*., 1990; Murphy *et al*., 2001*a*,*b*; Schmitz *et al*., 2002; Bloch *et al*., 2007; Janecka *et al*., 2007; Ni *et al*., 2010). The phylogenetic relationships between the anthropoid, tarsiid, lemuriform, omomyid and adapiform subgroups within the order Primates have also been debated repeatedly (Simons and Rasmussen, 1989; Kay *et al*., 1997; Dagosto, 2002; Ni *et al*., 2004, 2010; Franzen *et al*., 2009; Gingerich *et al*., 2010). Although some researchers prefer to use a small data matrix having a few “balanced” taxa for phylogenetic analysis, most researchers agree that a reliable analysis should be based on a large data matrix using total evidence.

Here, we reexamine the phylogenetic relationships of the euarchontans in the context of the largest total evidence analysis ever assembled. We developed a data matrix of 985 morphological characters and 658 molecular characters of short interspersed nuclear elements (SINEs) scored for 106 fossil taxa and 33 living taxa. The 985 morphological characters comprise 460 dental, 206 cranial, 289 postcranial and 30 soft tissue characters. These characters are updated from Ni *et al*. (2004, 2010), and include many newly defined characters. The SINEs data is from Kuryshev *et al*. (2001), Schmitz *et al*. (2001, 2002, 2005), Nishihara *et al*. (2002), Schmitz and Zischler (2003), Ray and Batzer (2005), Ray *et al*. (2005), Xing *et al*. (2005, 2007), Roy-Engel *et al*. (2008), Osterholz *et al*. (2009) and Konkel *et al*. (2010). Of the total 139 taxa, one insectivoran, *Echinosorex gymnura*, was designated as the outgroup. The ingroup comprises two living scandentians, nine living and extinct dermopterans, *Mixodectes*, 18 plesiadapiforms, and 108 anthropoid, tarsiid, lemuriform, omomyid, and adapiform primates.

Analysis based on the most parsimonious criterion reveals that the scandentians are the most basal euarchontan taxon, thereby supporting the monophyly of Primatomorpha (primates, plesiadapiforms and dermopterans) (Beard, 1991, 1993*a*,*b*). The plesiadapiforms included in this analysis, such as *Purgatorius*, *Plesiadapis*, *Carpolestes*, *Palenochtha*, and *Phenacolemur*, are closer to living dermopterans plus plagiomenids than they are to primates. Living and fossil dermopterans, *Mixodectes*, and plesiadapiforms form the sister group of primates. This result supports the common practice of many researchers to exclude plesiadapiforms from the order Primates (e.g., Fleagle, 1999; Covert, 2002). Within the order Primates, our analysis supports an early division between strepsirrhine and haplorhine primates. Adapiforms belong to the strepsirrhine division, and are more closely related to lemuriforms than to anthropoids. Adapiforms as a group is not monophyletic, but paraphyletic. The haplorhine division comprises tarsiids, omomyids and anthropoids. Omomyidae is not a natural monophyletic group. Living and fossil tarsiids fall into the Omomyidae family. Omomyids plus tarsiids form the sister group of anthropoids. The anthropoid clade is monophyletic, with eosimiids as the most basal taxon.

BEARD, K.C. (1990). Gliding behaviour and palaeoecology of the alleged primate family Paromomyidae (Mammalia, Dermoptera). Nature 345: 340–341.

BEARD, K.C. (1991). Vertical postures and climbing in the morphotype of Primatomorpha: Implications for locomotor evolution in primate history, In: Coppens, Y., Senut, B. (eds) Origine(s) de la bipédie chez les hominidés : Colloque international de la Fondation Singer-Polignac (5-8 juin 1990). Éditions du Centre National de la Recherche Scientifique, Paris, pp 79-87.

BEARD, K.C. (1993*a*). Phylogenetic systematics of the Primatomorpha, with special reference to Dermoptera. In: Szalay, F.S., Novacek, M.J., McKenna, M.C. (eds) Mammal Phylogeny, Volume 2, Placentals. Springer-Verlag, New York, pp 129-150.

BEARD, K.C. (1993*b*). Origin and evolution of gliding in early Cenozoic Dermoptera (Mammalia, Primatomorpha). In: MacPhee, R.D.E. (ed) Primates and Their Relatives in Phylogenetic Perspective. Plenum Press, New York and London, pp 63-90.

BLOCH, J.I., SILCOX, M.T., BOYER, D.M., SARGIS, E.J. (2007). New Paleocene skeletons and the relationship of plesiadapiforms to crown-clade primates. PNAS 104: 1159–1164.

COVERT, H.H. (2002). The earliest fossil primates and the evolution of prosimians: Introduction. In: Hartwig, W.C. (ed) The Primate Fossil Record. Cambridge University Press, Cambridge, pp 13-20.

DAGOSTO, M. (2002). The origin and diversification of anthropoid primates: Introduction. In: Hartwig, W.C. (ed) The Primate Fossil Record. Cambridge University Press, Cambridge, pp 125-132.

FLEAGLE, J.G. (1999). Primate Adaptation and Evolution, Second Edition. Academic Press, London, 596 pp.

FRANZEN, J.L., GINGERICH, P.D., HABERSETZER, J., HURUM, J.H., KOENIGSWALD, W.V., SMITH, B.H. (2009). Complete primate skeleton from the middle Eocene of Messel in Germany: Morphology and paleobiology. PLoS ONE 4: e5723.

Gingerich, P.D., Franzen, J.L., Habersetzer, J., Hurum, J.H., Smith, B.H. (2010). *Darwinius masillae* is a haplorhine – Reply to Williams et al. (2010). Journal of Human Evolution 59: 574-579.

Gunnell, G.F. (1989). Evolutionary History of Microsyopoidea (Mammalia, ?Primates) and the Relationship between Plesiadapiformes and Primates. Ann Arbor, University of Michigan, Museum of Paleontology, Papers on Paleontology. 157 pp.

Janecka, J.E., Miller, W., Pringle, T.H., Wiens, F., Zitzmann, A., Helgen, K.M., Springer, M.S., Murphy, W.J. (2007). Molecular and genomic data identify the closest living relative of primates. Science 318: 792–794.

Kay, R.F., Ross, C.F., Williams, B.A. (1997). Anthropoid origins. Science 275: 797-804.

Kay, R.F., Thorington Jr, R.W. Houde, P.W. (1990). Eocene plesiadapiform shows affinities with flying lemurs not primates. Nature 345: 342–344.

Konkel, M.K., Walker, J.A., Batzer, M.A. (2010). LINEs and SINEs of primate evolution. Evolutionary Anthropology: Issues, News, and Reviews 19: 236-249.

Kuryshev, V.Y., Skryabin, B.V., Kremerskothen, J., Jurka, J., Brosius, J. (2001). Birth of a gene: Locus of neuronal BC200 snmRNA in three prosimians and human BC200 pseudogenes as archives of change in the Anthropoidea lineage. Journal of Molecular Biology 309: 1049-1066.

Murphy, W.J., Eizirik, E., Johnson, W.E., Zhang, Y.P., Ryderk, O.A., O’Brien, S.J. (2001*a*). Molecular phylogenetics and the origins of placental mammals. Nature 409: 614–618.

Murphy, W.J., Eizirik, E., O'Brien, S.J., Madsen, O., Scally, M., Douady, C.J., Teeling, E., Ryder, O.A., Stanhope, M.J., de Jong, W.W., Springer, M.S. (2001*b*). Resolution of the early placental mammal radiation using Bayesian phylogenetics. Science 294: 2348-2351.

Ni, X., Meng, J., Beard, K. C., Gebo, D.L., Wang, Y., Li, C. (2010). A new tarkadectine primate from the Eocene of Inner Mongolia, China: Phylogenetic and biogeographic implications. Proceedings of the Royal Society B: Biological Sciences 277: 247-256.

Ni, X., Wang, Y., Hu, Y., Li, C. (2004). A euprimate skull from the early Eocene of China. Nature 427: 65–68.

Nishihara, H., Terai, Y., Okada, N. (2002). Characterization of novel Alu- and tRNA-related SINEs from the tree shrew and evolutionary implications of their origins. Molecular Biology and Evolution 19: 1964-1972.

Osterholz, M., Walter, L., Roos, C. (2009). Retropositional events consolidate the branching order among New World monkey genera. Molecular Phylogenetics and Evolution 50: 507-513.

Ray, D., Batzer, M. (2005). Tracking *Alu* evolution in New World primates. BMC Evolutionary Biology 5: 51.

Ray, D.A., Xing, J., Hedges, D.J., Hall, M.A., Laborde, M.E., Anders, B.A., White, B.R., Stoilova, N., Fowlkes, J.D., Landry, K.E., Chemnick, L.G., Ryder, O.A., Batzer, M.A. (2005). *Alu* insertion loci and platyrrhine primate phylogeny. Molecular Phylogenetics and Evolution 35: 117-126.

Roy-Engel, A.M., Batzer, M.A., Deininger, P.L. (2008). Evolution of human retrosequences: Alu. In: Encyclopedia of Life Sciences. John Wiley & Sons, Ltd., Chichester, DOI: 10.1002/9780470015902.a0005131.pub2.

Schmitz, J., Ohme, M., Suryobroto, B., Zischler, H. (2002). The colugo (*Cynocephalus variegatus*, Dermoptera): The primates’ gliding sister? Molecular Biology and Evolution 19: 2308-2312.

Schmitz, J., Ohme, M., Zischler, H. (2001). SINE insertions in cladistic analyses and the phylogenetic affiliations of *Tarsius bancanus* to other primates. Genetics 157: 777-784.

Schmitz, J., Roos, C., Zischler, H. (2005). Primate phylogeny: Molecular evidence from retroposons. Cytogenetic and Genome Research 108: 26-37.

Schmitz, J., Zischler, H. (2003). A novel family of tRNA-derived SINEs in the colugo and two new retrotransposable markers sparating dermopterans from primates. Molecular Phylogenetics and Evolution 28: 341-349.

Simons, E.L., Rasmussen, D.T., (1989). Cranial morphology of *Aegyptopithecus* and *Tarsius* and the question of the tarsier-anthropoidean clade. American Journal of Physical Anthropology 79: 1-23.

Xing, J., Wang, H., Han, K., Ray, D.A., Huang, C.H., Chemnick, L.G., Stewart, C.-B., Disotell, T.R., Ryder, O.A., Batzer, M.A. (2005). A mobile element based phylogeny of Old World monkeys. Molecular Phylogenetics and Evolution 37: 872-880.

Xing, J., Witherspoon, D.J., Ray, D.A., Batzer, M.A., Jorde, L.B. (2007). Mobile DNA elements in primate and human evolution. Yearbook of Physical Anthropology 50: 2-19.

Origin and early evolution of the grasping big toe in primates: New fossils and key characters evaluated within a phylogenetic context

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Some of the most striking postcranial differences between crown primates (=euprimates) and non-primate mammals, within crown primates, and between anthropoid and non-anthropoid primates can be found in the morphology of the first metatarsal (MTI). The MTIs of living and extinct "prosimian" primates (i.e., crown strepsirrhines, tarsiers, adapiforms, omomyiforms) generally differ from those of anthropoid primates and non-primate mammals in having conspicuously well-developed peroneal processes, deeply concave facets for articulation with the entocuneiform, relatively high physiological abduction angles (Fig. 1), and medially and plantarly notched proximal articular surfaces (e.g., Jacobs *et al.*, 2009). The absence of these features in other living and extinct euarchontans has called into question the polarity of these traits within the primate crown clade, particularly as it pertains to the origin of the anthropoid condition (e.g., Dagosto, 1990).

We employ new lines of evidence to test the hypothesis that the condition in anthropoids represents an evolutionary reversal from a more "prosimian"-like stem anthropoid ancestor. First, we describe two MTIs from Eocene deposits in Egypt that provide the oldest record of MTI morphology within the crown anthropoid and crown strepsirrhine clades. Second, we expand the character–taxon matrix of Boyer *et al.* (2010) to include the plesiadapoid *Carpolestes simpsoni* (Bloch and Boyer 2002) and a total of 16 characters from the MTI, representing not only previously recognized differences between "prosimians" and anthropoids, but also newly defined features that are characteristic of lower-level groupings. The expanded matrix includes 373 characters from all parts of the skeleton as well as soft-tissue and developmental features. As part of this exercise, we have studied the morphology of all described fossil MTIs from the early primate fossil record.

The MTI from the ~34 Ma Quarry L-41 (Jebel Qatrani Formation) is typically anthropoid-like in morphology, and on the basis of size and relative abundance is probably attributable to the oligopithecid anthropoid *Catopithecus browni* (Patel *et al.*, 2010). The morphology of *Catopithecus*' MTI is indistinguishable from the condition that is reconstructed as having been present at the crown anthropoid node, and provides no evidence for transitional morphology at this early point in anthropoid evolution. The MTI from the ~37 Ma Locality BQ-2 (Birket Qarun Formation) is strepsirrhine-like, and on the basis of size and morphology is most parsimoniously attributed to the basal crown strepsirrhine *Karanisia clarki* (Seiffert *et al.*, 2003). The *Karanisia* MTI is typically "prosimian"-like in having a relatively large peroneal process and a concave entocuneiform facet that is notched medially and plantarly.

Phylogenetic analysis of the expanded matrix, including the new scorings for *Catopithecus* and

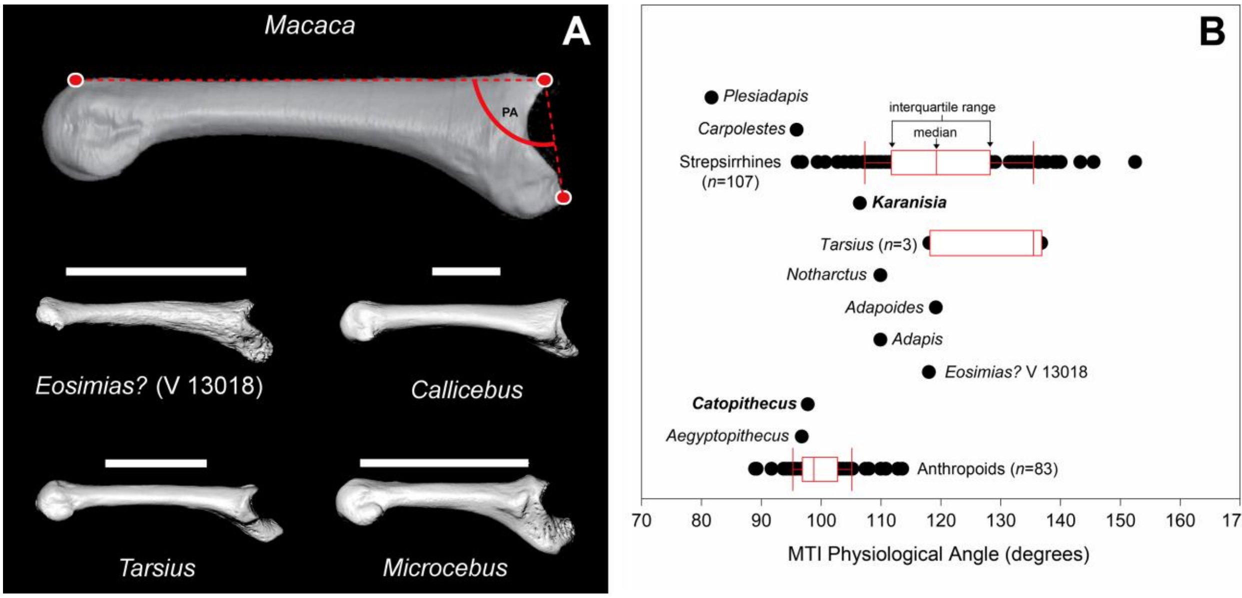

Figure 1. A) First metatarsal of the anthropoid *Macaca*, illustrating the measurement for physiological abduction angle; representative MTIs of an anthropoid (*Callicebus*), strepsirrhine (*Microcebus*), tarsier (*Tarsius*); and IVPP 13018, a middle Eocene MTI from Shanghuang, China, that might be attributable to the basal stem anthropoid *Eosimias*. Scale = 1cm. B) Measurements of physiological abduction angle in living and extinct primates.

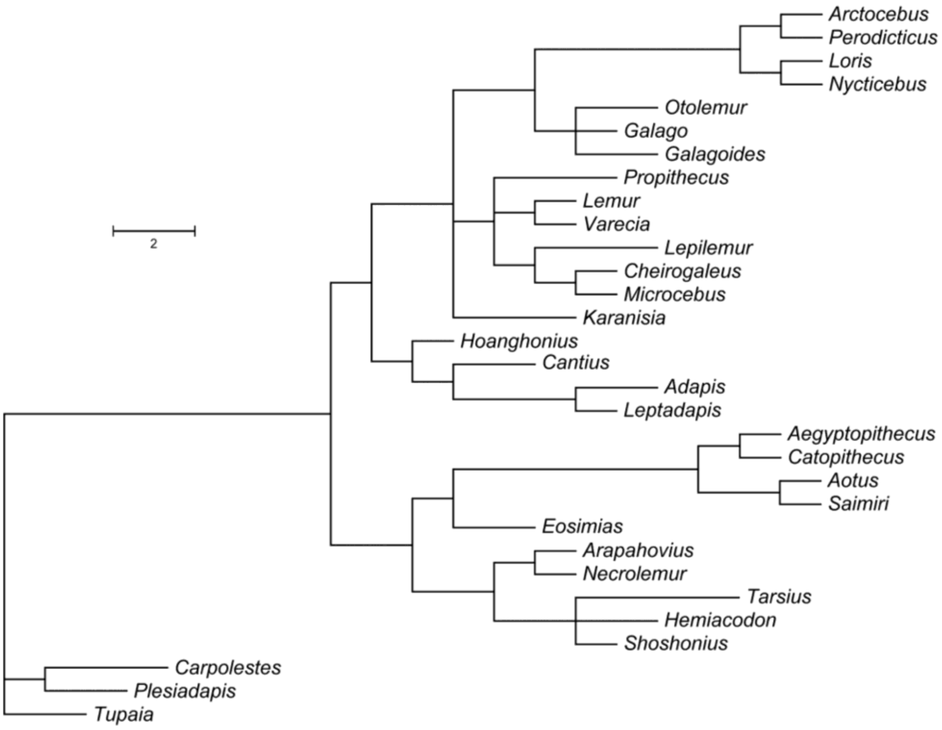

Figure 2. Phylogenetic relationships among primates in the expanded character-taxon matrix for which MTIs are known. Branches are scaled relative to the amount of character change in the 16 MTI characters, with 0-length branches given a length of 1 so that the branching sequence can be depicted.

Karanisia, continues to support groupings recovered previously, for instance 1) a haplorhine-strepsirrhine dichotomy, 2) placement of adapiforms as stem strepsirrhines, 3) an omomyiform-tarsiiform clade, and 4) the placement of *Catopithecus* as a stem catarrhine. The phylogenetic position of *Karanisia* relative to lorisiforms or lemuriforms could not be resolved, but it is clear that this genus lacks the highly specialized MTI morphology that is seen in extant lorisids, arguing against the hypothesis that *Karanisia* is a crown lorisid (Seiffert *et al.*, 2003).

We identify three phases in primate evolutionary history during which major changes occurred in MTI morphology: 1) along the primate stem lineage; 2) along the anthropoid stem lineage; and 3) along the lorisid stem lineage (Fig. 2). Our phylogenetic results suggest that most of the "prosimian"-like MTI features evolved along the primate stem lineage, and would have been present in the ancestral crown primate. This suite of features represents a significant departure from the condition seen in other non-primate mammals, and there are no known transitional fossils, suggesting either a rapid "burst" of MTI evolution along the primate stem lineage, or a long, unsampled ghost lineage. Given the phylogenetic relationships recovered in our analysis (Fig. 2), anthropoids are reconstructed as having undergone a series of reversals in MTI morphology for which there are also no known transitional forms. An MTI from middle Eocene deposits in Shanghuang, China (Fig. 1) that might be attributable to the basal stem anthropoid *Eosimias* (Gebo *et al.*, 2008) shows no derived features shared with anthropoids; if the bone does belong to *Eosimias*, it is clear that a significant gap exists in the fossil record documenting anthropoid MTI evolution.

Our analyses lend new support to the hypothesis that the MTI morphology seen in anthropoid primates represents a reversal from a "prosimian"-like stem anthropoid ancestor, perhaps associated with a transition to increased use of large-diameter, and perhaps more horizontal, arboreal substrates at some point early in the Eocene (e.g., Gebo *et al.*, 2000). A full understanding of this transition will only come from the recovery of more complete fossils along the anthropoid stem lineage.

Bloch, J.I., Boyer, D.M. (2002). Grasping primate origins. Science 298: 1606-1610.

Boyer, D.M., Seiffert, E.R., Simons, E.L. (2010). Astragalar morphology of *Afradapis*, a large adapiform primate from the earliest late Eocene of Egypt. American Journal of Physical Anthropology 143: 383-402.

Dagosto, M. (1990). Models for the origin of the anthropoid postcranium. Journal of Human Evolution 19: 121-139.

Gebo, D.L., Dagosto, M., Beard, K.C., Ni, X., Qi, T. (2008). A haplorhine first metatarsal from the middle Eocene of China. In: Fleagle, J.G., Gilbert, C.C. (eds) Elwyn Simons: A Search for Origins. Springer, New York, pp 229-242.

Gebo, D.L., Dagosto, M., Beard, K.C., Qi, T., Wang, J. (2000). The oldest known anthropoid postcranial fossils and the early evolution of higher primates. Nature 404: 276-278.

Jacobs, R.L., Boyer, D.M., Patel, B.A. (2009). Comparative functional morphology of the primate peroneal process. Journal of Human Evolution 57: 721-731.

Patel, B.A., Boyer, D.M., Jacobs, R.L., Seiffert, E.R., Simons, E.L. (2010). Anthropoid first metatarsal from the late Eocene of Egypt. American Journal of Physical Anthropology 50: 186.

Seiffert, E.R., Simons, E.L., Attia, Y. (2003). Fossil evidence for an ancient divergence of lorises and galagos. Nature 422: 421-424.

Geochronology and palaeontology of the Palaeogene deposits in the Sperrgebiet, Namibia

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STRATIGRAPHY AND AGE DETERMINATIONS

There has been considerable debate about the ages of the post-Proterozoic sediments of the Sperrgebiet, Namibia, ever since they were first mapped in the 1920s (Pickford *et al.*, 2008*b*). The deposits are generally quite thin (less than 20 metres), and outcrops are for the most part discontinuous. However, there are two widespread sedimentary horizons in the Sperrgebiet: the Blaubok Conglomerate (without phonolite pebbles and therefore older than the Klinghardt Volcanic Group), and the younger Gemsboktal Conglomerates (with phonolite clasts). Beneath the Blaubok Conglomerate occurs the Pomona Beds (quartzites) originally considered to be Cretaceous, and silicified limestones (Chalcedon Tafelberg), age estimates of which has varied in the literature from Cretaceous to middle Miocene (Pickford *et al.*, 2008*b*). Overlying the Blaubock Conglomerate is a suite of marine and continental deposits (Fig. 1).

Fossiliferous carbonate deposits (Black Crow, Silica North and Silica South) predate Klinghardt volcanism (Eocene-Oligocene) on the basis of stratigraphy and diagenesis. These carbonates have yielded plants, invertebrates and vertebrates, the age of which was estimated to be middle Eocene (Lutetian) on the basis of the mammalian biostratigraphy (Pickford *et al.*, 2008*a*). This age determination has been challenged by some authors, who consider that the fauna indicates a Priabonian or younger age (i.e., contemporary with Klinghardt volcanism). Previous estimates of the age of Klinghardt volcanism range from 29 to 37 Ma (Reid *et al.*, 1990). In the neighbourhood of Black Crow, phonolite cobbles from the Gemsboktal conglomerate, which unconformably overlies the fossil-bearing carbonates, have yielded K-Ar feldspar ages of 40.1±0.9 to 42.2±0.9 Ma and whole rock ages of 41.4±0.9 to 45.4±1.0 Ma, indicating an earlier onset of volcanism than previously thought. The data suggest that the faunas from the carbonates are older than the Priabonian, and that a Lutetian age, as originally inferred from the mammalian fauna, is likely to be retained.

PALAEONTOLOGY

A rich and diverse assemblage of Middle Eocene fossils discovered in palaeokarst deposits of the Sperrgebiet, Namibia, includes plants, invertebrates and vertebrates which indicate that the fossiliferous carbonates accumulated under a summer rainfall

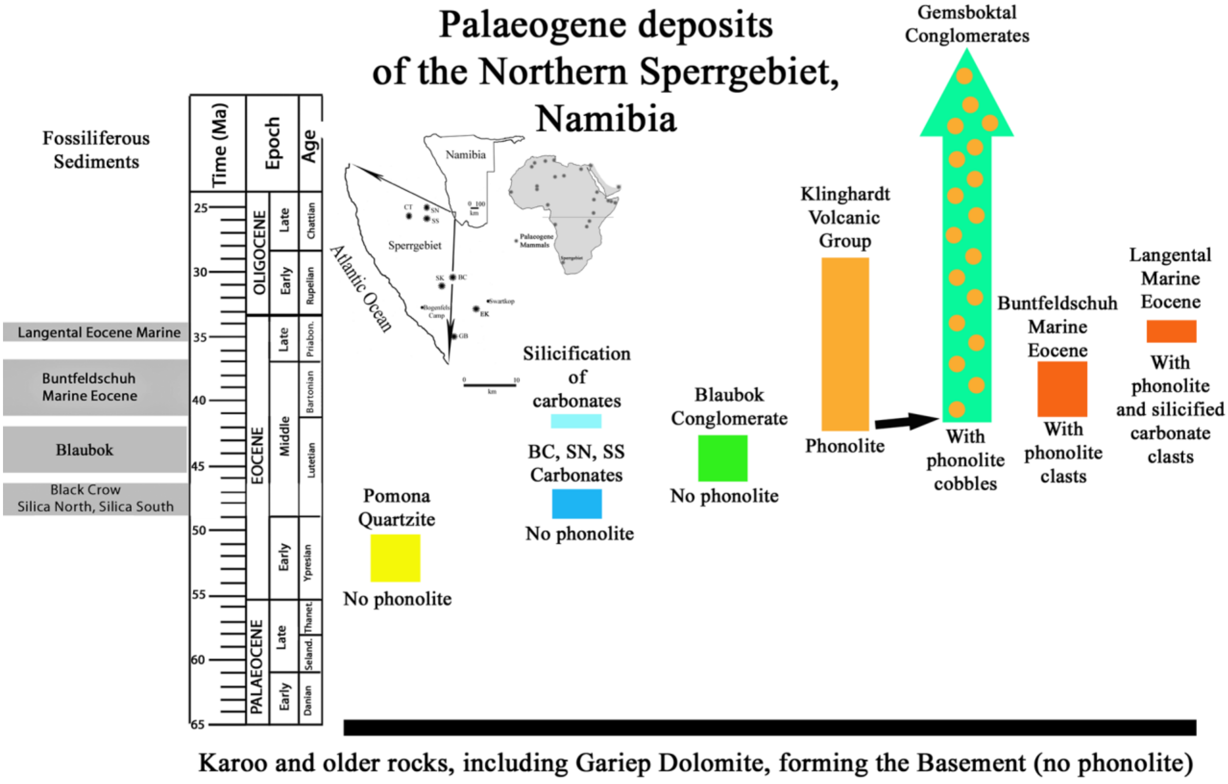

Figure 1. Palaeogene fossiliferous localities of Africa and stratigraphic succession in the Sperrgebiet, Namibia (BC – Black Crow, CT – Chalcedon Tafelberg, EK – Eisenkieselklippenbacke; GB – Gamachab, SK – Steffenkop, SN – Silica North, SS – Silica South).

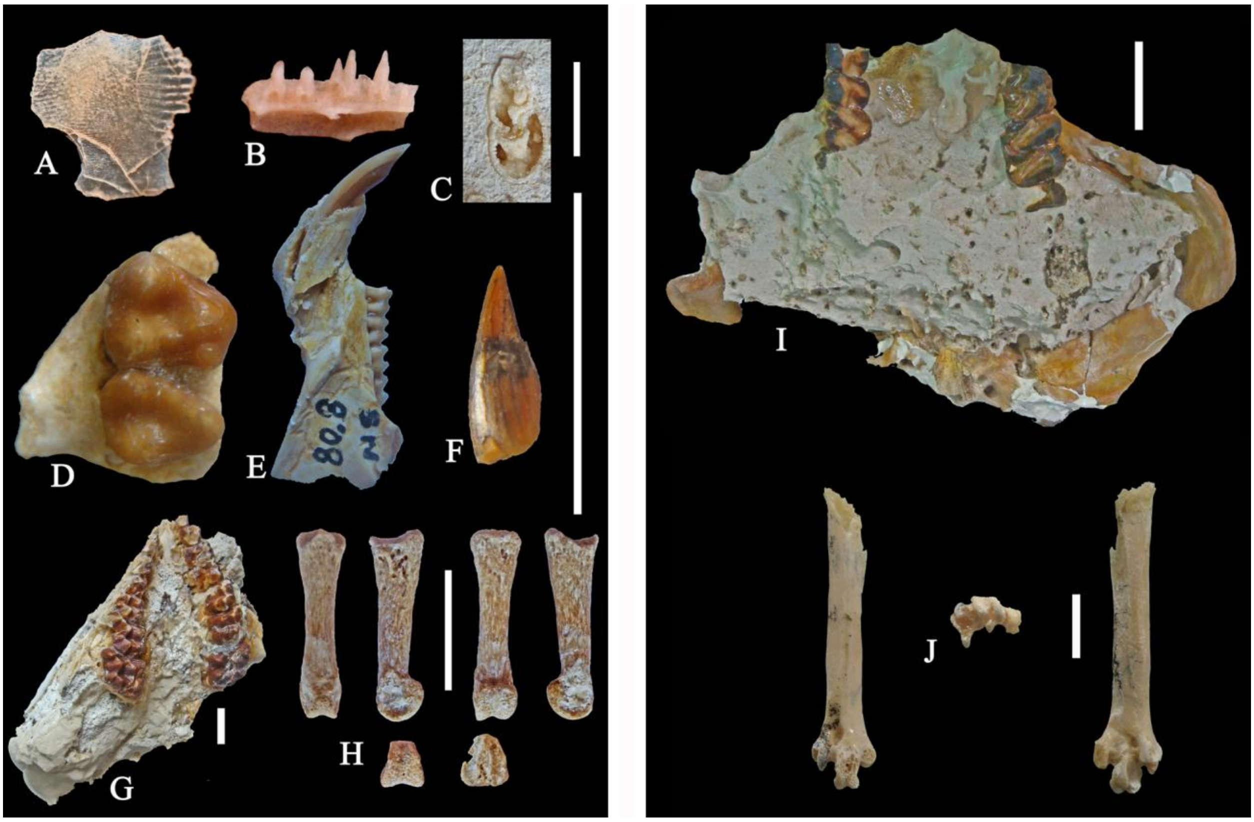

Figure 2. Invertebrates and vertebrates from the Lutetian deposits of the Northern Sperrgebiet, Namibia (A – fish scale; B – lacertilian jaw; C – land snail (*Xerocerastus*?); D – *Namaia* maxilla with M^2-M^3; E – *Prepomonomys* mandible; F – crocodile tooth; G – *Namahyrax* snout; H – possible xenarthran phalanx; I - palatal view of the skull of *Namatherium*, a primitive arsinoithere from Namibia; J – three views of the tarsometatarsus of *Namaortyx* (scale bars 10 mm, save for Fig. I, 5 cm).

regime. The plant remains belong to aquatic taxa, the invertebrates comprise both freshwater molluscs and land snails, and the vertebrates include fishes, reptiles (crocodiles and lizards), birds, and mammals (Fig. 2). *Namatherium* from Black Crow is more primitive than arsinoitheres from the Fayum, Egypt (late Priabonian-Rupelian), as is the brachyodont hyracoid *Namahyrax*.

A primate maxilla and lower premolar have been attributed to basal Anthropoidea (*Namaia*; Pickford *et al.*, 2008*a*), which, if correct, indicates a presence of the order in the continent earlier than previously considered possible. Rodents are moderately diverse, and comprise zegdoumyids, Diamantomyidae, Myophiomyidae, Phiomyidae and Bathyergidae. There is a macroscelidid from the deposits, which throws doubt on interpretations of some of the North African fossils previously considered to represent primitive macroscelideans, and there is a tooth that recalls erinaceomorphans. An enigmatic phalanx from Black Crow, previously attributed to Pholidota (Pickford *et al.*, 2008*a*), is in fact closer by its articular morphology (proximal articulation comprised of two parts separated by a vertical groove) to Xenarthra (Fig. 2), which raises the possibility of a connection to South American faunas at some stage in the early Palaeogene. Finally, two species of creodont and a todralestid complete the known mammal fauna. The bird from the deposits has recently been named *Namaortyx* (Pickford *et al.*, 2008*a*), and represents the earliest record of the Galliformes in Africa. The discovery of early Eocene fossils in Namibia is important for understanding the evolution and biogeography not only of African Palaeogene mammals, but also those from Europe which have long been known to contain elements of “African” (arsinoitheres) and, according to some authors “South American” (xenarthran) lineages.

Pickford, M., Senut, B., Morales, J., Mein, P., Sanchez, I.M. (2008*a*). Mammalia from the Lutetian of Namibia. Memoir of the Geological Survey of Namibia 20: 465-514.

Pickford, M., Senut, B., Morales, J., Sanchez, I. (2008*b*). Fossiliferous Cainozoic Carbonates of the Northern Sperrgebiet. Memoir of the Geological Survey of Namibia 20: 25-42.

Reid, D.L., Cooper, A.F., Rex, D.C., Harmer, R.E. (1990). Timing of post-Karoo volcanism in Southern Namibia. Geological Magazine 127: 427-433.

Locomotion in some Eocene mammals from Messel, seen from a biomechanical viewpoint

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Many mammals from the Messel site, especially Equoidea, primates and *Leptictidium*, seem to be “accelerators” (rather than “wanderers”). These are very good at rushing forward to attack prey or enemies and in escaping by sudden flight, because the total force (F) available in the animal’s body divided by low mass (m) yields high gain of speed (or acceleration (a)) during a time unit ($F = m*a$, or $a = F/m$). The force which accelerates the animal’s body is the reaction resulting from body weight and mass inertia. As long as the animal is moving forward, this resultant passes through or close to the hind feet (Peters and Preuschoft, 1984). An inevitable consequence during evolution is a reinforcement of the hindlimbs (Herkner, 1989; Christian, 1995, 1999) and the lumbar spine, as well as flexibility of the lumbar segments. An accompanying elongation of these elements permits extended contacts to the substrate during the phase of acceleration and therefore higher speed and less force (i.e., in leaping greater lengths and heights; Peters and Preuschoft, 1984). Both factors, reinforcement and elongation of the hindlimbs, can reach a point at which the forelimbs are no longer adequate partners of the hindlimbs and become reduced, for the sake of further strengthening the hindlimbs. If this is the case, a form of bipedality, e.g., hopping, as in *Leptictidium* (Christian, 1999), is developed.

An absolute must for a small animal in the sense of Fischer (1994), such as the mammals from Messel, is the ability to move safely on rough, discontinuous, and often inclined substrates. The best means of providing these cross-country capacities is a large area of support in combination with a low position of the centre of mass (CoM) – in other words, rather short or permanently flexed limbs (Cartmill, 1974; Witte *et al.*, 2002). The safest mode of locomotion (gait) is the walk. Two or three feet are on the ground for long periods, providing a large support. The swinging forward of the non-loaded limbs is dictated by the laws of pendulum and therefore does not need much energy (Witte *et al.*, 1991), but this also keeps down the frequency of locomotor cycles. Walking speed therefore is slow.

The next faster gait is the trot (or pace, or amble, depending on which limbs are moved simultaneously), in which the body is supported during the stance phase by two limbs at a time, interrupted by phases of aerial floating, which allow an increase of stride length. Trotting and similar running gaits are characterized by the influence of elastic elements (ligaments, muscle-tendon complexes), and this requires a rather constant rhythm. Stride frequencies are dictated by the own frequencies of tension-resistant materials and are higher than in the walk, so that higher speeds are possible while energy requirements are low. The rhythm of the trot, however, can be disturbed by discontinuities of the substrate.

Still faster and less prone to disturbance are asymmetric gaits such as bound, half-bound or gallop, because they contain longer phases of aerial suspension, and therefore longer stride lengths, while the frequencies tend toward lower values than the trot. “Small” mammals tend to use these asymmetric gaits more often (Fischer, 1994) than “large” or “cursorial” mammals, which reach comparable speeds in walking (Preuschoft *et al.*, 1994).

Aside from these generally valid conditions for locomotion, there is a fundamental difference between the substrates on which the animals move: one is the more or less horizontal, flat, and firm ground extending in two dimensions; the other comprises twigs, branches, and stalks, often steeply inclined against the horizontal, extending in three dimensions. Both substrates require different morphological “adaptations”.

Moving on a 2D-substrate means that primarily compressive forces acting at right angle to the ground are exchanged between substrate and animal, while only moderate force components are directed parallel to the ground. This holds true for the Messel equoids. A shortening of the toes is advantageous as a way to keep the necessary muscle forces low during roll-off. Shortening of the toes therefore allows a reduction of the muscle mass on the zygopodia and autopodia. Limbs become more slender this way and can be swung forward more rapidly (increased stride frequency) with low input of energy. Increased functional length of the stylo- and zygopodia, and especially the inclusion of the metapodia, lead to longer strides, and higher speed, without additional input of energy. The Equoidea from Messel (Franzen, 2007) show exactly these proportions.

Shortening of the toes also leads to smaller areas of contact between foot and ground. This concentrates the reaction force on a small area (compression = reaction force / contact area) and therefore favours the development of local reinforcements such as hooves or blunt claws (e.g., hooved animals, many land turtles, carnivores) and/or cushions (e.g., elephants, rhinos, hippos). Short toes and hoof-like terminal phalanges are present in the Messel equoids (Franzen, 2007), and this fits perfectly to their body proportions.

Moving within a 3-dimensional meshwork of substrates requires the transmission of compressive and tensile forces from the animal to the substrate (e.g., recent arboreal varanids and iguanids, some marsupials, sloths, many rodents such as squirrels, mustelids, paradoxurinae, and *Cryptoprocta*). Additional options for exploiting resources in the outer foliage and for safe locomotion on slender twigs are provided by the ability to transmit rotating moments between the animal and its substrate. This is the outstanding potential of truly prehensile autopodia, such as those characteristic of primates (Preuschoft, 2002) and chameleons (Fischer *et al.*, 2010). According to Kümmell (2009), prehensile properties occur very early in synapsids. Length and flexibility of the toes entail a large span of the grip and a large contact area, but require very strong muscles on the autopodia and zygopodia. This is equivalent to having heavy limbs and sets limits to stride frequencies (Witte *et al.*, 1991; Preuschoft *et al.*, 1994). Alone the shapes of the autopodia in the Messel primates classify them unequivocally as specialists for an arboreal lifestyle (Franzen, 2000; Franzen *et al.*, 2009).

Functional length of the free limbs is confined to the stylopodia and zygopodia, and implies advantages (long reach, high locomotor speed) as well as disadvantages (great moments of external forces, danger of loss of control in case of accidents). These conflicting conditions have been discussed in detail by Cartmill (1974, 1985), Preuschoft *et al.* (1992), and Preuschoft (2002). They have led to quite different results among living strepsirrhines and especially among haplorrhines. Their specific relevance for the various Messel primates (e.g., Franzen 2000; Franzen *et al.*, 2009) still needs to be investigated.

Some of the early quadrupedal mammals from the Messel site (equoids, *Leptictidium*, primates) represent and document marked crossroads in the evolution of terrestrial and arboreal adaptations.

Cartmill, M. (1974). Pads and claws in arboreal locomotion. In: Jenkins, P. (ed) Primate Locomotion. Academic Press, New York, pp. 45-83.

Cartmill, M. (1985). Climbing. In: Hildebrand, M., Bramble, D.M., Liem, K.F., Wake, D.B. (eds) Functional Vertebrate Morphology. Harvard University Press, Cambridge, MA, pp. 73-88.

Christian, A. (1995). Zur Biomechanik der Lokomotion vierfüßiger Reptilien. Courier Forschungs-Institut Senckenberg 180: 1-58.

Christian, A. (1999). Zur Biomechanik der Fortbewegung von *Leptictidium* (Mammalia, Proteutheria). Courier Forschungs-Institut Senckenberg 216: 1-18.

Fischer, M.M. (1994). Crouched posture and high fulcrum, a principle of locomotion in small mammals. Journal of Human Evolution 26: 501-521.

Fischer, M.M., Krause, C., Lilje, K.E. (2010). Evolution of chameleon locomotion, or how to become arboreal if being a reptile. Zoology 113(2): 67-74.

Franzen, J.L. (2000). *Europolemur kelleri* n. sp. von Messel und ein Nachtrag zu *Europolemur koenigswaldi* (Mammalia, Primates, Notharctidae, Cercamoniinae). Senckenbergiana lethaea 80: 275-287.

Franzen, J.L. (2006). Eozäne Equoidea (Mammalia, Perissodactyla) aus der Grube Messel bei Darmstadt (Deutschland). Funde der Jahre 1969–2000. Schweizerische Paläontologische Abhandlungen 127: 1-245.

Franzen, J.L., Gingerich, P.D., Habersetzer, J., Hurum, J.H., Koenigswald, W.v., Smith, H. (2009). Complete primate skeleton from the Middle Eocene of Messel in Germany: Morphology and paleobiology. PLoS ONE, 4(5): 1-27. (e5723. doi: 10.1371/journal.pone.0005723).

Herkner, B. (1989). Die Entwicklung der saltatorischen Bipedie bei Säugetieren innerhalb der Tetrapoden-Evolution. Courier Forschungs-Institut Senckenberg 111: 1-102.

Günther, M.M. (1989). Funktionsmorphologische Untersuchungen zum Springverhalten mehrerer Halbaffen. Dissertation Freie Universität Berlin, 183pp.

Kümmell, S. (2009). Die Digiti der Synapsida: Anatomie, Evolution und Konstruktionsmorphologie. Shaker Verlag, Aachen.

Peters, A., Preuschoft, H. (1984). External biomechanics of leaping in *Tarsius* and its morphological and kinematic consequences. In: Niemitz, C. (ed): Biology of Tarsiers. G. Fischer, Stuttgart, pp. 227–256.

Preuschoft, H. (2002). What does “arboreal locomotion” mean exactly and what are the relationships between “climbing”, environment and morphology? Zeitschrift für Morphologie und Anthropologie 83: 171-188.

Preuschoft, H., Günther, M.M. (1994). Biomechanics and body shape in primates compared with horses. Zeitschrift für Morphologie und Anthropologie 80: 149-165.

Preuschoft, H., Witte, H., Christian, A., Recknagel, S.T. (1994). Körpergestalt und Lokomotion bei grossen Säugetieren. Verhandlungen der Deutschen Zoologischen Gesellschaft, 87: 147-163.

Preuschoft, H., Witte, H., Demes, B. (1992). Biomechanical factors that influence overall body shape of large apes and humans. In: Matanao, S., Tuttle, R. Ishida, H., Goodman, M (eds) Topics in Primatology, Vol. 3, Evolutionary Biology. University of Tokyo Press, Tokyo, pp. 259-289.

Witte, H., Preuschoft, H., Fischer, M.S. (2002). The importance of the evolutionary heritage of locomotion on flat ground in small mammals for the development of arboreality. Zeitschrift für Morphologie und Anthropologie 83: 221-233.

Witte, H., Preuschoft, H., Recknagel, S.T. (1991). Human body proportions explained on the basis of biomechanical principles. Zeitschrift für Morphologie und Anthropologie 78:407-423.

3D reconstructions of Eocene and extant bats – Multimedia materials for public activities in the Year of the Bat 2011

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Messel is an extraordinary site for fossil bats. Whereas flying mammals are usually rare in fossil deposits, in Messel bats are by far the most frequent mammals (Habersetzer *et al.*, 1992). So far, about 700 individuals have been found in the oil-shale layers (age MP 11), many of them as complete skeletons with preserved gastrointestinal contents. According to SEM investigations of the gut contents, the Messel fossil bats fed on insects, and microradiographic examinations of skulls and cochleae showed that they already hunted using ultrasonic sounds (Habersetzer and Storch, 1992; Habersetzer *et al.*, 1994). Seven species of four families (Palaeochiropterygidae†, Archaeonycterididae†, Hassianycterididae†, Emballonuridae) have been described, forming the oldest known bat community in the world recovered with such excellent preservation.

The uniqueness of the Messel fossil site derives not only from the diversity of families found there, but also from *Tachypteron franzeni*, which is the only representative of an extant family among Messel bats and the worldwide oldest record of Emballonuridae (Storch *et al.*, 2002).

To illustrate the scientific relevance for the public, a 3D reconstruction of *Tachypteron franzeni* was prepared at Senckenberg in the traditional, or classic, way. It is the first 3D reconstruction of a Messel bat, and in recognition of the Year of the Bat 2011 the coloured model is published here for the first time (Fig. 1). A detailed description of the reconstruction will follow (Rabenstein *et al.*, in preparation)

Tachypteron franzeni was highly specialized for a straight, rapid, high-altitude flight. This fossil bat is characterized by a long and narrow wing, and the flight membranes have nearly the same outline as in extant *Taphozous* species, such as *Taphozous melanopogon* (Storch *et al.*, 2002).

A skull of the latter species from the Senckenberg mammal collection (SMF 46.334) was µCT-scanned and the dataset processed by E. S.-S. for rapid prototyping, generating a second model. The protocol will be published in detail (Rabenstein *et al.*, in preparation).

For the third 3D model a dissected cochlea from the extant neotropical leaf-nosed bat *Carollia perspicillata* (diameter ~ 1.5 mm) was scanned at a high-resolution synchroton radiation facility (SR-µCT, Habersetzer *et al.*, 2004). The cochlea of *C. perspicillata* morphologically resembles that of *Palaeochiropteryx tupaiodon*, which is the most common Messel bat. The cochlea was virtually cut open to expose the auditory canal and such delicate features as the diminutive foramina for the nerves. The models are on display at the newly opened Messel Visitor Center (Mangel, 2010).

Film sequences of virtual flights through the inner ear complement the static exhibits. They were developed, produced and published as part of the project Multimedia Materials Messel (Rabenstein and Habersetzer, 2007). The video published on CD-ROM (Habersetzer *et al.*, 2004) is available at the Messel Visitor Centre.

The high-resolution data were reworked in full high definition by E. S.-S. for the TV film *Urzeit am Geistersee* (Sparwasser *et al.*, 2011). The film shows research on bats conducted by R. R. in the field (Senckenberg Research Station "Chiquitos" in Bolivia) and by J. H. in high-tech laboratories and focuses on the evolution of bats. The film has been playing since 2010 in the Senckenberg Natural History Museum, Frankfurt.

Figure. 1. 3D reconstruction of *Tachypteron franzeni* by C. Weißbrod (Senckenberg Research Institute). Note the delicate and translucent wing membrane. Wingspan: 35 cm.

Current research results are vividly disseminated in certified training courses for teachers, in multimedia lectures for participants in various “bat nights”, and at special events at the Senckenberg Natural History Museum, Frankfurt, as well as for guided tours for VIPs, students, families and children. The “bat nights” in the Messel Pit receive an especially positive response from the public (Rabenstein, 2010). Pictures, animations, film sequences and 3D reconstructions in combination with pedagogical materials form the backbone of various guided tours and talks for the public. Heightened public activities in the Year of the Bat 2011 will help introduce fossil and extant species to the public as ambassadors for the protection of the unique geotope and impressive biotope that is Messel.

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HABERSETZER, J., RICHTER, G., STORCH, G. (1992). Bats: Already highly specialized insect predators. In: Schaal, S., Ziegler, W. (eds) Messel – An Insight into the History of Life and of the Earth. Clarendon Press, Oxford, pp 179-191.

HABERSETZER, J., RICHTER, G., STORCH, G. (1994). Paleoecology of early Middle Eocene bats from Messel, FRG. Aspects of flight, feeding and echolocation. Historical Biology 8: 235-260.

HABERSETZER, J., SCHERF, H., BECKMANN, F., SEIDEL, R. (2004). 3-D-Animation knöcherner Gesamtskelette und mikro-tomographischer Skelettdetails von Fossilien aus der Grube Messel. In: Habersetzer, J., Schaal, S. (eds) Current Geological and Paleontological Research in the Messel Formation. Courier Forschungsinstitut Senckenberg 252: 237-241.

HABERSETZER, J., STORCH, G. (1992). Cochlea size in extant Chiroptera and Middle Eocene microchiropterans from Messel. Naturwissenschaften 79: 462-466.

MANGEL, G. (2010). Faszination Welterbe Grube Messel: Zu Besuch in einer Welt vor 47 Millionen Jahren. Kleine Senckenberg Reihe 52, Frankfurt. 130 pp.

RABENSTEIN, R. (2010). Bats in the UNESCO World Heritage Site Messel Pit – Ambassadors of a palaeontological site for the protection of a geotope and biotope. Schriftenreihe der Deutschen Gesellschaft für Geowissenschaften 66: 116-117.

RABENSTEIN, R., J. HABERSETZER (2007). Von original bis multimedial: Senckenbergische Beiträge für das Besucherzentrum am Weltnaturerbe Grube Messel. Abhandlungen der Geologischen Bundesanstalt 60: 157-167.

SPARWASSER, K., HABERSETZER, J., RABENSTEIN, R. (2011). Urzeit am Geistersee & Ida completed, DVD 70 Min. + Bonusmaterial 30 Min. ISBN 978-3-929907-85-8.

STORCH, G., SIGÉ, B., HABERSETZER, J. (2002). *Tachypteron franzeni* n. gen., n. sp., earliest emballonurid bat from the Middle Eocene of Messel (Mammalia, Chiroptera). Paläontologische Zeitschrift 76 (2): 189-199.

Amphibians and squamates in the Eocene of Europe: What do they tell us?

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As far as the terrestrial realm of the Cainozoic is concerned, most studies have dealt with mammals. Other vertebrates were and are still more or less overlooked. However, amphibians and reptiles may afford significant information.

The abundance and diversity of amphibians and reptiles appears to be directly driven by environment rather than indirectly through the availability of food. The richness in reptiles depends on ambient energy, as they are strongly solar ectotherms; however, they do have limited thermoregulation capabilities. Amphibians, on the other hand, although sensitive to temperature as well, are highly dependent on moisture, and practically all of them require water at least for reproduction. Therefore, associations of amphibians and reptiles afford reliable information on environment, information that may be complementary to that provided by mammals.

However, concerning reptiles, only squamates are taken here into account. Like lissamphibians (the only amphibians present during the Cainozoic), they are small and therefore more numerous than larger animals. Turtles, crocodilians and choristoderans, the other reptiles known from the Cainozoic, are scattered and by far less frequent.

GEOGRAPHIC AND STRATIGRAPHIC BIASES

The present survey suffers several biases. Geographically, the Eocene vertebrate localities are markedly concentrated in western Europe. In addition, beds of early Eocene age are often of aquatic origin, mostly estuarian/deltaic, while localities of late Eocene age are generally of terrestrial origin (fissure-fills). Another bias may be the rarity of localities from the MP 11–MP 15 interval (middle Eocene).

BEFORE THE EOCENE

The fauna of amphibians and squamates from the Paleocene is poorly known in Europe. It lacks several taxa that were present during the latest Cretaceous (iguanids s.l., paramacellodids, teiids, and madtsoiids among the squamates). However, iguanids s.l. and perhaps teiids are present in the Eocene; consequently, their absence from the Paleocene record may be an artifact. However that may be, in Europe, the Paleocene fauna comprises (aside from various indeterminate and incertae sedis forms) salamandrids, dicamptodontids (salamanders), discoglossids, palaeobatrachids, bufonids (frogs), possibly lacertids, scincids, necrosaurids, amphisbaenians (lizards), and scolecophidians and boids (snakes).

SALIENT FEATURES OF AMPHIBIAN AND SQUAMATE HISTORY IN EUROPE DURING THE EOCENE

Remark: The marine deposits should be distinguished from other environments, the latter including estuarian and deltaic deposits that mainly produce terrestrial forms. The marine realm was inhabited by palaeophiid snakes, a group that died out at the end of the Eocene. These snakes, highly adapted to aquatic life, are still poorly known. They are potentially of interest to stratigraphy and, more specifically, to correlations between marine and continental deposits because they entered freshwater. However, identification at species level is difficult. They will not be discussed further, and the following deals only with non-marine faunas.

Four distinct assemblages of amphibians and squamates are discussed below: i) those of the level MP 7; ii) those of the levels MP 8+9 and MP 10; iii) the poorly known fauna from the MP 11–MP 15 interval; and iv) the assemblage of the MP 16–MP 19 interval, to which the problematic level MP 20 may (should?) be added.

THE MP 7 LEVEL (BASAL EOCENE)

The fauna from this level is markedly richer than that from the Paleocene. Among amphibians, salamanders appear to be approximately a continuation from the Paleocene, whereas the composition of the frog fauna changes with the arrival of Pelobatidae. The diversity of squamates increased more markedly. New taxa invaded Europe: iguanid s.l., agamid, gekkonid, anguid (glyptosaurines, anguines), varanid, helodermatid and perhaps cordylid lizards, as well as tropidophiid and perhaps russellophiid snakes; confirmed lacertid lizards are present. Among the newcomers are forms with North American affinities, but the geographic origin cannot be confidently recognized for all of the taxa. This tidal wave of immigrants represents one of the more prominent events that affected the history of squamates in Europe. It is also an important step toward the modern fauna, several immigrant families being still present in Europe today. Dispersals and the increased diversity of squamates, animals sensitive to temperature and sunshine, are likely the result of the PETM event.

THE MP 8+9 AND MP 10 LEVELS (EARLY EOCENE)

The faunas from MP 8+9 and MP 10 are rather homogenous. Among amphibians, MP 8+9 apparently marks the beginning of a slow demise of salamanders. Whereas salamanders were dominant in the late Cretaceous, the Paleocene and MP 7, from MP 8+9 onwards the relative number of frogs appears to increase. Squamates underwent diversification, although they do not differ at the family level from those of MP 7. Scincomorph lizards and boid snakes, mainly, become more numerous. Within snakes, boids begin their marked hegemony that will last up to the end of the Oligocene. In contrast, agamid and amphisbaenian lizards decrease.

It is not possible to establish whether diversification resulted from endemic evolution, immigration (what geographic origin?), or both. Members of the North American–European fauna are still present; they were perhaps joined (in MP 10) by a frog with South American affinities.

MP 11–MP 15 INTERVAL (MIDDLE EOCENE)

Localities from this time interval are rare, even though it comprises five levels. Most of the studied fossils are represented by well-preserved, articulated specimens from the German sites of Messel (MP 11) and Geiseltal (mostly MP 13). Such specimens are of high interest to precise phylogenetic studies, but they cannot easily be compared to isolated bones, i.e., nearly all other fossils from the Eocene of Europe. Aside from Messel and the Geiseltal sites, only two localities from this interval have been studied: St-Maximin (MP 13) and Lissieu (MP 14), both in France; they produced some disarticulated specimens. Paradoxically, despite Messel and Geiseltal fossils, MP 11–MP 15 appears mainly as a lacuna in our knowledge of the succession of events during the Eocene. Based on Messel, there is apparently no marked change between MP 10 and MP 11. The only noticeable event of this time interval is the possible appearance, in MP 13, of pelodytid frogs, a living family restricted to Europe today.

The main question concerning this interval is whether this paucity is the reflection of the actual biodiversity of that time. It is likely a bias as suggested by Messel and Geiseltal, at least for MP 11 and MP 13. However, the reduced number of localities may be also significant.

MP 16–MP 20 INTERVAL (LATEST MIDDLE AND LATE EOCENE)

Following the actually or artefactually depauperate MP 11–MP 15 period, a rich and diverse assemblage suddenly takes form in MP 16. Despite lower temperatures, these characteristics of the fauna remain in the younger levels up to MP 19. MP 20 is represented by very few localities that yielded poor faunas. In fact, aside from richness and diversity, there is no obvious difference between the assemblage from MP 16–MP 19 and the fauna from MP 20; the latter level is perhaps artificial and, here, MP 19 and MP 20 are regarded as a single level, MP 19+20. If a merging of MP 20 with MP 19 is accepted, amphibians and squamates from MP 16 through MP 19+20 form a homogenous assemblage.

The richness results from both arrival of new families and mainly diversification (local evolution?) of families already present. Ranid frogs and perhaps ‘aniliid’ snakes reached Europe by the time of MP 16, and the presence of pelodytids and frogs with South American affinities (‘leptodactylitids’) is now confirmed. Microhylid and rhacophorid frogs were reported as newcomers in MP 19+20, but this cannot be confirmed. Except for ‘leptodactylid’ frogs, geographic affinities of newcomers remain unknown. Taxa with North American affinities were still present, likely as offsprings of earlier European forms or survivors from earlier levels. Diversification within families occurred markedly in two steps, in levels MP 16 and MP 17. In these two levels, diversification is noticeable in iguanid s.l., lacertid and anguid lizards, while boid snakes (including boines) underwent a large radiation. Contrary to squamates, amphibians do not show clear diversification. This is perhaps the result of the aridification that took place during the late Eocene; this appears to be corroborated by the rarity of aquatic frogs (discoglossids, palaeobatrachids).

THE END OF THE EOCENE: THE ‘GRANDE COUPURE’

The transition between MP 19+20 and MP 21, i.e., the Eocene-Oligocene boundary, corresponds to an important faunal break, the ‘Grande Coupure’ (Great Break). About 45 taxa of amphibians and squamates are recorded from the MP 16–MP 19+20 interval, 36 of which are present in the last level (MP 19+20). Only five or six survived the Grande Coupure (two or three amphibians out of seven, three squamates out of 29). It should be noted that if MP 19 and MP 20 are really distinct, then the turnover occurred in two steps (mainly between MP 19 and MP 20, and then between MP 20 and MP 21). As is well known, this event would result from both the disturbances of environment and the collapse of the marine barrier that separated Europe from Asia.

A parallel could be drawn between the diversity of squamates at the end of the Eocene and the decline of diversity in various mammalian groups after MP 18. It may be entertained whether squamates took advantage of niches deserted by mammals.

The Grande Coupure marks the end of a fauna of squamates that includes Euro-American components. It was replaced by a fauna that likely comprises Asian taxa, the main step in the change occurring in MP 22 (early Oligocene). It should be kept in mind that this event is recorded from western Europe only; several taxa necessarily survived elsewhere (including in Europe), permitting subsequent repopulation.

CONCLUSION

The Eocene appears as one of the main crossroads in the history of amphibians and squamates. It comprises both ‘old’ and ‘modern’ taxa. ‘Old’ taxa were inherited from the latest Cretaceous and Paleocene faunas that were more or less common to North America and Europe. ‘Modern’ taxa are families, and perhaps even genera, that are part of the present fauna, including the European one, but not only that from Europe. Some taxa with South American affinities are recorded in the European Eocene. During the Eocene, amphibian faunas evolved relatively slowly, with no obvious changes at the family level, in contrast to squamate ones that underwent a series of changes. The ‘quiet’ evolution of amphibians is surprising in view of their high dependence on water availability. Most taxa, including ‘modern’ ones that died out locally, did not survive the end of the Eocene, at least in western Europe.

Dental microwear texture analysis of three large-bodied adapids from the late Eocene of the Quercy fissure fillings (France)

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During the Eocene, climates were warmer and more constant than those of the Paleocene, leading to the widespread development of tropical rainforests throughout much of the Holarctic ecozone. Such conditions were auspicious for primates, whose rapid diversification marked the Eocene epoch. The first Euprimates can be divided into two major groups, Omomyiformes (Haplorrhini-related) and Adapiformes (Strepsirrhini-related). The latter have often been compared to Malagasy lemurs. Adapiformes radiated during the Eocene in Europe, as well as in the other regions of the Holarctic Province. From the tiny *Anchomomys* to the large-bodied *Leptadapis*, they colonised a wide spectrum of ecological niches. However, the Eocene-Oligocene transition was a time of major climatic change and faunal turnover. It is also marked by the disappearance of primates from the fossil record in Europe and in North America, at a time when temperatures were cooling down and environments were becoming more open.

This study is focused on how primates coped with the changing environmental conditions of the latest Eocene, in the run-up to the faunal turnover at the Eocene-Oligocene transition. Diet is of paramount importance in a primate's life and can be one of the best indicators of its ecology, as the available food depends directly on the environment in which it lives. Therefore, this study focuses on the dietary reconstruction for three large-bodied adapids, which existed from MP 17 to MP 19, i.e., leading up to the Eocene-Oligocene transition. The taxa included in this study occur in the emblematic fissure fillings from the Quercy region of the South of France: *Leptadapis magnus* (N=6; body mass=4000 g) from Perrière (MP 17b, 37 Ma), *Cryptadapis tertius* (N=6; body mass=2500 g) from Sainte Néboule (MP 18, 36 Ma), and *Adapis parisiensis* (N=7; body mass= 1300 g) from Rosières (MP 19, 35 Ma). Perrière (MP 17b, 37 Ma) has previously been described as a wooded savannah, with the possible appearance of a dry season (Legendre, 1988). Sainte-Néboule (MP 18, 36 Ma) and Rosières 2 (MP 19, 35 Ma) correspond to slightly more open environments, in the run-up to the events of the Eocene–Oligocene transition. Previous studies have described both *Adapis* and *Leptadapis* as leaf eaters. No dietary hypothesis as been described for *Cryptadapis*, although this genus has been compared to extant cercopithecids (Godinot, 1984).

Diet will be characterized using dental microwear texture anaylsis, the study of the scar patterns left on the enamel surface as a result of tooth–food abrasion. Here, we use the protocol laid out by Scott *et al.* (2006) for dental microwear texture analysis using a Sensofar Plμ white-light scanning confocal imaging profiler (housed at the Anthropology Department of the University of Arkansas). Analysis was carried out on phase II crushing facets of lower or upper molars, which corresponds to the surfaces against which food is reduced. Five microwear variables are used in this study. Complexity (Asfc, or area-scale fractal complexity) is a measure of the roughness at a given scale. For example, the surface of a tooth may appear smooth to the naked eye, but looking through a microscope will reveal the numerous pits and scratches which scar the enamel surface. The scale of maximum complexity quantifies the range over which Asfc is calculated. Anisotropy (epLsar, or length-scale anisotropy of relief) measures the orientation concentration of surface roughness. Textural fill volume is a function of the shape and the texture of a given surface at a coarse (Tfv) or fine scale (Ftfv). The final variable, heterogeneity (HAsfc, heterogeneity of area-scale fractal complexity), quantifies the amount of variation observed between adjoining scans or even within a single one. All variables have been described in further detail in previous studies (e.g., Scott *et al.*, 2006; Ungar *et al.*, 2007; Merceron *et al.*, 2010). Statistical tests were then used in order to highlight potential differences in microwear texture between taxa. As microwear data violated conditions for parametric tests, it was rank transformed before analysis. Individual ANOVAs coupled with least significant difference multi-comparison tests were used to pinpoint sources of significant variation.

Although most results fall within the range of extant leaf-eating primates, they do highlight significant differences between the three taxa. *Adapis* (Fig. 1) has a higher Asfc than the two other adapids. Asfc has been used in previous studies (Scott *et al.*, 2006) to distinguish between diets based on hard foods and those based on tougher ones. As such, Asfc results indicate two possibilities. Either *Adapis* incorporated harder items in its diet than *Cryptadapis* or *Leptadapis* (Fig. 1), or the latter two taxa incorporated a higher quantity of tougher items in their diet. Anisotropy can be used to separate diets based on hard and tough items. Results for epLsar will be higher for a surface exhibiting numerous scratches in the same direction. Anisotropy is higher in *Cryptadapis* than in *Adapis* and *Leptadapis*, indicating *Cryptadapis* might have had a tougher diet than the other large adapids, i.e., including a higher quantity of leaves in its diet than both *Leptadapis* and *Adapis*. Anisotropy also shows differences between *Adapis* and *Leptadapis*. The epLsar results indicate *Leptadapis* included tougher elements in its diet than *Adapis*, perhaps pointing to a larger amount of leaves. Heterogeneity is higher for *Adapis* and *Leptadapis* than for *Cryptadapis*, which could point to more variability in their diet. Tfv and Ftfv show significant differences between *Adapis* and *Leptadapis*. The higher values seen in *Adapis* could denote a slightly larger quantity of fruit in *Adapis*' diet. Tfv and Ftfv do not highlight any differences between *Adapis* and *Leptadapis*.

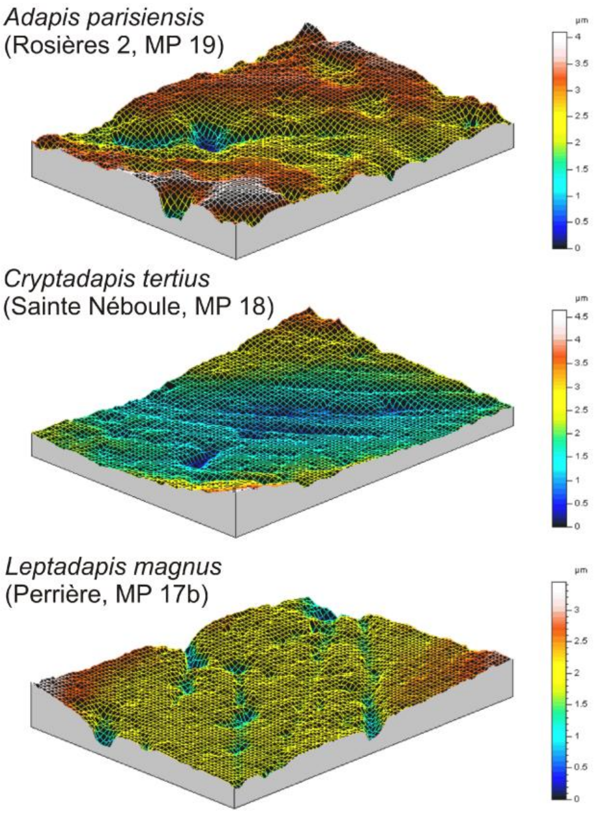

Figure 1. Meshed axiomatic representations of microwear surfaces in three dimensions for *Adapis*, *Cryptadapis*, and *Leptadapis.*

In summary, dental microwear texture analysis has allowed us to characterise the diet of these three large-bodied adapids. *Leptadapis* (MP 17, 37 Ma) was most probably a leaf eater, incorporating a small amount of fruit in its diet. *Adapis* was also a leaf eater, but would have incorporated a larger amount of fruit in its diet than *Leptadapis*. This contrasts with previous views which have mostly described this taxon as a leaf-eater (e.g., Gingerich, 1980; Gingerich and Martin, 1981). Based on the anatomy of mastication in primates, Perry (2008) concludes that *Adapis* has a strong bite force, which is coherent with the hard food elements in the diet suggested by microwear results. However, the height of the condyle indicates less capacity for gape when compared to *Leptadapis* (Perry, 2008). Thus, a larger amount of fruit in its diet than *Leptadapis* seems surprising. Perry (2008) proposes a diet based on tough foods such as mature leaves and small fruit with tough rinds. Such a diet is coherent with microwear results and could explain different morphological adaptations exhibited by this taxon (e.g., dental morphology, body mass, cranial crests). *Cryptadapis* seems to be the most folivorous of the three large-bodied adapids. Although no previous dietary estimation has been formulated for this taxon, this result would fit with previous comparisons to extant cercopithecids. *Adapis* and *Leptadapis* show more plasticity in their diet than *Cryptadapis*. Such a capacity could have conferred an advantage to cope with the harsher seasonal environments of the end of the Eocene. *Cryptadapis*, on the other hand, appears to be strictly folivorous, with a diet seemingly less variable than the two other large-bodied adapids. A less variable diet might imply a diminished capacity to cope in times of food shortage, such as might have occurred in the run-up to the Eocene–Oligocene transition. However, further investigations need to be carried out to investigate this hypothesis.

Gingerich, P.D. (1980). Dental and cranial adaptations in Eocene Adapidae. Zeitschrift für Morphologie und Anthropologie 71: 135-142.

Gingerich, P.D., Martin, R.D. (1981). Cranial morphology and adaptations in Eocene Adapidae. II. The Cambridge skull of *Adapis parisiensis*. American Journal of Physical Anthropology 56: 235-257.

Godinot, M. (1984). Un nouveau genre témoignant de la diversité des adapinés (Primates, Adapidae) à l'Eocène terminal. Comptes-rendus des séances de l'Académie des sciences. Série 2, Mécanique-physique, chimie, sciences de l'univers, sciences de la terre 299: 1291-1296.

Legendre, S. (1988). Les communautés de mammifères du Paléogène (Eocène supérieur et Oligocène) d'Europe occidentale: Structures, milieux et évolution. Dissertation, Université des Sciences et Techniques du Languedoc, Montpellier.

Merceron, G., Scott, J., Scott, R.S., Geraads, D., Spassov, N., Ungar, P.S. (2009). Folivory or fruit/seed predation for *Mesopithecus*, an earliest colobine from the Late Miocene of Eurasia? Journal of Human Evolution 57:732-738.

Perry, J.M.G. (2008). The Anatomy of Mastication in Extant Strepsirrhines and Eocene Adapines, Dissertation, Duke University, Durham.

Scott, R.S., Ungar, P.S., Bergstrom, T.S., Brown, C.A., Childs, B.E., Teaford, M.F., Walker, A. (2006). Dental microwear texture analysis: technical considerations. Journal of Human Evolution 51: 339-349.

Ungar, P.S., Merceron, G., Scott, R. (2007). Dental microwear texture analysis of Varswater bovids and early Pliocene paleoenvironments of Langebaanweg, Western Cape Province, South Africa. Journal of Mammalian Evolution 14: 163-181.

Eocene Chiroptera from Tunisia and Algeria: New insight into the early evolution of bats in North Africa

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From the Afro-Arabian Paleogene, quite all African bat fossils are limited to the northern regions of the continent and are essentially documented by dental remains and jaw fragments (Fig. 1; Sigé, 1985, 1991; Gunnell *et al.*, 2003, 2008; Tabuce, 2005; Eiting and Gunnell, 2009). A notable exception is the middle Eocene bat *Tanzanycteris mannardi* (Gunnell *et al.*, 2003) from Mahenge, Tanzania, known by a partial skeleton. Despite the fragmentary nature of the fossils, including primarily isolated teeth and jaw fragments, this bat record reveals that chiropterans were already well diversified in these regions by the early Paleogene. The oldest occurrence of the Chiroptera in Africa is documented in the middle early Eocene from El Kohol (Algeria; Ravel *et al.*, 2011). These specimens are the first primitive bats ("Eochiroptera") recorded in North Africa, although this group exhibits a widespread distribution including Europe, South Asia, North America, South America?, Tanzania and Australia (Gunnell and Simmons, 2005). Beyond these primitive bats, Afro-Arabian deposits have yielded the earliest representatives of extant microchiropteran families as early as the early Eocene (Fig. 1). For instance, the locality of Chambi (Tunisia) documents the late early Eocene Philisidae, *Dizzya exultans*, which is considered to be an archaic vespertilionoid, and an indeterminate rhinolophoid (Sigé, 1991). The Fayum deposits (late Eocene–early Oligocene, Egypt) yield Philisidae as well as modern bat families, among them Rhinopomatidae, Megadermatidae, Vespertilionidae and Emballonuridae (Sigé, 1985; Gunnell *et al.*, 2008). One bat tooth is reported in the middle Eocene of Aznag (Ouarzazate Basin, Morocco; Tabuce *et al.*, 2005), and is an indeterminate taxon. The Early Oligocene of Oman (Taqah) documents also Philisidae and modern families, including members of the Nycteridae, Hipposideridae and Emballonuridae (Sigé *et al.*, 1994).

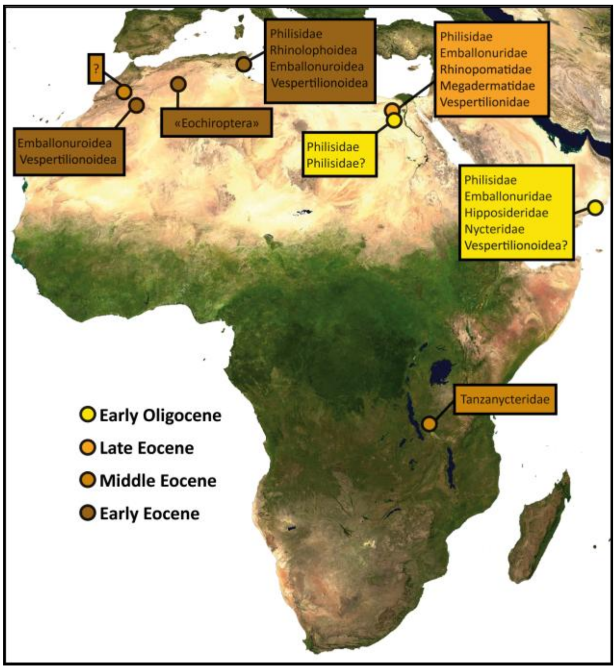

Figure 1. Paleogene bat fossil record in Africa and Arabia.

In the framework of the paleontological program PALASIAFRICA in the early Tertiary of Algeria and Tunisia, our yearly field seasons have yielded abundant new dental remains of Chiroptera. In Tunisia, our continuing field efforts in the vicinity of Chambi have led, after acid treatment of the indurate sediment of a new locality, about 500 isolated teeth of bats. This new bat fauna includes at least 5 new taxa of modern aspect (Fig. 1; Emballonuroidea, Rhinolophoidea and Vespertilionoidea). Among these new bat remains, a noticeably large upper molar attributable to the genus *Witwatia* (Chiroptera, Vespertilionoidea, Philisidae) has been found. This specimen represents a new species, which exhibits distinctive Philisidae characteristics. The tooth is similar in size and morphology to *W. schlosseri* and *W. eremicus,* which are the most common and the largest microbat fossils from the early late Eocene of Quarry BQ-2 in the Fayum (Egypt; Gunnell *et al.*, 2008). *Witwatia* nov. sp. represents the oldest occurrence of *Witwatia* in the African fossil record, thereby suggesting an early appearance of the large-sized microbats, probably during the early Eocene. Like the largest extant microbats, the large size of *Witwatia* suggests a tendency to the opportunistic diet of this taxon, thereby contrasting with the strict insectivory characterizing primitive bats found in other continents at the same epoch.

In Algeria, the middle member of the Glib Zegdou Formation in the Gour Lazib (late early or early middle Eocene; Adaci *et al.*, 2007) have produced about 50 isolated teeth of microbats. This material reveals three new taxa that belong to extant superfamilies (Fig. 1; Emballonuroidea and Vespertilionoidea). This new material includes also a distinctly large specimen (a lower molar), which could represent a new species of *Witwatia*. Indeed, this specimen displays a suite of dental features otherwise found only in *Witwatia* but also a submyotodont structure of the talonid, which is somewhat unusual for philisids, as it differs from the myotodonty of *Witwatia* (Gunnel *et al.*, 2008) and the nyctalodonty of Dizzya (Sigé, 1991). This new specimen testifies to the success of the large-sized philisids in North Africa during the Paleogene.

The new Eocene chiropterans from North Africa shed new light on the origin and the early radiation of modern bats in this part of the globe. Interestingly, all these African bat fossils were found in non-karstic Paleogene sites (fluvio-limnic deposits). This raises a critical question regarding the ecological behavior of the early bats, notably on the type of roosts (tree cavities, boles, furled leaves, etc.). All African Paleogene chiropterans, except the Algerian primitive bat from El Kohol, are representatives of extant superfamilies (Emballonuroidea, Rhinolophoidea and Vespertilionoidea), which include 5 extant families (Emballonuridae, Rhinopomatidae, Nycteridae, Megadermatidae and Vespertilionidae) and one extinct family (Philisidae). In other continents (Europe, Asia, North America), the modern microbats become gradually dominant during the Middle to the late Eocene, while the primitive "Eochiroptera" seem to disappear at the same epoch (Simmons, 2005; Gunnell and Simmons, 2005; Eiting and Gunnell, 2009). The current available fossil record of bats in North Africa suggests that a turnover could have occurred during the late early Eocene. The early explosion of extant families in North Africa challenges the hypothesis of a Laurasian origin for these bats (Teeling, 2005). In contrast, Sigé (1991) suggested a southern (Gondawanian) origin for modern bats, a hypothesis which is now strongly supported by the new fossil evidence. Unfortunately, the understanding of the origin and pattern of dispersal of early bats remain a delicate subject of discussion given their ability of dispersion (by flight), and because of both the incompleteness and scarcity of the earliest bats, notably in Africa.

Eiting, T.P., Gunnell, G.F. (2009). Global completeness of bat fossil record. Journal of Mammalian Evolution 16: 151-173.

Gunnell, G.F., Jacobs, B.F., Herendeen, P.S., Head, J.J., Kowalski, E., Msuya, C.P., Mizambwa, F.A., Harrison, T., Habersetzer, J., Storch, G. (2003). Oldest placental mammal from sub-Saharan Africa: Eocene microbat from Tanzania - Evidence for early evolution of sophisticated echolocation. Palaeontologica Electronica 5(3): 1-10.

Gunnell, G.F., Simmons N.B. (2005). Fossil evidence and the origin of bats. Journal of Mammalian Evolution, 12: 209-246.

Gunnell, G.F., Simons, E.L., Seiffert, E.R. (2008). New bats (Mammalia: Chiroptera) from the Late Eocene and Early Oligocene, Fayum Depression, Egypt. Journal of Vertebrate Paleontology 28(1): 1-11.

Ravel, A., Marivaux, L., Tabuce, R., Adaci, M., Mahboubi, M., Mebrouk, F., Bensalah, M. (2011). The oldest African bat from the Early Eocene of El Kohol (Algeria). Naturwissenschaften 28 (5): 397-405.

Sigé, B. (1985). Les chiroptères oligocènes du Fayum, Egypte. Geologica et Palaeontologica 19: 161-189.

Sigé, B. (1991). Rhinolophoidea et Vespertilionoidea (Chiroptera) du Chambi (Eocène inférieur de Tunisie). Aspect biostratigraphique, biogéographique et paléoécologique de l'origine des chiroptères modernes. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 182(3): 355-376.

Sigé, B., Thomas, H., Sen, S., Gheerbrant, E., Roger, J., Al-Sulaimani, Z. (1994). Les chiroptères de Taqah (Oligocène inférieur, Sultanat d'Oman). Premier inventaire systématique. Münchner Geowissenschaftliche Abhandlungen 26(A): 35-48.

Simmons, N.B. (2005). Chiroptera. In: Rose, K.D., Archibald, J.D. (eds) The rise of placental mammals: origins and relationships of the major extant clades. The Johns Hopkins University Press Baltimore, Maryland, Volume Chapter 11, pp 159-173.

Tabuce, R., Adnet, S., Cappetta, H., Noubhani, A., Quillevere F. (2005). Aznag (bassin d'Ouarzazate, Maroc), nouvelle localité à sélaciens et mammifères de l'Eocène moyen (Lutétien) d'Afrique. Bulletin de la Société Géologique de France 176(4): 381-400.

Teeling, E.C., Springer, M.S., Madsen, O., Bates, P., O'brien, J.S., Murphy, W.J. (2005). A molecular phylogeny for bats illuminates biogeography and the fossil record. Science 307: 580-584.

The edge of the sea at the time of Messel: Mangroves and related coastal wetlands in the Eocene of the Helmstedt mining district

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Lake Messel was situated in the centre of a large Central European island, and the plant remains of the early middle Eocene at Messel represent a primeval paratropical forest closely surrounding an inland lake. The fossiliferous oil shale deposited in the lake opens a window into the greenhouse world of the middle Eocene restricted to a few hundred thousand years. In contrast, an almost continuous section covering about 10 million years of the early to middle Eocene has been exposed by lignite mining in the vicinity of Helmstedt, less than 400 km north of Messel. Throughout this time the area was situated near the mouth of a broad estuary at the southern shore of the North Sea Basin and exposed to changing sea levels, varying sediment transport, and subsidence due to subsurface salt migration. Thus, the section is composed of alternating marine and terrestrial sediments showing considerable variations in environments transitional between land and sea, thus allowing the development of coastal plant communities and environments to be traced through time.

Since macroscopic remains of plants are rare and calcareous shells and bones are not preserved, the reconstruction of palaeovegetation and palaeoenvironments focussed on palynological and sedimentological information, including trace fossils.

The younger parts of the section, which most probably are early middle Eocene in age, revealed repeated evidence of true mangrove communities, including genera such as *Rhizophora*, *Avicennia* and *Nypa* (Lenz, 2005) (Fig. 1). High-resolution studies of pollen even show a characteristic succession of mangrove elements with decreasing marine influence closely comparable to those existing in the Indo-Pacific region today. The approximately contemporaneous coexistence of mangrove communities at

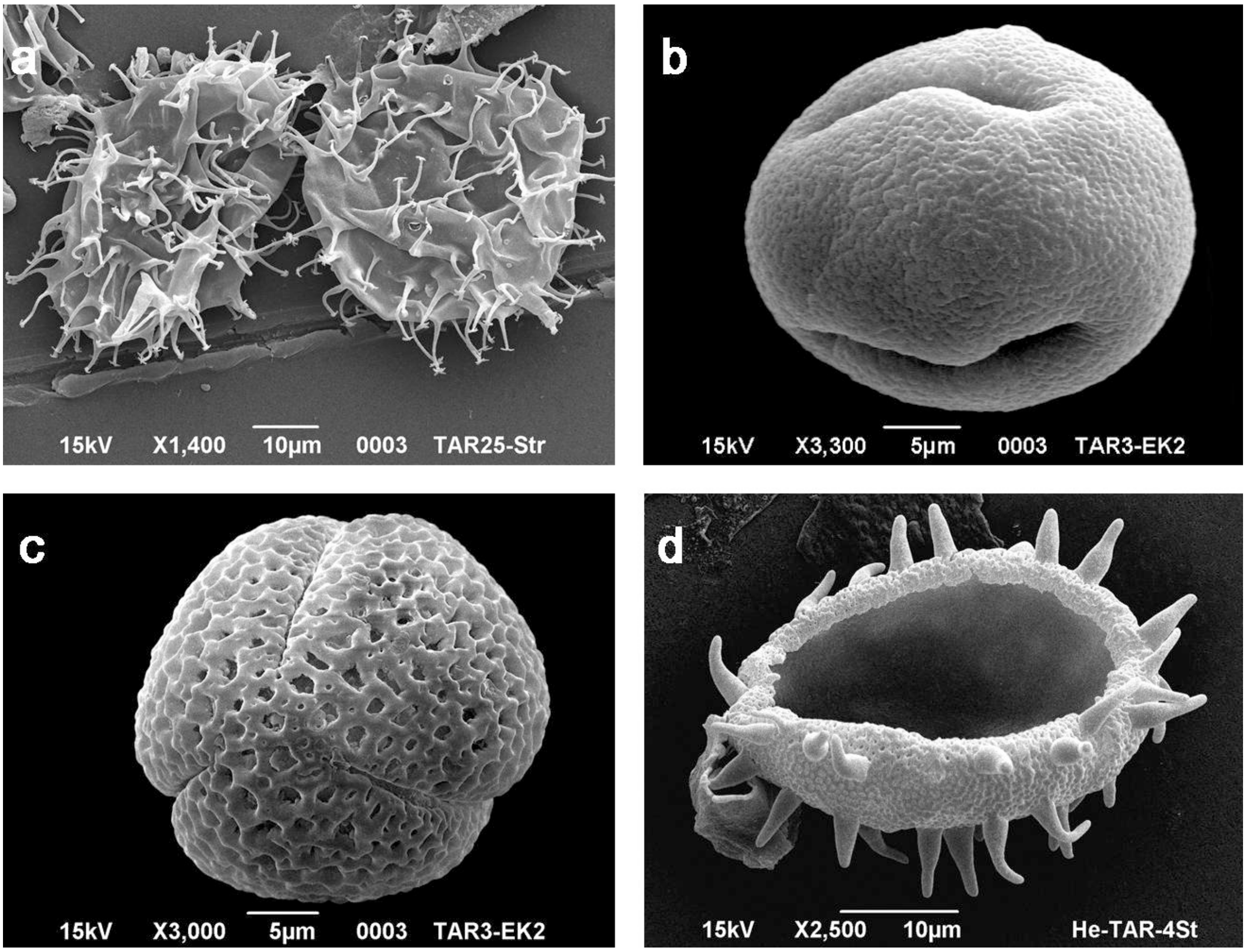

Figure 1. Phytoplankton and mangrove pollen from the middle Eocene of the Helmstedt mining district: a) cysts of dinoflagellates, *Apectodinium* sp., b) pollen of Red Mangrove, *Rhizophora*, c) pollen of Black Mangrove, *Avicennia*, d) pollen of *Nypa*.

Helmstedt and a paratropical rain forest around Lake Messel supports the predominance of a persistent equable warm and humid climate for that time.

In contrast to the middle Eocene, pollen of true mangroves are strikingly rare to even absent throughout the early Eocene portion of the Helmstedt sections, and a distinctly zoned mangrove fringe cannot be identified there. Instead, marine/terrestrial transitions are frequently accompanied by unique successions, such as a distinctive *Thomsonipollis-Pistillipollenites* assemblage possibly representing an ecotone substituting the typical mangrove under alternative climatic and hydrodynamic conditions. That climate played a significant role is indicated by the evidence of fundamentally different fire regimes in the early and the middle Eocene at Helmstedt (Riegel *et al.*, 2000).

Apart from mangroves and mangrove substitutes the Eocene sections at Helmstedt include additional rare and exceptional examples of coastal plant communities. For instance, seagrass meadows of considerable extent have been observed in situ in sands beneath one of the seams. They document a shallow marine environment and show evidence of sediment fixation comparable to recent situations. Thin coal seams rich in *Sphagnum* remains and charcoal are sandwiched between tidal and intensively bioturbated clastic sediments and suggest the existence of ombrogenous herbaceous peat mires at sea level and high frequency of alternating wet and dry conditions. Near the early to middle Eocene transition numerous succeeding horizons of palm tree stumps still rooted in well-sorted white sands are vivid reminders of palm-fringed tropical or subtropical beaches that once bordered the shores of the North Sea. The diversity and abundance of marine phytoplankton and the proportion of freshwater phytoplankton in the clastic interbeds provide a measure of salinity to which these coastal wetlands were exposed and adapted.

Thus, the manifold repetition of marine/terrestrial transitions exposed in the mines of the Helmstedt district offer a unique opportunity to study the development of coastal wetlands under varying environmental conditions and through an extended greenhouse period which encompasses the time of Messel.

LENZ, O.K. (2005). Palynologie und Paläoökologie eines Küstenmoores aus dem Mittlere Eozän Mitteleuropas — Die Wulfersdorfer Flözgruppe aus dem Tagebau Helmstedt, Niedersachsen. Palaeontographica B 271: 1-157.

RIEGEL, W., BODE, T., HAMMER, J., HAMMER-SCHIEMANN, G., LENZ, O., WILDE, V. (2000). The paleoecology of the Lower and Middle Eocene at Helmstedt, Northern Germany - A study in contrasts. Acta Palaeobotanica Supplementum, 2 (for 1999): 349-358, 7 Abb.

Importance of Messel for interpreting Eocene Holarctic mammalian faunas

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The Messel Pit Fossil Site has produced an extraordinary vertebrate fauna of 132 species, including at least 44 species of mammals in 31 genera (Morlo *et al.*, 2004). Virtually all of the mammalian species are represented by complete or nearly complete articulated skeletons, providing a unique window on the anatomical structure and paleobiology of Eocene mammals. No other site in the world has provided such an extensive and diverse database of Eocene mammal skeletons. The penecontemporaneous coals of Geiseltal near Halle have produced some specimens comparable to those from Messel (e.g., Thalmann, 1994; Erfurt, 2000), but skeletons are less numerous and the Geiseltal fauna is much less well documented.

Similar preservation to that at Messel is known outside of Europe from the late Wasatchian Fossil Butte Member of the Green River Formation in southwestern Wyoming, but only a small number of mammalian taxa and skeletons are known (eight species, most of which are represented by only one or two specimens; e.g., Koenigwald *et al.*, 2005*a*; Rose and Koenigswald, 2005; Simmons *et al.*, 2008; Grande, in press). Nevertheless, at least half of the Green River taxa have close relatives at Messel, prompting comparisons. The late early-middle Eocene Bridger Formation of Wyoming, approximately coeval with Messel, has produced a large and diverse mammalian fauna, with relatively complete skeletal material known for many genera (e.g., Matthew, 1909; Gregory, 1920; Simpson, 1931; Gunnell and Gingerich, 1993). Here, too, many genera are closely related to Messel taxa. The Willwood Formation of the Bighorn Basin, Wyoming, spanning nearly all of the Wasatchian, has produced the largest and most diverse samples of early Eocene mammals from anywhere. The close faunal similarity to early Eocene European mammal faunas has long been known (e.g., McKenna, 1975). As McKenna noted, the North Atlantic connection between North America and Europe was disrupted by the end of the early Eocene; consequently, one might expect the resemblance between Willwood and Messel faunas to be as great as, or greater than, that between Bridger and Messel faunas. Nearly half of all Messel genera have closely related counterparts from the Willwood and Bridger formations.

Eocene Asian faunas generally show less similarity to the Messel fauna, probably because the Obik Sea and Turgai Strait presented a formidable barrier to dispersal between Europe and Asia. Even so, at least a quarter of Messel genera have close relatives in the recently discovered early Eocene Vastan local fauna from Gujarat, India (e.g., Rose *et al.*, 2006), indicating that some degree of faunal exchange between India and western Europe took place in the

Figure 1. Apatemyids: A. *Heterohyus nanus* from Messel; B. *Apatemys chardini* from Fossil Butte; both to same scale. Inset compares manual digit lengths.

early or middle Eocene. Surprisingly, the Vastan fauna shows closer resemblance to contemporaneous western European and North American faunas than it does to those from Asia (e.g., Rana *et al.*, 2008; Kumar *et al.*, 2010).

The diversity of mammals at Messel, belonging to 13 different orders, allows broad comparisons with close relatives from other faunas. For many Eocene taxa the Messel fossils provide the best or only view of the complete animal (e.g., *Macrocranion*, various rodents, marsupials). In other cases Messel skeletons offer important insight into variation within genera or families (e.g., apatemyids, artiodactyls, leptictidans, pantolestids), or provide critical stages for understanding evolutionary transitions (Pholidota, Euprimates). I review here the role of certain Messel taxa in our understanding of other important Eocene faunas.

Bats are by far the most common mammals at Messel, but they are rare in most other Eocene deposits, most species being represented by only jaws or isolated teeth. Skeletons of related bats are known from the Fossil Butte Member (e.g., Simmons and Geisler, 1998; Simmons *et al.*, 2008). The most diverse early Eocene bat fauna, consisting of jaws, teeth, and isolated bones, unexpectedly comes from Vastan and includes two genera in common with Messel and several other closely related taxa (Smith *et al.*, 2007). Knowledge of the paleoecology of Messel bats (e.g., Habersetzer and Storch, 1989) enhances our understanding of these early bat assemblages.

The two genera of marsupials from Messel show that the herpetotheriid *Amphiperatherium* was more terrestrial than the arboreally adapted “*Peradectes*” (Koenigswald and Storch, 1992; Kurz, 2001). This ecomorphological distinction has allowed tentative allocation of isolated tarsals from the Willwood Formation to *Herpetotherium* and *Peradectes*. Similarly, complete skeletons of the amphilemurid eulipotyphlan *Macrocranion* (e.g., Storch, 1993) have enabled identification of very similar isolated elements from Willwood quarry samples in which *Macrocranion* is common. One of Messel’s most curious denizens was the leptictidan *Leptictidium*, whose three species are characterized by elongate hind limbs and very short forelimbs (e.g., Storch and Lister, 1985). Dentally, and in many postcranial aspects (but not the separate tibia and fibula), *Leptictidium* is more derived than any leptictid. But all Eocene and Oligocene leptictids had a fused tibia-fibula and longer metatarsals than in *Leptictidium* (Rose, 1999*a*). Moreover, the tibia and fibula are already fused in the oldest known Paleocene leptictids, indicating that *Leptictidium* must have diverged from leptictids not later than the early Paleocene (Rose, 2006).

Two obscure groups now usually considered to be cimolestan derivatives or placed in their own orders — apatemyids and pantolestids — are known from exquisite skeletons from both Messel and the Fossil Butte Member (e.g., Koenigswald *et al.*, 2005*b*). In these examples of closely allied genera, we have the opportunity to examine intrafamilial anatomical diversity at levels of detail rarely possible. Both *Heterohyus* from Messel and *Apatemys* from Fossil Butte possess arboreally adapted skeletons with an unusually specialized manus: the central digits are disproportionately long, as in extant *Daubentonia* and *Dactylopsila* — an adaptation for probing for wood-boring insects (Koenigswald, 1990; Koenigswald *et al.*, 2005*a*). But in both apatemyids the elongate digits are the second and third, not the third and fourth as in the two unrelated living taxa, and they are distinctly longer in *Heterohyus* than in *Apatemys* (Fig. 1). Thus we can infer that apatemyids preyed on wood-boring insects long before *Daubentonia* did, but in a similar manner, and that *Heterohyus* was more specialized for this role than was *Apatemys*. Quite a different niche was occupied by the otter-like

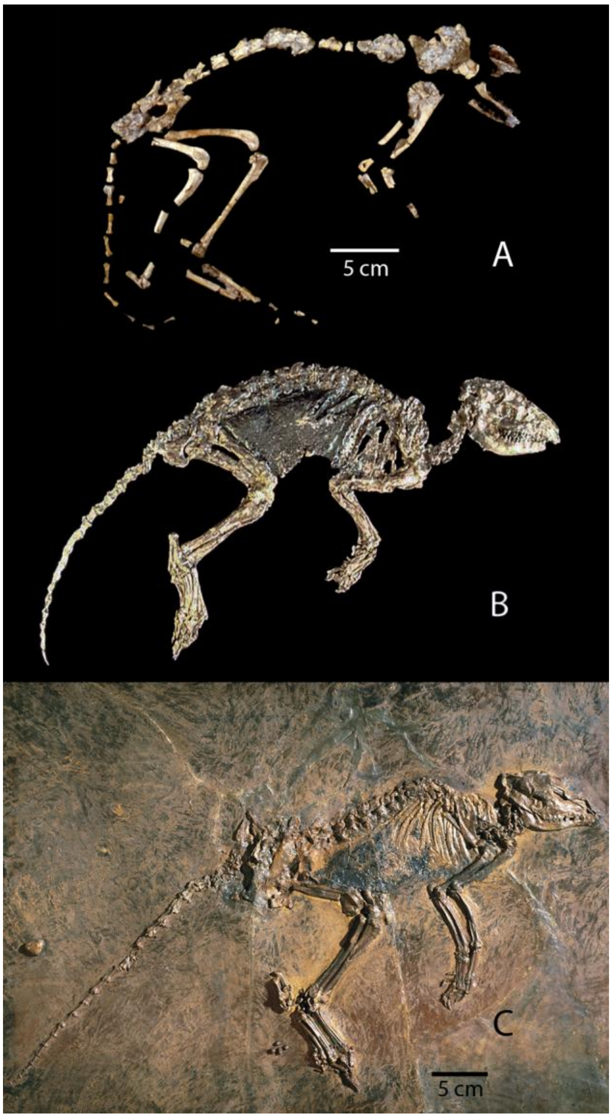

Figure 2. Dichobunoid artiodactyls: A. *Diacodexis metsiacus* from the Willwood Formation; B. *Aumelasia* cf. *gabineaudi* from Messel; C. *Messelobunodon schaeferi* from Messel. A and B to same scale.

pantolestids *Buxolestes* (Messel), *Palaeosinopa* (Fossil Butte and Willwood), and *Pantolestes* (Bridger). All show very similar adaptations for semiaquatic and semifossorial habits, and they differ in few features except for the longer tail in *Palaeosinopa* (Rose and Koenigswald, 2005), underscoring their close relationship. Skeletons of both *Buxolestes* and *Palaeosinopa* even contain fish remains in the abdomen.

The dichobunoid artiodactyls *Messelobunodon* and *Aumelasia* are very similar in postcranial anatomy to early Eocene *Diacodexis* (Fig. 2), the oldest known artiodactyl (Franzen, 1983, 1988; Rose, 1985). All have a rabbit-like, cursorially specialized skeleton with relatively short forelimbs, long hind limbs, and especially long distal segments. Both *Messelobunodon* and *Diacodexis* are plesiomorphic in retaining a femoral third trochanter, lost in nearly all other artiodactyls. Nevertheless, like virtually all other early and middle Eocene artiodactyls, they resemble primitive ruminants postcranially more than they do other artiodactyls, suggesting either that they have a special relationship to ruminants or that small size may have constrained basal artiodactyls to this bauplan. *Diacodexis* was a widespread Holarctic genus, and recently discovered remains from the early Eocene of India show the same postcranial features as in North American *Diacodexis* and *Messelobunodon* (Kumar *et al.*, 2010).

The adapoid primates from Messel, particularly *Europolemur*, bear striking similarities to North American *Notharctus* and *Smilodectes* (Bridger) and *Cantius* (Willwood). The Messel primates are discussed by Gingerich (2011).

The last example included here is the basal pholidotan *Eomanis*, now known from several skeletons from Messel (Storch, 1978, 2003). Numerous features now inextricably tie *Eomanis* to later pholidotans, such as North American late Eocene *Patriomanis* (e.g., Emry, 2004). At the same time, other traits — one in the dentary and several in the postcranial skeleton — afford strong evidence that *Eomanis*, and likely *Eurotamandua* as well, are closely allied with (and probably derived from) palaeanodonts (e.g., Rose, 1999*b*; Gaudin *et al.*, 2009). The fossorially adapted skeletons of *Palaeanodon* (Willwood), *Metacheiromys* (Bridger), *Eomanis*, and *Eurotamandua* share numerous derived features of the forelimb, in particular, that are similar in detail and unlike those of other fossorial mammals. Thus *Eomanis* provides a critical link between metacheiromyid palaeanodonts and later undoubted pholidotans.

By virtue of their exceptional preservation and completeness, the Messel mammals paint an unusually vivid picture of mammalian paleobiology in central Europe during the Lutetian. Equally important, they provide unique insights into the anatomy, paleobiology, and phylogenetic relationships of related taxa from elsewhere in Laurasia during a critical period in the history of mammals.

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EMRY, R.J. (2004). The edentulous skull of the North American pangolin, *Patriomanis americanus*. Bulletin of the American Museum of Natural History 285: 130-138.

ERFURT, J. (2000). Rekonstruktion des Skelettes und der Biologie von *Anthracobunodon weigelti* (Artiodactyla, Mammalia) aus dem Eozän des Geiseltales. Hallesches Jahrbuch für Geowissenschaften, Reihe B (12): 57-141.

FRANZEN, J.L. (1983). Ein zweites Skelett von *Messelobunodon* (Mammalia, Artiodactyla, Dichobunidae) aus der "Grube Messel" bei Darmstadt (Deutschland, S-Hessen). Senckenbergiana lethaea 64: 403-445.

FRANZEN, J.L. (1988). Skeletons of *Aumelasia* (Mammalia, Artiodactyla, Dichobunidae) from Messel (M. Eocene, W. Germany). Courier Forschungsinstitut Senckenberg 107: 309-321.

GAUDIN, T.J., EMRY, R.J., WIBLE, J.R. (2009). The phylogeny of living and extinct pangolins (Mammalia, Pholidota) and associated taxa: A morphology based analysis. Journal of Mammalian Evolution 16: 235-305.

GINGERICH, P.D. (2011). Primates in the Eocene. In: Lehmann, T., Schaal, S.F.K. (eds) The World at the Time of Messel: Puzzles in Palaeobiology, Palaeoenvironment, and the History of Early Primates. 22nd International Senckenberg Conference. 15th – 19th November 2011, Frankfurt am Main. Conference Volume. Senckenberg Gesellschaft für Naturforschung, Frankfurt am Main. pp. 67-68.

GRANDE, L. (in press). Snapshots from Deep Time: The 52 Million-Year-Old Community of Fossil Lake, Locked in Stone. University of Chicago Press, Chicago.

GREGORY, W.K. (1920). On the structure and relations of *Notharctus*, an American Eocene primate. Memoirs of the American Museum of Natural History 3: 49-243.

GUNNELL, G.F., GINGERICH, P.D. (1993). Skeleton of *Brachianodon westorum*, a new middle Eocene metacheiromyid (Mammalia, Palaeanodonta) from the early Bridgerian (Bridger A) of the southern Green River Basin, Wyoming. Contributions from the Museum of Paleontology, The University of Michigan 28: 365-392.

HABERSETZER, J., STORCH, G. (1989). Ecology and echolocation of the Eocene Messel bats. In: Hanak, V., Horacek, I., Gaisler, J. (eds) European Bat Research 1987. Charles University Press, Praha, pp 213-233.

KOENIGSWALD, W.V. (1990). Die Paläobiologie der Apatemyiden (Insectivora s.l.) und die Ausdeutung der Skelettfunde von *Heterohyus nanus* aus dem Mitteleozän von Messel bei Darmstadt. Palaeontographica Abteilung A, 210:41-77.

Koenigswald, W.v., Rose, K.D., Grande, L., Martin, R.D. (2005*a*). First apatemyid skeleton from the lower Eocene Fossil Butte Member, Wyoming, compared to the European apatemyid from Messel. Palaeontographica Abteilung A 272: 149-169.

Koenigswald, W.v., Rose, K.D., Grande, L., Martin, R.D. (2005*b*). Die Lebensweise eozäner Säugetiere (Pantolestidae und Apatemyidae) aus Messel (Europa) im Vergleich zu neuen Skelettfunden aus dem Fossil Butte Member von Wyoming (Nordamerika). Geologisches Jahrbuch Hessen 132: 43-54.

Koenigswald, W.v., Storch, G. (1992). The marsupials: Inconspicuous opossums. In: Schaal, S., Ziegler, W. (eds) Messel – An Insight into the History of Life and of the Earth. Clarendon Press, Oxford, pp 155-158.

Kumar, K., Rose, K.D., Rana, R.S., Singh, L., Smith, T., Sahni, A. (2010). Early Eocene artiodactyls (Mammalia) from western India. Journal of Vertebrate Paleontology 30: 1245-1274.

Kurz, C. (2001). Osteologie einer Beutelratte (Didelphimorphia, Marsupialia, Mammalia) aus dem Mitteleozän der Grube Messel bei Darmstadt. Kaupia – Darmstädter Beiträge zur Naturgeschichte 11:83-109.

Matthew, W.D. (1909). The Carnivora and Insectivora of the Bridger Basin, Middle Eocene. Memoirs of the American Museum of Natural History 9: 291-567.

McKenna, M.C. (1975). Fossil mammals and early Eocene North Atlantic land continuity. Annals of the Missouri Botanical Garden 62: 335-353.

Morlo, M., Schaal, S., Mayr, G., Seiffert, C. (2004). An annotated taxonomic list of the Middle Eocene (MP 11) Vertebrata of Messel. Courier Forschungsinstitut Senckenberg 252: 95-108.

Rana, R.S., Kumar, K., Escarguel, G., Sahni, A., Rose, K.D., Smith, T., Singh, H., Singh, L. (2008). An ailuravine rodent from the lower Eocene Cambay Formation at Vastan, western India, and its palaeobiogeographic implications. Acta Palaeontologica Polonica 53(1): 1-14.

Rose, K.D. (1985). Comparative osteology of North American dichobunid artiodactyls. Journal of Paleontology 59(5): 1203-1226.

Rose, K.D. (1999*a*). Postcranial skeleton of Eocene Leptictidae (Mammalia), and its implications for behavior and relationships. Journal of Vertebrate Paleontology 19(2): 355-372.

Rose, K.D. (1999*b*). *Eurotamandua* and Palaeanodonta: convergent or related? Paläontologische Zeitschrift 73: 395-401.

Rose, K.D. (2006). The postcranial skeleton of early Oligocene *Leptictis* (Mammalia: Leptictida), with a preliminary comparison to *Leptictidium* from the middle Eocene of Messel. Palaeontographica Abteilung A, 278: 37-56.

Rose, K.D., Koenigswald, W.v. (2005). An exceptionally complete skeleton of *Palaeosinopa* (Mammalia, Cimolesta, Pantolestidae) from the Green River Formation, and other postcranial elements of the Pantolestidae from the Eocene of Wyoming. Palaeontographica Abteilung A 273: 55-96.

Rose, K.D., Smith, T., Rana, R.S., Sahni, A., Singh, H., Missiaen, P., Folie, A. (2006). Early Eocene (Ypresian) continental vertebrate assemblage from India, with description of a new anthracobunid (Mammalia, Tethytheria). Journal of Vertebrate Paleontology 26: 219-225.

Simmons, N.B., Geisler, J.H. (1998). Phylogenetic relationships of *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* to extant bat lineages, with comments on the evolution of echolocation and foraging strategies in Microchiroptera. Bulletin of the American Museum of Natural History 235: 1-182.

Simmons, N.B., Seymour, K.L., Habersetzer, J., Gunnell, G.F. (2008). Primitive early Eocene bat from Wyoming and the evolution of flight and echolocation. Nature 451: 818-821.

Simpson, G.G. (1931). *Metacheiromys* and the Edentata. Bulletin of the American Museum of Natural History 59: 295-381.

Smith, T., Rana, R.S., Missiaen, P., Rose, K.D., Sahni, A., Singh, H., Singh, L. (2007). High bat (Chiroptera) diversity in the Early Eocene of India. Naturwissenschaften 94(12): 1003-1009.

Storch, G. (1978). *Eomanis waldi*, ein Schuppentier aus dem Mittel-Eozan der “Grube messel” bei Darmstadt. Senckenbergiana lethaea 59: 503-529.

Storch, G. (1993). Morphologie und Paläobiologie von *Macrocranion tenerum*, einem Erinaceomorphen aus dem Mittel-Eozän von Messel bei Darmstadt (Mammalia, Lipotyphla). Senckenbergiana Lethaea 73:61-81.

Storch, G. (2003). Fossil Old World “edentates”. Senckenbergiana Biologica 83: 51-60.

Storch, G., Lister, A.M. (1985). *Leptictidium nasutum*, ein Pseudorhyncocyonide aus dem Eozän der “Grube Messel” bei Darmstadt (Mammalia, Proteutheria). Senckenbergiana Lethaea 66:1-37.

Thalmann, U. (1994). Die Primaten aus dem eozänen Geiseltal bei Halle/Saale (Deutschland). Courier Forschungsinstitut Senckenberg 175: 1-161.

Functional morphology, fossils and the origins of the tarsier and anthropoid lineages

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Identifying the origins of tarsiers has been one of the more vexing and controversial problems for systematists, and it has equally plagued discussions of anthropoid origins. The alternative views of current schools of thought are well known: 1) *Tarsius* is the sister-taxon of Anthropoidea; 2) *Tarsius* is a divergent relic of indeterminate affinities within the paraphyletic Tarsiiformes or Omomyoidea, the taxonomic group considered most likely to include the ancestral stock of anthropoids; 3) *Tarsius* is part of a clade of genera currently classified within the Tarsiiformes. Hypothesis #1 (the tarsier-anthropoid hypothesis), receives its support from neontological studies of the cranium; from parsimony-based studies of living and extinct primates involving supermatrices of characters and taxa; and, from arguing that contravening similarities shared by *Tarsius* and fossil tarsiiforms are either primitive or convergent. Hypothesis #2 has limited standing as a testable proposition, although its underlying arguments merit consideration. It asserts the position of *Tarsius* among tarsiiforms is unknowable because it is so highly modified and possible links are unacceptable for any number of reasons – no fossils are transformationally appropriate in a morphoclinal sense; others are autapomorphous, thus removed from possible ancestry; others are plesiomorphic or homoplasious; no synapomorphies are present. Hypothesis #3 (the necrolemur-tarsier hypothesis) relies on similarities shared by tarsiers and some fossil tarsiiforms proposed as synapomorphies. Advocates reject Hypothesis #1, interpreting its supporting anatomical evidence as analogies or ambiguous similarities of questionable phenetic and cladistic merit, and by challenging the credibility and phyletic valence of the parsimony-based results. The resolution of these controversies has consequences for the interrelationships of tarsiers and anthropoids and for reconstruction of the morphotype conditions of euprimate higher taxa, which influences how Eocene fossils lacking surefire cranial information are interpreted with regard to the anthropoid origins.

A new functional morphology model proposes a two-step evolutionary scenario to explain the extremely modified tarsier head (Rosenberger, 2010). It begins with the evolution of enormous eyes, followed by selection for a new mid-cranial head carriage system designed to support a cranium that is eccentrically loaded by massive, rostrally positioned eyeballs. In conjunction, a radical form of vertical-clinging-and-leaping (VCL) positional behaviors evolves to complement cranial biomechanics and facilitate an adaptive shift from pursuit hunting to ambush predation. The cranial correlates of this system involve an extensive pattern of derived, integrated features in the face, neurocranium and basicranium, such as the quasi-postorbital plate, flared orbital margins, huge orbital floor, development of extensive maxillary paralveolar shelving, compressed nasal capsule, uptilted basicranial axis, rounded neurocranium, rostrally shifted and enlarged foramen magnum, laterally displaced otic capsule, and abbreviation of the external auditory meatus. This model can be applied in a character analysis to test hypotheses concerning the homologies and polarities of features associated with each of the proposals concerning tarsier origins, and the weights we might ascribe to character of consequence.

Nearly ten genera of Eocene tarsiiforms that preserve relevant anatomy, spanning North America and Europe and displaying varied dental and postcranial morphologies, exhibit parts of this complex, often in combination and in exquisitely similar patterns (Rosenberger, 2011). Apparently, all had large to hypertrophic eyeballs, but none suggest a configuration achieved by an alternate paradaptive pathway, i.e., convergently. Forms such as *Shoshonius* present a mosaic: facial features align with tarsiers while neuro- and basi-cranial features remain primitive, indicating the advanced head carriage and VCL elements were not yet developed, as is confirmed by the postcranial skeleton. Others, such as *Strigorhysis* (Fig. 1–2), suggest that eyeball size for some fossil tarsiiforms was probably in the range of a modern tarsier's, in this case *Tarsius pumilus*. These and other large-eyed fossils comprise a clade of small to tiny nocturnal predators, with galago- and tarsier-like locomotor repertoires, all referable to a monophyletic Family Tarsiidae characterized by the large-eyed syndrome, at a minimum. The existence of this group calls for a second look at the systematics of several small-eyed forms frequently allocated to the "omomyids," such as *Teilhardina* and *Rooneyia* (here regarded as non-tarsiiform), and even the eponymous *Omomys*.

Reconsideration of the cranial features supporting the tarsier-anthropoid hypothesis suggests some are unlikely to be valid phenetic resemblances with homology implications – they are "verbal characters" – while others are homoplastic at best. Purported anthropoid synapomorphies in auditory bulla morphology, such as the "perbullar" pathway of the carotid artery and the "anterior accessory cavity," can be stated only as resemblances if one accepts an unreasonably coarse similarity criterion. In other words, these morphologies have evolved independently in

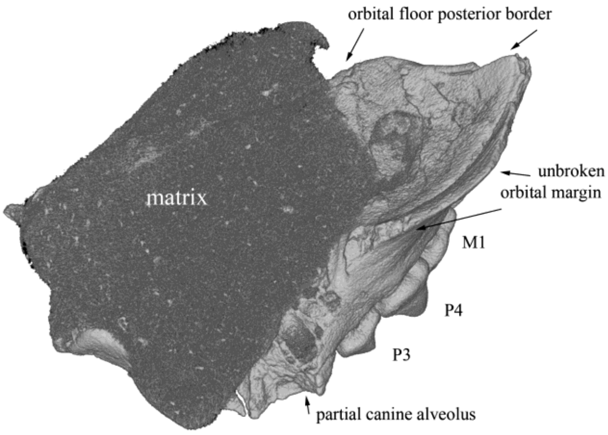

Figure 1. Three-quarters view into the orbital floor of *Strigorhysis*.

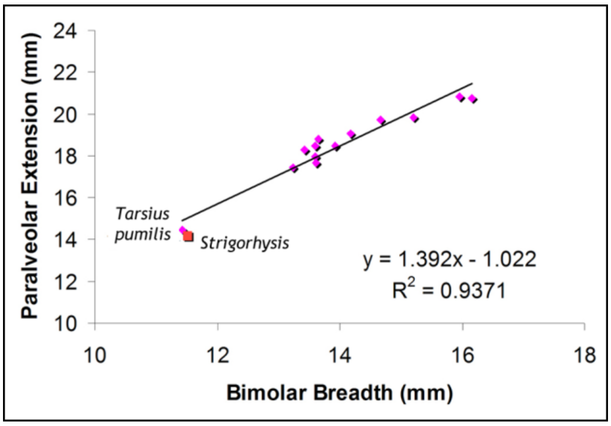

Figure 2. *Strigorhysis* orbital floor proportions compares with *Tarsius pumilus*.

Tarsius and are not part of a tarsier-anthropoid morphocline. They represent different features or character states. Both are more likely to be autapomorphic corollaries associated with a reshaping of the basicranium under selection for a new head carriage, rather than abstract morphotype conditions that might potentially evolve into anthropoid anatomy. The *Rooneyia* bulla, for example, is a much better phenetic match and structural model for a pre-anthropoid ear region than the bulla of *Tarsius* or any fossil tarsiiform. The conformation of the postorbitum in tarsiers and anthropoids is also a mismatch. Anthropoids, for functional reasons still unclear, close the orbital fossa by enlarging the zygomatic and recessing the eyeballs below an enlarged, roofing frontal bone. Tarsiers leave the fossa open, but flare the postorbital bar/zygomatic, as well as the frontal and maxilla, to accommodate the ectopic, rostrad eyeballs. Its postorbital plate is a slave to eyeball hypertrophy, as is the entire orbital surround. The plate's role as a partition to insulate the eye from temporalis contractions is probably secondary.

This line of functional analytical reasoning challenges use of these same features in the numerical cladistic studies, and this extends to the large number of dental characters employed as well. Included in these matrices are serial homologues treated as separate characters, characters that co-vary and are non-independent, traits of micro- not macro-evolutionary relevance, etc. When analyzed in concert, they reduce the cladistic component of the analysis and exaggerate its phenetic power. The frequently conforming branching sequences evident in these studies does not provide independent validation of any of the hypotheses therein, as they are based essentially on the same data matrices and employ the same methods. This is not to say they are irrelevant. Only that they are best seen as heuristic models of possible affinities built with a mixture of cladistic and phenetic information, with some nodes being more cladistic than others.

The highly derived cranial morphology of *Tarsius* is an abundant reservoir of high-weight traits whose polarities are clear owing to their functional integration into one of the most radical ecophylogenetic syndromes of the Order Primates. This phenomenon simplifies homology recognition when surveying fossils with potential significance for tarsier and anthropoid origins. The novelty and success of the tarsier adaptive zone, its ancient roots, the geographical dispersion of fossils that are potentially if not actually close relatives – all these are clues that the lineage must have experienced a major adaptive radiation within an insectivore-frugivore sphere of which *Tarsius* is but one genus. Unraveling this evolutionary history would be a major accomplishment. And, if the cranial morphology can help us navigate the more plentiful and hard-to-sort dental and postcranial anatomy of Eocene haplorhines, perhaps we can cleave away more of the tarsiids and thus isolate those nearer to the ancestry of Anthropoidea and/or Euprimates.

ROSENBERGER, A.L. (2010). The skull of *Tarsius*: Functional morphology, eyeballs, and the nonpursuit predatory lifestyle. International Journal of Primatology 31: 1032–1054.

ROSENBERGER, A.L. (2011). *Strigorhysis*: Another large-eyed Eocene North American fossil tarsiiform. Anatomical Record DOI: 10.1002/ar.21367.

New Ascomycota from Eocene forests and their interactions with plants and arthropods

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Fungi are essential components of all terrestrial ecosystems. However, their delicate and ephemeral structures are only rarely preserved as fossils. Yet ambers and fine-grained sediments occasionally contain fossil Eocene fungi in excellent condition. In the last decade, several new ascomycetes were recovered from Eocene ambers, and also from the sediments of the Eckfeld Maar. This talk reviews recent discoveries of fossil Ascomycota, which have provided new insights into interactions of Eocene fungi with both plants and arthropods.

(1) *MYCORRHIZAL FUNGI*.
The Lower Eocene amber from Gujarat (western India) preserves the first known ectomycorrhizae associated with an angiosperm (Fig. 1). Different developmental stages of the fossil mycorrhizae are delicately preserved in the ancient resin. The mycobiont is considered to be an anamorphic ascomycete, and the phytobiont is likely a representative of the amber-producing Dipterocarpaceae. Ectomycorrhizae may have conferred an evolutionary advantage on dipterocarps, allowing them to become the prevalent overstory trees in India, from whence they spread into South East Asia, where they are still predominant today. The amber fossils reveal that ectomycorrhizae occurred in early tropical broadleaf forests by the Lower Eocene.

(2) *EPIPHYTIC FUNGI*.
Sooty moulds are a group of saprophytic fungi of the Capnodiales, which produce colonies on the surface on living plants. Their branched hyphae of globular dark-coloured cells are recorded as far back as the Lower Cretaceous (Girard *et al.*, 2009), and have also been found in several pieces of Eocene Baltic amber (Rikkinen *et al.*, 2003). Many sooty moulds obtain their nutrients primarily from the excretions of such insects as aphids, scale insects and other producers of honeydew, or directly from plant exudates (Hughes, 1976). The Eocene fossils are morphologically assignable to the modern genus *Metacapnodium*. These fungi are an example of the morphological stability of taxa which, once adapted to particular microhabitats such as the bark of trees, have preserved their morphological features for more than 100 million years. A remarkable association of a thrips and sooty moulds has recently been discovered from the Lower Eocene Oise amber of France. Remains of hyphae, as well as conidia of sooty moulds, have been found attached to the cuticle of a specimen of *Uzelothrips* sp., a new fossil species of the previously monospecific extant family Uzelothripidae (Thysanoptera). This arthropod-fungus association is not considered accidental, since these same fungi are also found on extant specimens of uzelothripids, suggesting very specific long-term interactions and strong habitat specificity. The new fossil uzelothripids provide evidence of long-term ecological stability in their association with dark-coloured fungi of the Dothideomycetes. It is further hypothesized that the morphological stability of this group of thrips (reproducing over significant geologic periods) is correlated with the long-term stability of micro-habitats and food sources, resulting in less selection pressure.

(3) *RESINICOLOUS FUNGI*.
Resinicolous fungi, such as ascomycetes of the Mycocaliciales, are adapted to their special substrate and are also able to grow on fresh and hardened resin (Tibell and Titov, 1995). Therefore, they may be found in places where herbivorous insects induce long-term resin flows (Rikkinen, 1999; Rikkinen and Poinar, 2000). Representatives of the extant genus *Chaenothecopsis* were found entrapped in Baltic amber. Both the mycelium and the stalked apothecia of this fungus are completely preserved in the resin; this represents an exceptional taphonomic situation in which this fungus was covered and preserved by its own substrate.

(4) *PARASITIC FUNGI*.
Aspergillus collembolorum is an example of parasitic anamorphs of the Ascomycota, which are found in Baltic amber still attached to their substrates (Dörfelt and Schmidt, 2005). *Aspergillus collembolorum* infested a springtail (Collembola), and later sporulated, even continuing to sporulate when embedded in the liquid resin. Other Ascomycota found in Baltic amber are associated with plant remains, or possibly with other fungi. The extant anmorphic genus *Gonatobotryum* and related genera, such as *Gonatobotrys* and *Nematogonum*, largely contain mycoparasites of lignicolous fungi. Several representatives of the genus *Gonatobotryum* were found in Baltic amber on various substrates, mainly on plant remains. However, it is hard to decide whether these fungi parasitized the plants themselves or other fungi growing inside these plants as they decayed (Dörfelt and Schmidt, 2007).

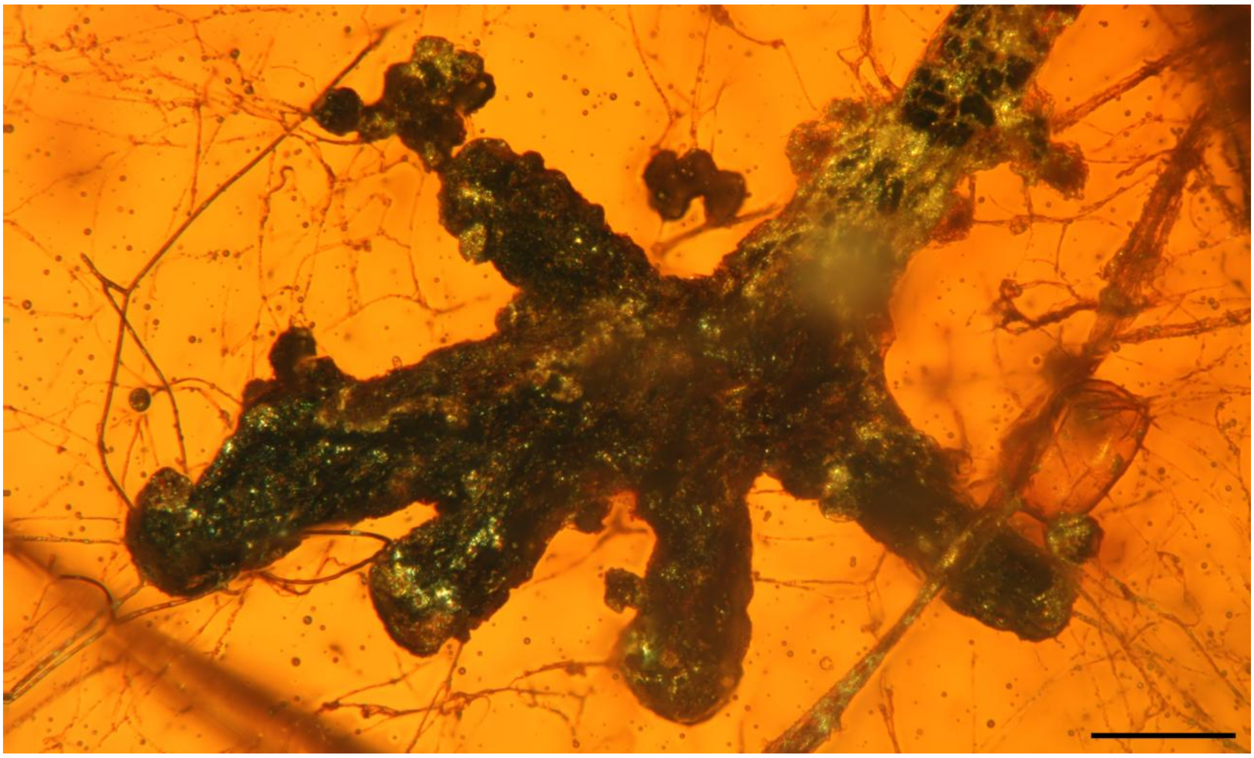

Figure 1. Ectomycorrhizal system from Eocene amber of India (scale bar = 100 µm).

(5) LIGNICOLOUS FUNGI.

Dense crusts of numerous perithecial ascomata were discovered at the surface of wood fragments from the middle Eocene Eckfeld Maar. The ascomata possess ostioli on very short rostra, some of which still contain dark-pigmented fusiform spores. The septation of these mostly four-celled spores is quite variable, and is distinguished from any extant taxon. The spores possess either a central septum or a central unseptate cell. These fungi most probably belong to the Sordariomycetes, or to the Dothideomycetes (Pleosporales).

DÖRFELT, H., SCHMIDT, A.R. (2005). A fossil *Aspergillus* from Baltic amber. Mycological Research 109: 956-960.

DÖRFELT, H., SCHMIDT, A.R. (2007). A conifer seedling with two herbicolous fungi from the Baltic amber forest. Botanical Journal of the Linnean Society 155: 449-456.

GIRARD, V., SCHMIDT, A.R., STRUWE, S., PERRICHOT, V., BRETON, G., NÉRAUDEAU, D. (2009). Taphonomy and palaeoecology of mid-Cretaceous amber-preserved microorganisms from southwestern France. In: Perrichot, V., Néraudeau, D. (eds) Cretaceous ambers from south-western France: Geology, taphonomy, and palaeontology. Geodiversitas 31: 153-162.

HUGHES, S.J. (1976). Sooty moulds. Mycologia 68: 693-820.

RIKKINEN, J. (1999). Two new species of resinicolous *Chaenothecopsis* (Mycocaliciaceae) from western North America. The Bryologist 102: 366-369.

RIKKINEN, J., DÖRFELT, H., SCHMIDT, A.R., WUNDERLICH, J. (2003). Sooty moulds from European Tertiary amber, with notes on the systematic position of *Rosaria* (Cyanobacteria). Mycological Research 107: 251-256.

RIKKINEN, J., POINAR, G.O., JR. (2000). A new species of resinicolous *Chaenothecopsis* (Mycocaliciaceae, Ascomycota) from 20 million year old Bitterfeld amber, with remarks on the biology of resinicolous fungi. Mycological Research 104: 7-15.

TIBELL, L., TITOV, A. (1995). Species of *Chaenothecopsis* and *Mycocalicium* (Caliciales) on exudate. The Bryologist 98: 550-560.

Eocene Embrithopoda (Mammalia) from Turkey and their paleobiogeographic implications

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Among mammals, the Embrithopoda are classified as an infraorder of the order Paenungulata and of the suborder Tethytheria, together with the proboscideans, sirenians and presumably desmotylians (McKenna and Bell, 1997; Rose, 2006). On a larger scale, the embrithopods are thus considered putative Afrotheria, a clade based on molecular biology data (Stanhope *et al.*, 1998), which band together paenungulates, macroscelids, tenrecoids, and aardvarks (Tabuce *et al.*, 2008). The best-known representative of embrithopods is *Arsinoitherium zitteli* Beadnell, 1902 from the early Oligocene of Fayum, Egypt. This animal is of the size of a large rhinoceros and has graviportal and pillar-like limb bones similar to those of elephants. Its large skull bears a pair of large anterior horn cores on the nasal bones directed upward and forward, and another pair of horn cores, much smaller, above the orbits on the frontals.

Arsinoitherium long remained a symbol of the endemism of African mammalian faunas during the Paleogene. Embrithopods are known from seven localities in Africa (Fayum, Dor el Talha, Grigema, Melembe, Losidok, Chilga, and Black Crow) and three in the Arabian peninsula (Aydim, Thaytiniti, and Taqah) dated between middle Eocene and late Oligocene (Pickford, in press). The specimens from Black Crow (Namibia) have been referred to a different genus, *Namatherium*, whereas the other African and Arabian records were referred to *Arsinoitherium*. However, embrithopods have also been recorded outside of Africa, for example in Turkey (*Palaeoamasia* and *Hypsamasia*) and Romania (*Crivadiatherium*). These discoveries imply that embrithopods existed on both sides of the Tethys seaway during the Paleogene. Such dispersal pattern does not fit in the "Island Africa" model developed by paleogeographic reconstitutions (e.g., Barrier and Vrielynck, 2008).

The type locality of *Palaeoamasia kansui* Ozansoy, 1966 is the Eski Çeltek lignite mine in north-central Turkey. Its age is Ypresian, based on the planktonic foraminifera from a thin marine intercalation above the mammal-bearing lignite seam (Koç and Türkmen, 2002). Recent discoveries at Eski Çeltek improved our knowledge of the skull morphology and the dentition of *P. kansui. Palaeoamasia* was recorded in four other localities in Turkey, which are all early-?middle Eocene lignite mines (Sen and Heintz, 1979; Kaya, 1995).

Hypsamasia seni is another embrithopod from Turkey, documented by some fragmentary teeth from the early Lutetian (Maas *et al.*, 1998) or late Paleocene (Kazanci and Gökten, 1986) deposits near Ankara. Because the tooth pattern of *Hypsamasia* is very similar to that of *Palaeoamasia*, its generic status is questioned. In Romania, *Crivadiatherium* is represented by two species from the late Eocene of the Hateg depression (Radulescu and Sudre, 1985). Both species are known from their lower dentition, which is similar in size to that of *Palaeoamasia*, but is more lophodont and has molarized posterior premolars.

The relationships and composition of Embrithopoda are still debated. On the one hand, the late Paleocene Phenacolophidae (consisting of the genera *Phenacolophus* from China and Mongolia, as well as *Minchenella* and perhaps *Radinskya* from China) could be included in the Embrithopoda as the sister family of the arsinotheres from Africa and Europe, implying an East Asian origin for the infraorder (McKenna and Manning, 1977). On the other hand, arsinotheres, being included in the order Paenungulata together with proboscideans and sirenians (Gheerbrant *et al.*, 2005; Rose, 2006), are putative afrotherians. Noticeably, Gheerbrant *et al.* (2005) also suggested that the poorly documented *Phenacolophus* should be considered a stem Tethytheria.

In the light of the early Paleogene occurrences of embrithopods in Turkey and Romania, the long-supposed endemism of the African Paleogene mammalian faunas can be criticized. Moreover as shown by Gheerbrant and Rage (2006), several mammalian groups originated in Eurasia and reached Africa during the Paleogene.

Studying the morphology and functional anatomy of the skull and limb bones of *Arsinoitherium*, Court (1993) showed that this animal was a massive, graviportal herbivore with forelimbs adapted for strong retraction. Such features are consistent with a semi-aquatic habitat. In other words, this animal lived in rather warm, humid, and highly vegetated environments. The occurrence of *Palaeoamasia* and *Crivadiatherium* in Turkey and in Romania in swamp deposits may also indicate that they were preferably inhabitants of wet environments.

The age of the localities yielding embrithopods suggests an origin in southeastern Europe for the African embrithopods, and that their dispersal across the Tethys seaway probably occurred during the late Paleocene or early Eocene (Gheerbrant *et al.*, 2005). During this time interval, the Afro-Arabian plate was isolated from Eurasia, as well as from the island arcs situated along its southern rims, by the Neo-Tethys seaways, which formed a marine barrier. In such a paleogeographic context, the dispersal of embrithopods may be explained only by sweepstake migration of mammals adapted to wet environments. This hypothesis would explain the occurrence of embrithopods on both sides of the Neothethys ocean.

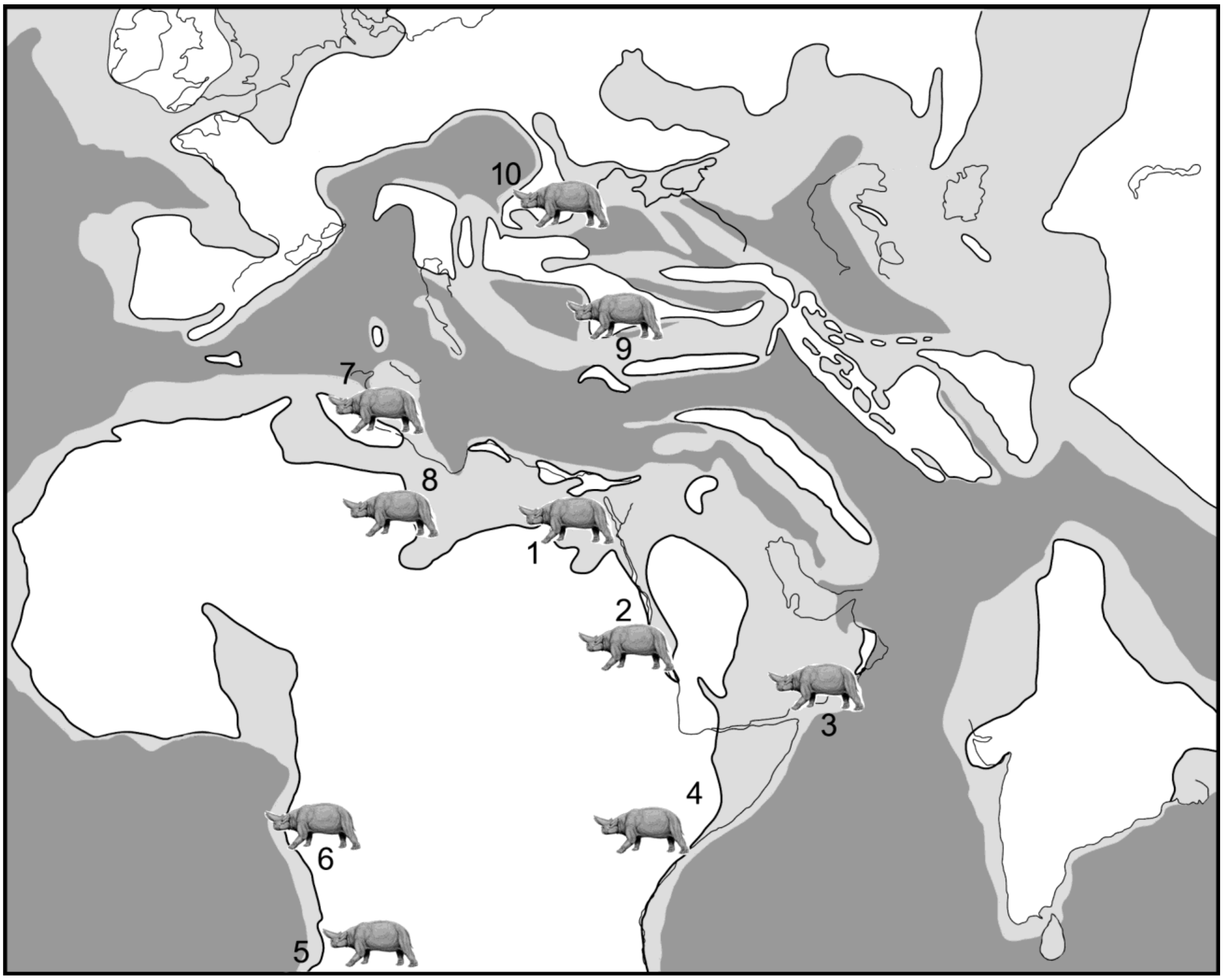

Figure 1. Geographic distribution of embrithopods during the Paleogene (Ypresian map modified from Barrier and Vrielynck, 2008). 1: Fayum, Egypt; 2: Chilga, Ethiopia; 3: Aydim, Thaytiniti and Taqah, Oman; 4: Losidok, Kenya; 5: Black Crow, Namibia; 6: Melembe, Angola; 7: Grigema, Tunisia; 8: Dor el Talah, Lybia; 9: Turkey; 10: Romania.

Barrier, E., Vrielynck, B. (2008). Palaeotectonic maps of the Middle East. Tectono-sedimentary-palinspastic maps from Late Norian to Pliocene. CGMW/CCGM, Paris, 14 maps.

Court, N. (1993). Morphology and functional anatomy of the postcranial skeleton in *Arsinoitherium* (Mammalia, Embrithopoda). Palaeontographica 226: 125-169.

Gheerbrant, E., Domming, D.P., Tassy, P. (2005). Paenungulata (Sirenia, Proboscidea, Hyracoidea, and relatives). In: Rose, K.D., Archibald, J.D. (eds) Placental Mammals: Origins and Relationships of the Major Clades. Johns Hopkins University Press, Baltimore, MD. pp. 84-105.

Gheerbrant, E., Rage, J.C. (2006). Paleobiogeography of Africa: How distinct from Gondwana and Laurasia? Palaeogeography, Palaeoclimatology, Palaeoecology 241: 224-246.

Kaya ,T. (1995). *Palaeoamasia kansui* (Mammalia) in the Eocene of Bultu-Zile (Tokat, Norteastern Turkey) and systematic revision of *Palaeoamasia*. Turkish Journal of Earth Sciences 4: 105-111.

Kazanci, N., Gökten, E. (1986). Sedimentary characteristics of terrestrial Paleocene deposits in northern Ankara region, Turkey. Communications of the Faculty of Sciences, University of Ankara C 4: 153-163.

Koç, C., Türkmen, I. (2002). Suluova (Amasya) kuzeyindeki kömürlü Eosen çökellerinin sedimantolojik özellikleri. Yerbilimleri 26: 101-117.

Maas, M.C., Thewissen, J.G.M., Kappelman, J.W. (1998). *Hypsamasia seni* (Mammalia: Embrithopoda) and other mammals from the Eocene Kartal Formation of Turkey. In: Beard K.C., Dawson M.R. (eds) Dawn of the Age of Mammals in Asia. Bulletin of Carnegie Museum of Natural History 34: 286-297.

McKenna, M.C., Bell, S.K. (1997). Classification of Mammals above the Species Level. Columbia University Press, New York, 631pp.

McKenna, M.C., Manning, E. (1977). Affinities and palaeobiogeographic significance of the Mongolian Paleocene genus *Phenacolophus*. Geobios 10 (Supplément 1): 61-85.

Pickford M. (in press). *Arsinoitherium* from Tunisia. Notes du Service géologique de Tunisie.

Radulescu, C., Sudre, J. (1985). *Crivadiatherium iliescui* n. sp., nouvel embrithopode (Mammalia) dans le Paléogène ancien de la Dépression de Hateg (Roumanie). Palaeovertebrata 15: 139-157.

Rose, K.D. (2006). The Beginning of the Age of Mammals. Johns Hopkins University Press, Baltimore, 428pp.

Sen, S., Heintz, E. (1979). *Palaeoamasia kansui* Ozansoy, 1966, Embrithopode (Mammalia) de l'Eocène d'Anatolie. Annales de Paléontologie 65: 73-91.

Stanhope, M.J., Madsen, O., Waddell, V.G., Cleven, G.C., de Jong, W.W., Springer, M.S. (1998). Highly congruent molecular support for a diverse superordinal clade of endemic African mammals. Molecular Phylogenetics and Evolution 9: 501-508.

Tabuce, R., Asher, R.J., Lehmann, T. (2008). Afrotherian mammals: A review of current data. Mammalia 72: 2-14.

Palaeogene primates from the Sperrgebiet, Namibia

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Since the early 1990s, research in geology and palaeontology has been carried out in Namibia in collaboration with the Geological Survey of Namibia and Namdeb to evaluate the age of the diamond-bearing deposits of the Sperrgebiet. During the 2008 field season, we discovered Palaeogene deposits at 3 localities (older than 42 Ma) which have not been registered in this part of the world before (Pickford *et al.*, 2008*a*; Pickford *et al.*, 2011; Fig. 1). African Early Tertiary sediments which have yielded primates are known not only in North Africa (Maghreb, Sultanate of Oman, Egypt), but also in Tanzania, where one locality (in the Rukwa Basin) is recorded, and in Angola (Malembe, Cabinda) (Fig. 2). The Namibian fossils are diverse, including plants, gastropods, fish, crocodiles, frogs, lizards, snakes, birds, and several mammals. But the most unexpected finds were remains (a maxillary fragment and a lower premolar) of small primates found at two sites: Black Crow and Silica North (Pickford *et al.*, 2008*b*). One of them in particular seems to recall North African primates known in the Fayum (Egypt), but is morphologically more primitive and much smaller.

The specimens consist of a right maxillary fragment (BC 6'08) with M^2 and M^3 and an isolated right lower P_4 (SN 15'08) and have been attributed to *Namaia bogenfelsi* (Fig. 2). The teeth are bunodont, with no buccal cingulum in the upper molars, and the M^2 exhibits a large hypocone (different from *Altiatlasius*), well-defined paraconule and metaconule (which are well developed as in many strepsirhines, but can also occur in simiiforms from Northern Africa), paracone and hypocone exhibit sloping buccal walls; three cusps are present on the M^3. The molars differ from the Northern African genera *Biretia* and *Algeripithecus* and from the Fayum genera *Proteopithecus* and *Catopithecus* by the absence of cingulum, a stronger hypocone at the M^2, larger paracone and metacone, and a more bucco-lingually compressed protocone. The teeth are generally small compared to Propliopithecoidea. The Namibian fossils also differ from most North African taxa, including *Talahpithecus* from Libya, by the absence of buccal and lingual cingulum in the molars. The right P_4 from Silica North is a small bunodont tooth with a trapezoidal occlusal outline. The protoconid is large and joins a tiny metaconid by a low but well-defined crest.

In general morphology, the Namibian primates appear to differ from most of the strepsirrhines described from Northern Africa and appear to be closer to Simiiformes. The problem is complex, as some primates previously interpreted as anthropoids (in Algeria, for example) are now considered by some authors to belong to the strepsirrhines. The polarity of the features being difficult to establish for the moment, the debate is far from over. It is important to find more cranial remains to throw light on systematics and phylogeny.

Conclusion

The discovery of possible Palaeogene Simiiformes in South West Africa, far from the classical sites of Northern Africa, is of extreme importance for the debate about the origins of Simiiformes and for the Palaeogene history of mammals as a whole. It suggests the possibility of other scenarios for the origins of Anthropoidea in the Old World.

Acknowledgements

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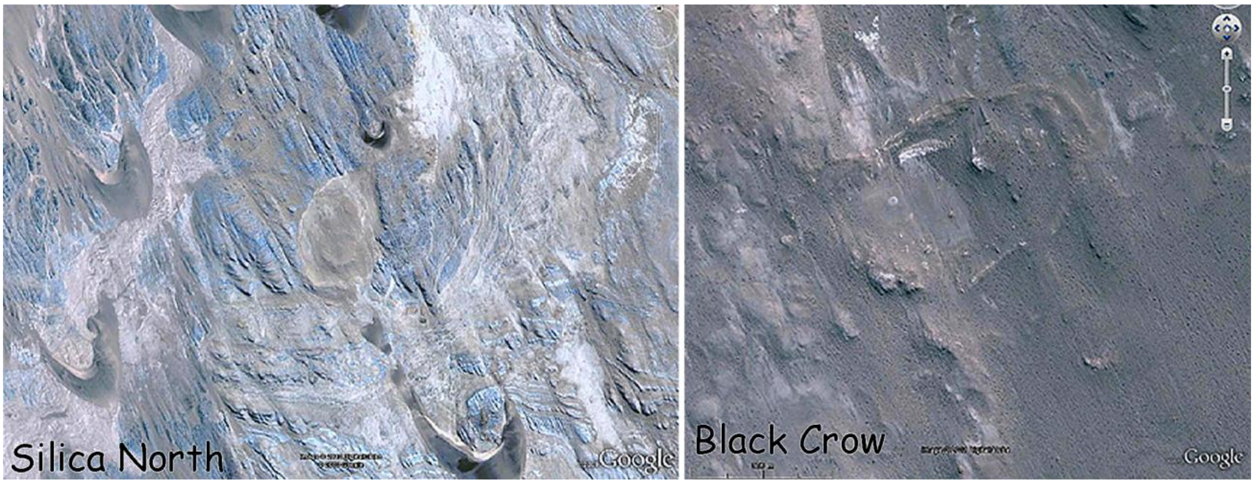

Figure 1. Palaeogene sites in the Sperrgebiet (satellite images).

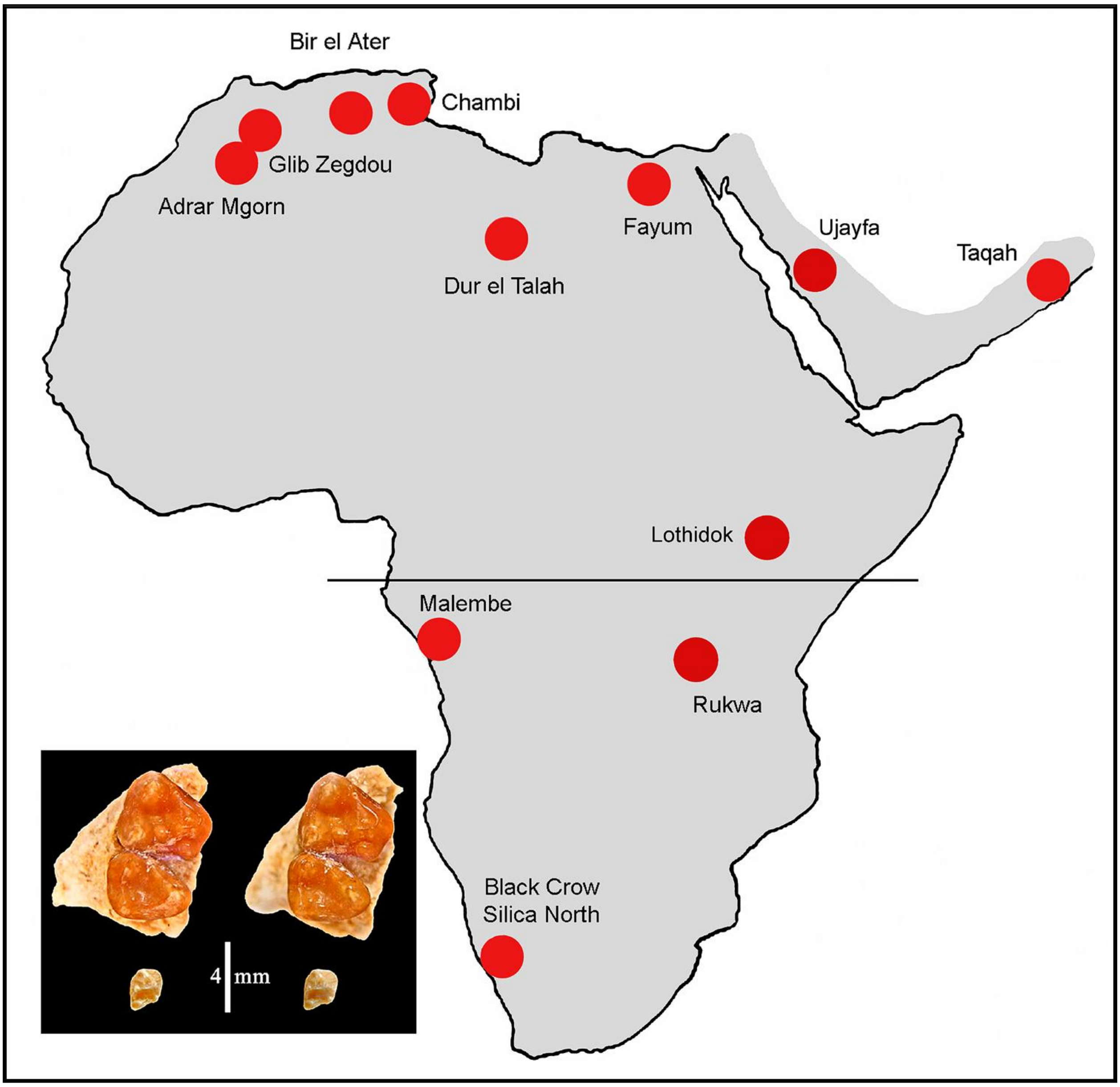

Figure 2. Palaeogene primate-bearing localities of Afro-Arabia including a stereo image of Palaeogene primates from the Sperrgebiet (top: BC 6'08, right maxilla; bottom: SN 15'08, lower P_4).

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Pickford, M., Sawada, Y., Senut B. (2011). Geochronology and palaeontology of the Palaeogene deposits in the Sperrgebiet, Namibia. In: Lehmann, T., Schaal, S.F.K. (eds) The World at the Time of Messel: Puzzles in Palaeobiology, Palaeoenvironment, and the History of Early Primates. 22nd International Senckenberg Conference. 15th – 19th November 2011, Frankfurt am Main. Conference Volume. Senckenberg Gesellschaft für Naturforschung, Frankfurt am Main. pp. 129-130.

Pickford, M., Senut, B., Morales, J., Mein, P., Sanchez, I. (2008*a*). Mammalia from the Lutetian of Namibia. Memoir of the Geological Survey of Namibia 20: 465-514.

Pickford, M., Senut, B., Morales, J., Sanchez, I. (2008*b*). Fossiliferous Cainozoic carbonates of the Northern Sperrgebiet. Memoir of the Geological Survey of Namibia 20: 25-42.

A nycterid bat from late Oligocene paleokarstic fillings, Quercy, SW France

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Today, twelve living nycterid species are geographically widely distributed in non-Saharan Africa and insular SE Asia (Hill and Smith, 1984). Like other bats, their way of life consists mostly of nocturnal winged predation, a diet of insects, and diurnal roosting in caves. As reported by classic authors, the hard-tissue morphology of nycterids, particularly their teeth, makes them very distinctive. The family status of the Nycteridae was recognized long ago, but subordinal relationships remained unclear. Long after Miller (1907) considered them to be closely related to emballonurids, they were thought to be related to rhinolophoid bats (Simpson, 1945; McKenna and Bell 1997).

The cave-roosting habits of nycterids should favour them to be preserved as fossils within cave deposits. Nevertheless, until recently their global fossil record has remained poor. During the decades since the early 1960s, field research of the many Paleogene Quercy paleokarstic clay fillings in SW France has produced rich vertebrate faunas, typically including abundant bat material. However, nycterid remains have been found in only two Quercy localities so far: Mas de Pauffié and Lazedev. The Mas de Pauffié nycterid was found first and initially noted as "Emballonurid indet.“ in Remy *et al.* (1987, Tab. 4); the rarer Lazedev nycterid, representing the same species, has been recognised only during very recent investigations. These are the oldest fossil *Nycteris* records to date. The species is so far unknown from other Quercy or any localities, including those close in age. This late Oligocene occurrence of *Nycteris* at Quercy is well outside the present geographic distribution of nycterids, a situation not uncommon among vertebrates over geological time.

In the Quercy specimens, characteristic nycterid features (some # being shared with emballonurids) include the puncturing shape of the upper canine #; shape of P^4 #; complete absence of P^2 to P^3, such that C and P^4 are in contact; the well-extended postero-distal heel of M^1 and M^2 #; absence of postprotocrista; indented labial border anterior to mesostyle # (rather than the more symmetrical mesostyle border of rhinolophoids); and reduced entoconid of lower molars and its close proximity to metaconid. Furthermore, various features of tooth morphology shared by the Mas de Pauffié and Lazedev nycterids and recent *Nycteris* species significantly supports a close phylogenetic relationship between nycterid and emballonuroid bats, as expressed by Miller (1907), rather than with rhinolophoids. Shared features can be very clearly seen in the general shape of the upper molars, notably the typical posteriorly extended heel of M^1–M^2.

The occurrence of fossil *Nycteris* in two Quercy localities provides an unexpected and significant new addition to the late Paleogene SW European bat record, despite the rich and generally well-sampled nature of the many localities known to date. The remains are evidence that unexpected occurrences can occur! The presence of nycterids at Mas de Pauffié and Lazedev suggests a relatively recent paleogeographic invasion, perhaps without prolonged presence of these bats subsequently. Similar biogeographic movements among bats during the latest Paleogene and Miocene of SW Europe have been recorded in various other groups, such as pteropodids, emballonurids, and rhinopomatids.

HILL, J.E., SMITH J.D. (1984). Bats, a Natural History. British Museum (Natural History), London. Publication No 877, 243pp.

MCKENNA M.C., BELL S.K. (1997). Classification of Mammals above the Species Level. Colombia University Press, New York, 631pp.

MILLER, JR., G.S. (1907). The Families and Genera of Bats. Smithsonian Institution, United States National Museum, Bulletin 57: 282pp.

REMY, J.A., CROCHET, J.-Y., SIGÉ, B., SUDRE, J., BONIS, L. DE, VIANEY-LIAUD, M., GODINOT, M., HARTENBERGER, J.-L., LANGE-BADRÉ, B., COMTE, B. (1987). Biochronologie des phosphorites de Quercy: Mise à jour des listes fauniques et nouveaux gisements de mammifères fossiles. Münchner Geowissenschaftliche Abhandlungen A (10): 169-88.

SIMPSON, G.G. (1945). The Principles of Classification and a Classification of Mammals. Bulletin of the American Museum of Natural History 85: 350pp.

Diversity and biogeography of early bats

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Early bats mainly comprise “eochiropterans” (Eochiroptera Van Valen, 1979 is a controversial paraphyletic group composed of primitive taxa; see Simmons and Geisler (1998) for an overview) and a few taxa representing the first members of modern families. They are known from the early and early to mid- middle Eocene (Ypresian and Lutetian and global equivalents, encompassing European mammalian reference levels MP7 through MP13). The fossil record for early bats consists mainly of cranial and dental remains with the exception of two world-famous lagerstätten that have yielded many complete skeletons – the early Eocene Green River Formation in Wyoming, and the middle Eocene Messel Formation in Germany. However, these two areas account for only a portion of the known diversity of early and middle Eocene bats. Here we review the earliest records of bats from all continents and provide updated dental diagnoses and discussion based on the fossil material presently available.

The highest diversity of early bats occurs in Europe with the presence of species representing Icaronycteridae, Onychonycteridae, Archaeonycteridae, Hassianycteridae, Palaeochiropterygidae, Mixopterygidae, Emballonuridae, Hipposideridae, and several taxa of uncertain taxonomic status (Smith *et al.*, 2011).

The oldest bats from Asia have recently been described from the early Eocene Vastan Lignite Mine in Gujarat, western India (Smith *et al.*, 2007). Among the families represented, Icaronycteridae and Archaeonycteridae show the most plesiomorphic features, whereas Hassianycteridae and Palaeochiropterygidae are more derived. Other derived species are present but are difficult to relate to a known family. In total, eight species belonging to at least five genera and four families are present in the same level of the same locality. Their high diversity and close relationship with bats from Western Europe, especially with those from Messel, highlight our understanding of early bat dispersal and suggest Paleocene or earlier Eocene biotic contact between India and Europe before the Indian-Asian collision.

In Eastern Asia the oldest bats are recorded from the late middle Eocene of China and are represented with certainty only by Palaeochiropterygidae (Tong, 1997). In Australia, only the early Eocene genus *Australonycteris* (family indeterminate) is known (Hand *et al.*, 1994).

In North America, early Eocene Icaronycteridae and Onychonycteridae from the Green River and Wind River basins in Wyoming are the only families recognized (Simmons *et al.*, 2008), suggesting a possible geographic origin from Europe. In South America, only one record (taxon indeterminate) is present in the early Eocene (Tejedor *et al.*, 2005).

In Africa, Tanzanycteridae are known from the middle Eocene of Tanzania, and Philisidae and an “eochiropteran” bat are recorded from the early Eocene of Tunisia and Algeria (Gunnell *et al.*, 2003; Sigé, 1991; Ravel *et al.*, 2010).

Taken together, known records of early bats indicate that their highest diversity was around the Greater Tethys Seaway extending from Gibraltar to Indo-Pakistan.

GUNNELL, G.F., JACOBS, B.F., HERENDEEN, P.S., HEAD, J.J., KOWALSKI, E., MSUYA, C.P., MIZAMBWA, F.A., HARRISON, T., HABERSETZER, J., STORCH, G. (2003). Oldest placental mammal from sub-Saharan Africa: Eocene microbat from Tanzania—Evidence for early evolution of sophisticated echolocation. Palaeontologica Electronica 5: 1-10.

HAND, S., NOVACEK, M., GODTHELP, H., ARCHER, M. (1994). First Eocene bat from Australia. Journal of Vertebrate Paleontology 14: 375–381.

RAVEL, A., MARIVAUX, L, TABUCE , R., MAHBOUBI, M., 2010. Oldest bat (Chiroptera, Eochiroptera) from Africa: Early Eocene from El Kohol (Algeria). Journal of Vertebrate Paleontology 28: 149A.

SIGÉ, B. (1991). Rhinolophoidea et Vespertilionoidea (Chiroptera) du Chambi (Eocène inférieur de Tunisie). Aspects biostratigraphique, biogéographique et paléoécologique de l’origine des chiroptères modernes. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 182: 355-376.

SIMMONS, N.B., GEISLER, J.H. (1998). Phylogenetic relationships of *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* to extant bat lineages, with comments on the evolution of echolocation and foraging strategies in Microchiroptera. Bulletin of the American Museum of Natural History 235: 1–182.

SIMMONS, N.B., SEYMOUR, K.L., HABERSETZER, J., GUNNELL, G.F. (2008). Primitive early Eocene bat from Wyoming and the evolution of flight and echolocation. Nature 451: 818–822.

SMITH, T., HABERSETZER, J., SIMMONS, N.B., GUNNELL, G.F. (2011). Chapter 2. Systematics and paleobiogeography of early bats. In: Gunnell, G.F., Simmons, N.B. (eds) Evolutionary History of Bats: Fossils, Molecules and Morphology. Cambridge University Press, Cambridge (in press).

SMITH, T., RANA, R.S., MISSIAEN, P., ROSE, K.D., SAHNI, A., SINGH, H., SINGH, L. (2007). High bat (Chiroptera) diversity in the Early Eocene of India. Naturwissenschaften 94: 1003–1009.

TEJEDOR, M.F., CZAPLEWSKI, N.J., GOIN, F.J., ARAGON, E. (2005). The oldest record of South American bats. Journal of Vertebrate Paleontology 25: 990–993.

TONG, Y-S. (1997). Middle Eocene small mammals from Liguanqiao Basin of Henan province and Yuanqu Basin of Shanxi province, Central China. Palaeontologica Sinica 18, New Series *C* 26: 1-256.

VAN VALEN, L. (1979). The evolution of bats. Evolutionary Theory 4: 103-121.

On new material of *Kopidodon macrognathus* (Mammalia, Paroxyclaenidae) from Messel

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Since its first description in 1933, twelve specimens of *Kopidodon macrognathus*, ranging from a mandible fragment to complete skeletons, have been recovered from the middle Eocene fossil locality of Messel. They are housed in the Hessisches Landesmuseum Darmstadt (HLMD), the Senckenberg Museum Frankfurt (SMF), and in private collections. Four of these have never been described. Here, we will focus on one of them (HLMD-Me-17750) and add two new specimens including a juvenile one (SMF ME 11116 and 11287). These specimens help us to implement our knowledge on the anatomy and ontogeny of this rare paroxyclaenid.

The juvenile specimen (SMF ME 11287), with yet unfused epiphyses in some long bones and phalanges, and the adult specimen (SMF ME 11116) are both lying such that their left side is visible, whereas HLMD-Me-17750 offers its right side (Fig. 1). The adult specimens are complete, whereas the heavily crushed head of the juvenile one has been severed from the body. In all three specimens the legs are in a semi-flexed position, often considered typical for drowned animals (Clemens and Koenigswald, 1993). All three specimens also show a body outline with a noticeable bushy tail.

The skull of the adult (SMF ME 11116) is fairly crushed but suggests that the orbit is facing laterally, not frontally. A very developed sagittal crest is visible in connection to a distinct nuchal crest. The occipital plane is inclined at about 140° to the base of the skull. This area is missing in the juvenile (SMF ME 11287), hindering comparisons and timing of the formation of the crests in relation, for example, to the fusion of the epiphyses. Conversely, this juvenile skull still preserves the right deciduous canine (dC), so that a double set of canines is visible, with the permanent one (C) erupting a little in front (Fig. 1C). It seems that, as in HLMD-Me-7576 described by Koenigswald (1983: Fig. 5), the C is the last tooth to erupt in *K. macrognathus*. This author explained that the eruption period for such a large tooth is contingent on the room generated in the tooth-row during growth. Usually, the milk tooth is not shed until after the permanent one is sufficiently erupted to be functional

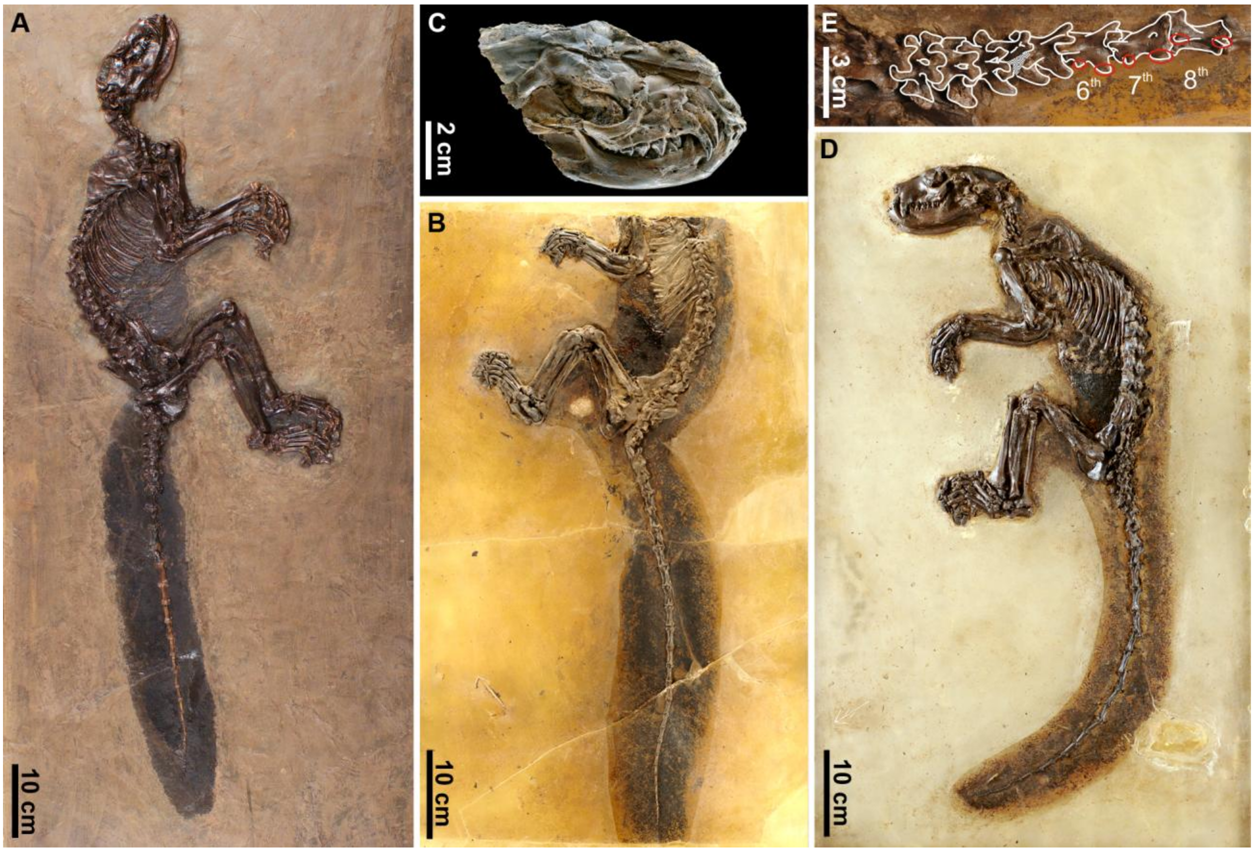

Figure 1. A) Lateral view of the adult specimen HLMD-Me-17750; B) Lateral view of the juvenile specimen, SMF ME 11287; C) Detail of the right side of the cranium of SMF ME 11287: note the retention of the deciduous canine; D) Lateral view of the adult specimen SMF ME 11116; E) Detail of the first caudal vertebrae of SMF ME 11116: the outline emphasis the two separated transverse processes on Ca6-8.

(Ewer, 1998: p61). As the tip of the C has not reached the level of the dC in SMF ME 11287, it is assumed that the C is not yet functional. In contrast, the permanent left canine is fully erupted and there is no trace of a milk tooth. This could suggest that the eruption of the canine is asynchronous in *Kopidodon macrognathus*. Such configuration would in return allow the animal to have always at least one functional canine during tooth replacement. On the other hand, the retention of the dC could also be a pathological condition, as is occasionally encountered in extant dogs (e.g., Hobson, 2005).

The adult specimen (SMF ME 11116) displays a complete vertebral column with seven cervicals, 20 thoraco-lumbar vertebrae, three sacral, and 31 caudal vertebrae. The axis is very well preserved in lateral aspect and shows a very large dorsal spine. The neck appears overall short and robust, with a large articulation surface at the postzygapophyses. The 13 ribs visible on the left side of SMF ME 11116 correspond to 13 thoracic vertebrae, as in specimen SMF ME 2401 (Clemens and Koenigswald 1993). Conversely, for other specimens of *K. macrognathus*, Koenigswald (1983) counted 10 to 12 thoracic vertebrae. In SMF ME 11287 and HLMD-Me-17750, the number of ribs cannot be assessed, as the more rostral ones are either missing or hidden by the scapula and humerus. Seven lumbar vertebrae can be discerned in the adult specimens SMF ME 11116 and HLMD-Me-17750, a count which differs from other specimens for which nine lumbars were described (Clemens and Koenigswald, 1993; Koenigswald, 1983). The sacrum of SMF ME 11116 clearly consists of three vertebrae fused by their centra but not their processes, whereas Koenigswald (1983) described potentially four sacral vertebrae in another specimen. The first five caudal vertebrae of the two adult specimens show a posteriorly elongated transverse process decreasing in size caudally, which has not been described in other specimens (Fig. 1E). The sixth caudal shows a similar transverse process in the caudal part but bears an additional shorter anterior process merging with the posterior one at the level of the centrum. From the seventh caudal vertebra onwards, there are two clearly separated transverse processes, whose size decreases until the 13th one (visible only on SMF ME 11116). The tail of *Kopidodon* thus bears some resemblances with the long and possibly prehensile tail of *Chriacus*, a Paleogene arctocyonid adapted for climbing (Rose, 1987).

Based on the known specimens, *K. macrognathus* shows a highly variable number of thoracic, lumbar, sacral and certainly caudal vertebrae, but displays the seven cervicals typical of almost all mammals. Despite these variations, all specimens have more than 19 thoracolumbar vertebrae, a possible apomorphic character for afrotherians (Sánchez-Villagra *et al.*, 2007). Further analyses on vertebral variability should be considered, as a high proportion of anomalies (e.g., cervical rib) and a high level of intraspecific diversity in vertebral count have been suggested to be typical of recent southern placentals (in opposition to boreoeutherians) (Asher *et al.*, 2009).

In SMF ME 11116 the head of the humerus is proximally more elevated than the greater tubercle. It is well rounded and probably enabled rotational movement. The deltopectoral crest is marked with its largest extension in about the middle of the humerus length. The brachial crest is broad and extends proximally as far as the deltoid crest. According to Clemens and Koenigswald (1993), these features are characteristic of arboreal or scansorial mammals. Similarly well-developed brachial crests can, however, be found in digging mammals (Hildebrandt, 1985). The olecranon fossa is shallow, seems very small and is oval in shape. Ulna and radius remain separated in all three specimens. The femoral head is set on a short and thick neck. As a long neck is usually associated with a high mobility of the hindlimb (MacPhee, 1994), a somewhat limited mobility can be assumed for *Kopidodon* here. To the best of our knowledge, specimens SMF ME 11116 and HLMD-Me-17750 are the first to show an almost complete scapular blade, enabling a more detailed description. A very prominent and strong scapular spine as well as a second crest along the axillary border marked in the distal half and tapering off to the proximal rim are present. Unnoticed so far is the extension of the proximal third of the axillary border of the scapula towards the thorax. This area is the origin of the musculus teres major, which inserts into the bicipital groove on the humerus and rotates the arm. Finally, as noticed by other authors (e.g., Clemens and Koenigswald, 1993), both hands and feet bear curved and laterally flattened ungual phalanges specialised for climbing.

Based on the morphological observations of the post-cranial skeleton of the three new specimens, we support the view that *Kopidodon* was a rather arboreal or scansorial animal with a fairly specialized forelimb and a more generalized hind limb.

Asher, R.J., Bennett, N., Lehmann, T. (2009). The new framework for understanding placental mammal evolution. BioEssays 31: 853-864.

Clemens, W.A., Koenigswald, W.v. (1993). A new skeleton of *Kopidodon macrognathus* from the Middle Eocene of Messel and the relationships of Paroxyclaenids and Pantolestids based on postcranial evidence. Kaupia 3: 57-73.

Ewer, R.F. (1998). The Carnivores. Ithaca, Cornell University Press. 500pp.

Hobson, P. (2005). Extraction of retained primary canine teeth in the dog. Journal of Veterinary Dentistry 22 (2): 132-137.

Koenigswald, W.v. (1983). Skelettfunde von *Kopidodon* (Condylarthra, Mammalia) aus dem mitteleozänen Ölschiefer von Messel bei Darmstadt. Neues Jahrbuch für Geologie und Paläontologie 167: 1-39.

MacPhee, R.D.E. (1994). Morphology, adaptations, and relationships of *Plesiorycteropus*, and a diagnosis of a new order of Eutherian mammals. Bulletin of the American Museum of Natural History 220: 1-220.

Rose, K.D. (1987). Climbing adaptation in the Early Eocene mammal *Chriacus* and the origin of Artiodactyla. Science 236: 314-316.

Sánchez-Villagra, M.R., Narita, Y., Kuratani, S. (2007). Thoracolumbar vertebral number: The first skeletal synapomorphy for afrotherian mammals. Systematics and Biodiversity 5: 1-7.

The herpetofauna from the late Uintan of West Texas

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Initial collecting efforts in the Middle Eocene Devil's Graveyard Formation (=DGF; Stevens *et al.*, 1984) of West Texas were focused on recovering mammalian fossils to facilitate biostratigraphic and biochronologic correlations with other Eocene faunas (e.g., Wilson, 1977). During those and subsequent expeditions, numerous fossils representing the herpetofauna were recovered, though little work was done to identify those fossils or to utilize them to address broader questions concerning saurian evolution in one of the southernmost Eocene localities in North America. Numerous saurian taxa, including boids, glyptosaurs, crocodylians, turtles, and amphisbaenians, were collected from this locality, but only the turtles have been described recently (Burroughs, pers. com.). Here we report on amphisbaenians and new crocodylians from the DGF and use apomorphic morphological characters to elucidate the alpha taxonomy and phylogenetic position of these new specimens to address saurian response to climate change in the middle Eocene (Zachos *et al.*, 2001). The DGF is time-calibrated by multiple radioisotopic dates (Stevens *et al.*, 1984; Prothero, 1996) as well as paleomagnetic data (Walton, 1992) and relative ages based on mammalian biostratigraphy and biochronology (e.g., Wilson *et al.*, 1968), resulting in excellent temporal precision for investigating paleobiological questions. Although herpetological material has often been collected and associated with the mammalian specimens from the late Uintan of West Texas, the saurian material remains unstudied and has never been fully identified or integrated into a holistic assessment of the local faunas. Previous hypotheses proposed that changes in the herpetofauna of other North American Eocene sections were correlated with the decrease in temperature and increase in aridity through the Eocene and into the Oligocene (Hutchison, 1992; Smith, 2006). Those hypothesized correlations between climate change, saurian faunal evolution, and methodological inferences for large-scale studies are problems that will be addressed with the West Texas herpetological material.

Questions regarding saurian diversity and biogeographic response to climate change are addressed using two disparate groups, amphisbaenians and crocodylians, from the DGF localities. Those taxa represent extremes in body size, (amphisbaenian average skull length of 1 cm versus crocodylian SL of 29 cm), providing two ends of a size spectrum with which to examine potential evolutionary changes in a time of climate flux. Amphisbaenians and crocodylians also represent fossorial and semi-aquatic taxa, respectively. Examining those two taxa in concert has the potential to provide environmental and climatic information based on the range of their extant ecologies and paleobiological histories.

Previously, fossil specimens of amphisbaenians from the Eocene of North America were known exclusively from deposits in Wyoming (Kearney, 2003). Therefore, documentation of individuals from the DGF results in a biogeographic range extension of the clade, because they represent rare lower-latitude specimens that can now be incorporated into interpretations of squamate fossil history. At least four amphisbaenian skulls are now known from a single sub-locality within the DGF. These specimens are hypothesized to represent new taxa based on anatomical features clarified by CT data. Recent phylogenetic analysis of squamate relationships recovered amphisbaenians as the sister taxon to Serpentes (Conrad, 2008), and this topology has interesting implications for the origins of both clades and for the evolution of characters associated with limblessness fossoriality.

Crocodylians were documented previously from the DGF, with most specimens from West Texas assigned to *Pristichampsus* based on isolated, mediolaterally compressed teeth (Brochu, 2000) as well as other cranial material (Busbey, 1986). *Pristichampsus* was reported in Bridgerian age deposits (Langston, 1975; Westgate, 1989) as well as Uintan age deposits (Bramble and Hutchison, 1971; Busby, 1986). Some of the more robust crocodylian teeth from West Texas were assigned to *Allognathosuchus* (Busby, 1986; Westgate, 1989); and *Borealosuchus* was recognized from the DGF based on associated vertebral centra, osteoderms, phalanges, and teeth (Brochu, 2000). A partial mandibular symphysis, a partial dentary, and several teeth were referred to *Globidontia* (Brochu, 2000) as the southernmost North American Tertiary occurrences of an alligatoroid with durophagous dentition. A new specimen collected in 2010 is the most complete specimen of an alligatorid with durophagous dentition from the DGF.

The herpetological material from the DGF increases the recognized diversity of both the crocodylians and the amphisbaenians from the Eocene of North America. Examination of the herpetological specimens from the DGF of West Texas using an apomorphy-based method of specimen identification results in a set of identifications that are testable hypotheses based on observable morphological data.

Recognition of these taxa from the DGF allows comparison of the herpetological components of the Uintan of West Texas with other previously identified Eocene herpetological assemblages across North America, resulting in a clearer understanding of the taxonomic composition and faunal dynamics of the Eocene reptiles from West Texas and a more complete picture of how middle Eocene faunas responded to large-scale climate changes associated with this time period.

Brochu, C. (2000). Fossil crocodylians from the Eocene Devil's Graveyard and Canoe Formations, Brewster County, Texas. The Texas Journal of Science 52: 3–12.

Busby, A.B., III. (1986). *Pristichampsus* cf. *P. vorax* (Eusuchia; Pristichampsinae) from the Uintan of West Texas. Journal of Vertebrate Paleontology 6: 101–103.

Conrad, J.L. (2008). Phylogeny and systematics of Squamata (Reptilia) based on morphology. Bulletin of the American Museum of Natural History 310: 1-182.

Hutchison, J.H. (1992). Western North American reptile and amphibian record across the Eocene/Oligocene boundary and its climatic implications. In: Prothero, D.R., Berggren, W.A. (eds) Eocene-Oligocene Climatic and Biotic Evolution. Princeton University Press, Princeton, pp 451-463.

Kearney, M. (2003). Systematics of the Amphisbaenia (Lepidosauria: Squamata) based on morphological evidence from recent and fossil forms. Herpetological Monographs 17: 1-74.

Langston, W., Jr. (1975). Ziphodont crocodiles: *Pristichampsus vorax* (Troxell), new combination, from the Eocene of North America. Fieldiana 33: 291–314.

Prothero, D.R. (1996). Magnetostratigraphy of the Eocene-Oligocene transition in Trans Pecos Texas. In: D.R. Prothero and R.J. Emry (eds) The Terrestrial Eocene-Oligocene Transition in North America. Cambridge University Press, Cambridge, pp. 189–198.

Smith, K. T. (2006). A diverse new assemblage of late Eocene squamates (Reptilia) from the Chadron Formation of North Dakota, U.S.A. Palaeontologia Electronica, 9.2.5A, 44pp.

Stevens, J.B., Stevens, M.S., Wilson, J.A. (1984). Devil's Graveyard Formation (new) Eocene and Oligocene Age Trans-Pecos Texas. Texas Memorial Museum Bulletin 32: 1-21.

Walker, R.J. (1999). An analysis of the herpetofauna and paleoenvironment of the Wasatch and Bridger Formations (Middle Eocene), at South Pass, Wyoming. Unpublished PhD dissertation. Michigan State University, East Lansing. 536pp.

Walton, A.H. (1992). Magnetostratigraphy of the lower and middle members of the Devil's Graveyard Formation (Middle Eocene), Trans-Pecos Texas. In: Prothero, D.R., Berggren, W.A. (eds) Eocene-Oligocene Climatic and Biotic Evolution. Princeton University Press, Princeton, pp. 74-87.

Westgate, J.W. (1989). Lower vertebrates from an estuarine facies of the Middle Eocene Laredo Formation (Claiborne Group), Webb County, Texas. Journal of Vertebrate Paleontology 9: 282-294.

Wilson, J.A. (1977). Stratigraphic occurrence and correlation of Early Tertiary vertebrate faunas Trans-Pecos Texas Part 1: Vieja area. Texas Memorial Museum Bulletin 25: 1-42.

Wilson, J.A. (1986). Stratigraphic occurrence and correlation of Early Tertiary vertebrate faunas, Trans-Pecos Texas: Agua Fria-Green Valley areas. Journal of Vertebrate Paleontology 6: 350-373.

Wilson, J.A., Twiss, P.C., DeFord, R.K., Clabaugh, S.E. (1968). Stratigraphic succession, potassium-argon dates, and vertebrate faunas, Vieja Group, Rim Rock County, Trans-Pecos Texas. American Journal of Science 266: 590-604.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K. (2001). Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292: 686–693.

The early Eocene radiation of Hyracoidea (Mammalia, Afrotheria): New fieldwork evidence from northwestern Africa

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Hyracoids are poorly diversified today, with only three small-sized genera restricted to Africa and the Middle East. In contrast, during the Paleogene they represented the dominant 'ungulate' group on the Arabo-African continent. Late Eocene to Oligocene sites from the Fayum in Egypt are particularly famous for their hyracoid fossil record (Rasmussen and Gutiérrez, 2010; Barrow *et al.*, 2010, and references cited therein). The beginning of the hyracoid radiation, however, is less well documented, since rare fragmentary specimens are known from only a few early to middle Eocene sites in North Africa. The oldest and most primitive hyracoid, *Seggeurius amourensis*, is known by few dental remains from the early Eocene of El Kohol, Algeria (Court and Mahboubi, 1993) and Ouled Abdoun Basin, Morocco (Gheerbrant *et al.*, 2003). Only three other early Paleogene fauna have yielded hyracoids: the Gour Lazib, Algeria, where three species have been described so far (*Microhyrax lavocati*, *Megalohyrax gevini*, and *Titanohyrax mongereaui*) (Sudre, 1979; Tabuce *et al.*, 2001, 2007), Chambi, Tunisia, with one species (*T. tantulus*) (Court and Hartenberger, 1992), and Black Crow, Namibia, also with one species (*Namahyrax corvus*) (Pickford *et al.*, 2008).

Our recent palaeontological fieldwork in the Gour Lazib and Chambi has led to the recovery of numerous mammalian specimens, among which are dental, cranial, and postcranial elements of hyracoids. All current data, including unpublished results, suggest that the faunas from the Gour Lazib and Chambi are penecontemporaneous, and date from the late early to earliest middle Eocene.

From Chambi, careful acid etching of the freshwater limestone helped in finding several new dental specimens belonging to *Titanohyrax tantulus*, including the previously unknown lower and upper premolars. This material, as well as a skull from the Gour Lazib (see below), confirms that the holotype bears a part of dP^2 and dP^3–M^1, as suggested by Barrow *et al.* (2010). More interestingly, the new material also documents the presence of two other species. The first one is significantly larger than *T. tantulus* and is represented by a fragmentary maxillary bearing badly preserved P^4–M^2. The relatively simple P^4 lacking a mesostyle, the bunoselenodont molars with protocone and hypocone of subequal size, and the moderately developed ectoloph with rounded styles suggest affinities with the genus *Megalohyrax*. The second species recently discovered at Chambi is *Microhyrax lavocati*. It is known from a partial juvenile mandible bearing $dP_{2\text{-}4}$ and from some isolated upper teeth.

The Gour Lazib area comprises now more than fifteen mammalian sites. Except for the locality HGL49 from the Glib Zegdou, which is the type-locality of *Titanohyrax mongereaui*, all the fossiliferous levels are situated in the middle member of the Glib Zegdou Formation and have delivered hyracoids through quarrying, screen washing, and acid-etching of sandstone. In particular, the localities HGL50, HGL51, and HGL53 from the Glib Zegdou, HGL10 from the east part of the Gour Lazib, and HGL61 from the Gour Idergane have yielded remarkable material, including associated craniodental and postcranial remains. In summary, our ongoing paleontological expeditions in this area have led to the recovery of at least seven penecontemporaneous hyracoid species, making the Gour Lazib the richest area documenting the early stage of hyracoid radiation. These taxa can be ecologically distinguished from each other thanks to their different dental morphologies that indicate several dietary specializations ranging from omnivory to folivory. Their estimated body-mass ranges from 3 kg to over 1000 kg. Moreover, several morphologicaly different astragali indicate generalist, arboreal and cursorial adaptations.

Among these seven species, *Microhyrax lavocati* is the smallest one. The new material includes several isolated teeth, fragmentary dentaries, and maxillaries from the Glib Zegdou (HGL50 and HGL51), as well as two partial skulls from HGL10 and HGL61. These specimens document, for the first time, the upper dentition of *Microhyrax* (the maxillary and upper molar published by Tabuce *et al.* (2001, 2007) are now attributed to *Helioseus*). At HGL61, several lower jaws represent a new species of *Microhyrax* slightly larger than *M. lavocati*. *Helioseus insolitus* is another small species, which is very abundant at HGL51. It is characterized by plagiaulacoid premolars, a morphology which is unique within the order Hyracoidea (Tabuce *et al.*, 2010). *Helioseus* is now documented by numerous postcranial elements and partial skeletons. A medium-sized taxon is represented by a single upper tooth, probably a molar, discovered at HGL50. Its preliminary assignment to ?*Thyrohyrax* sp. (Tabuce, in Adaci *et al*., 2007) is still uncertain. Until now, the largest species of the fauna were *Megalohyrax gevini* and *Titanohyrax mongereaui*, both only known by their holotype. The few new specimens referable to *M. gevini* do not enable to clarify the recently discussed generic status of this species (see Barrow *et al*., 2010). The same is true for *T. mongereaui*, which is still known only from its holotype. Another large-bodied species known from several isolated teeth and postcranial elements represents another species of *Titanohyrax*. The generic assignment is supported by the occurrence of well-developed metastylids on molars and spatulate (not hyperpectinate) lower incisors. This taxon differs from *T. mongereaui* in being higher crowned. Finally, a third titanohyracid, *T.* cf. *tantulus*, is represented at HGL10 by a damaged ?P^4 and at HGL53 by a yet undescribed complete skull. With the exception of *T. tantulus* from Chambi, which is slightly smaller, *T.* cf. *tantulus* from the Gour Lazib differs notably from all other members of the genus by its small size (it is half as large as *Titanohyrax* nov. sp. from L-41; see Rasmussen and Gutiérrez, 2010), less molariform premolars (P^2 without mesostyle), and less labially expanded styles.

To conclude, the diversity of hyracoids in the first part of the Maghrebian Eocene is remarkable and surprising at such an early age. This diversity is comparable to that found later in the Fayum. Moreover, as in the Egyptian localities and following the recent taxonomy proposed by Rasmussen and Guttiérez (2010), the discovered genera belong to the Geniohyidae (*Seggeurius*), Saghatheriidae (e.g., *Microhyrax* and *Megalohyrax*), and Titanohyracidae. This diversity and the degree of specialization of some taxa (e.g., *Helioseus insolitus* and *Titanohyrax tantulus*) indicate that the basal radiation of hyracoids occurred no later than the early Eocene, or even earlier. Recently, Barrow *et al.* (2010) proposed a large-scale phylogeny of basal Afrotheria, among which most of the Paleogene hyracoids. The inferred taxonomy of hyracoids resulting from this phylogenetic analysis differs significantly from the formal taxonomy proposed by Rasmussen and Guttiérez (2010). Among other results, Barrow *et al.* (2010) rejected the monophyly of Saghatheriidae and argued that *Microhyrax* and *Seggeurius* are basal hyracoids along with *Dimaitherium* from the Priabonian Birket Qarun Formation, Fayum. They also suggested that *Megalohyrax gevini* and *Titanohyrax mongereaui* from the Gour Lazib do not necessarily belong to their respective genera. They concluded that there is no compelling evidence for an early Eocene (or Paleocene) divergence of the Fayum hyracoid lineages. Importantly, Barrow *et al.* (2010) insisted that their phylogeny could be potentially biased by our current poor knowledge of the early Eocene hyracoids. So, ongoing studies of both the craniodental and postcranial anatomy of the hyracoids from the Gour Lazib and Chambi will undoubtedly clarify the basal phylogeny of this mammalian order.

Adaci, M., Tabuce, R., Mebrouk, F., Bensalah, M., Fabre, P.-H., Hautier, L., Jaeger, J.-J., Lazzari, V., Mahboubi, M., Marivaux, L., Otero, O., Peigné, S., Tong, H. (2007). Nouveaux sites à vertébrés paléogènes dans la région des Gour Lazib (Sahara Nord-occidental, Algérie). Comptes Rendus Palevol 6: 535–544.

Barrow, E.C., Seiffert, E.R., Simons, E.L. (2010). A primitive hyracoid (Mammalia, Paenungulata) from the early Priabonian (late Eocene) of Egypt. Journal of Systematic Palaeontology 8: 213-244.

Court, N., Hartenberger, J.-L. (1992). A new species of the hyracoid mammal *Titanohyrax* from the Eocene of Tunisia. Palaeontology 35: 309-317.

Court, N., Mahboubi, M. (1993). Reassessment of lower Eocene *Seggeurius amourensis*: aspect of primitive dental morphology in the mammalian order Hyracoidea. Journal of Paleontology 67: 889-893.

Gheerbrant, E., Sudre, J., Cappetta, H., Mourer-Chauviré, C., Bourdon, E., Iarochene, M., Amaghzaz, M., Bouya, B. (2003). Les localités à mammifères des carrières de Grand Daoui, bassin des Ouled Abdoun, Maroc, Yprésien : Premier état des lieux. Bulletin de la Société Géologique de France 174: 271-278.

Pickford, M., Senut, B., Morales, J., Mein, P., Sanchez, I.M. (2008). Mammalia from the Lutetian of Namibia. Memoir of the Geological Survey of Namibia 20: 465-514.

Rasmussen, D.T., Gutierrez, M. (2010). Hyracoidea. In: Sanders, W. J., Werdelin, L. (eds) Cenozoic Mammals of Africa. University of California Press, pp 123-145.

Sudre, J. 1979. Nouveaux mammifères éocènes du Sahara Occidental. Palaeovertabrata 9: 83-115.

Tabuce, R., Mahboubi, M., Sudre, J. (2001). Reassessment of the Algerian Eocene Hyracoid *Microhyrax*: The early diversity and basal phylogeny of the Order Hyracoidea (Mammalia). Eclogae geologica Helvetiae 94: 537-545.

Tabuce, R., Adaci, M., Hautier, L., Mennecart, B., Mahboubi, M. (2010). Solving the mystery of the enigmatic mammal *Helioseus insolitus*: A highly derived hyrax from the Eocene of Gour Lazib, Algeria. Journal of Vertebrate Paleontology, SVP Program and Abstracts Book, 2010, 173A.

Middle Eocene rodents from the Rocky Mountains: Temporal variation in diversity

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After the Bridgerian Crash, North American mammalian faunas went through a major reorganization as climates deteriorated. At a continental level, mammals experienced a major drop in taxonomic richness at the end of the Early Eocene Climatic Optimum (EECO) and then underwent another diversity increase towards the end of the middle Eocene (Woodburne *et al*., 2009).

Rodents went through a major diversification after the EECO, with an increase in generic richness during the Uintan North America Land Mammal Age (NALMA) from the preceding Bridgerian NALMA (Gunnell *et al.*, 2009; Woodburne *et al.*, 2009). The aim of this pilot study is to begin to evaluate the mechanisms that regulate rodent diversity by focusing on temporal variation in diversity within a restricted region: the Rocky Mountain intermontane basins of Utah and Wyoming. During the transition from the Bridgerian to the Uintan NALMA, global cooling continued and likely had an effect on both local and regional faunas (Zachos *et al.*, 2001; Zachos *et al.*, 2008; Townsend *et al.*, 2010).

High-resolution stratigraphic fossil assemblages from the Green River Formation, Wyoming, and Uinta Formation, Utah, have increased both the known samples and taxa for both Bridgerian and Uintan NALMA mammals. The rodent faunal list from the Bridgerian NALMA of Wyoming has 86 species from six families, while the younger Uintan NALMA faunas from Utah have 63 species and as many as eight families. The body size diversity of these two rodent faunas is also quite different: there is an increase of larger-bodied rodents in the Uintan NALMA that were not present during the Bridgerian NALMA. Body mass estimates for Bridgerian rodents indicate the largest taxa were only 1.5 kg, whereas some species from the Uintan are more than 1 kg heavier. Both assemblages maintain very small rodents. This suggests that as the composition of these communities changed through time, species richness was not maintained.

GUNNELL, G.F., MURPHEY, P.C., STUCKY, R.K., TOWNSEND, K.E., ROBINSON, P., ZONNEVELD, J.P., BARTELS, W.S. (2009). Biostratigraphy and biochronology of the latest Wasatchian, Bridgerian, and Uintan North American Land-Mammal “Ages”. In: Albright, B. (ed) Geology, Vertebrate Paleontology, and Biostratigraphy in Honor of Michael O. Woodburne. Museum of Northern Arizona Bulletin v. 65, pp 279-330.

TOWNSEND, K.E.B., RASMUSSEN, D.T., MURPHEY, P.C., EVANOFF, E. (2010). Middle Eocene habitat shifts in the North American Western interior: A case study. Palaeogeography, Palaeclimatology, Palaeoecology 297: 144-158.

WOODBURNE, M.O., GUNNELL, G.F., STUCKY, R.K. (2009). Land mammal faunas of North American rise and fall during the Early Eocene Climatic Optimum. Annals of Denver Museum of Nature and Science 1: 1-74.

ZACHOS, J., DICKENS, G., ZEEBE, R. (2008). An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. Nature 451: 279-283.

ZACHOS, J., PAGANI, M., SLOAN, L., THOMAS, E., BILLUPS, K. (2001). Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292: 686–693.

Exceptional geochemical preservation of vertebrate remains from the Eocene Messel Pit, Germany – Paleoenvironmental and paleoecological implications of the stable isotope signatures

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The 47-Myr-old middle Eocene oil shale deposits of the UNESCO World Heritage Site Messel (Mertz and Renne, 2005) are famous for their exceptionally well-preserved articulated vertebrate fossils that often still display soft tissue preservation. The cause is the special taphonomic situation – anoxic bottom-water conditions – of the Lagerstätte, which prevailed during the more than 600 ka existence of the Messel maar lake.

The isotopic compositions of oxygen, carbon and strontium were analyzed from the fossil skeletal remains of some of Messel's terrestrial (propalaeothere) and aquatic vertebrates (fish, turtle and crocodile) to determine the condition of geochemical preservation. Phosphatic coprolites, authigenic phosphate (messelite, montgomeryite), and carbonate (siderite) minerals, as well as the embedding oil shale, were also analyzed to characterize the isotope compositions of diagenetic mineral phases.

The oil shale and siderite have values of $\delta^{18}O_{CO3}$ (0.3 to 1.5‰) and $\delta^{13}C_{CO3}$ (14.8 to 17.8‰); these are much higher than those of all vertebrate remains (Fig. 1). Such positive values are typical for siderite from Messel and other Eocene anoxic lake settings (Felder and Gaupp, 2006). The strong ^{13}C enrichment is likely due to methanogenesis in the anoxic bottom water of Lake Messel. The enamel of *Propalaeotherium,* a European genus of early hippomorph perissodactyls, has preserved, low $\delta^{13}C$ values of around −8.8±0.7‰ (n=6), typical for C_3 plant feeders (Fig. 1). This is in accordance with its presumed leaf-dominated diet in a C_3-plant ecosystem. In contrast, the dentin of the same teeth has about 17‰ higher $\delta^{13}C$ values, which indicates a significant diagenetic alteration of the dentin. Bone and dentin of the aquatic vertebrates also have positive $\delta^{13}C$

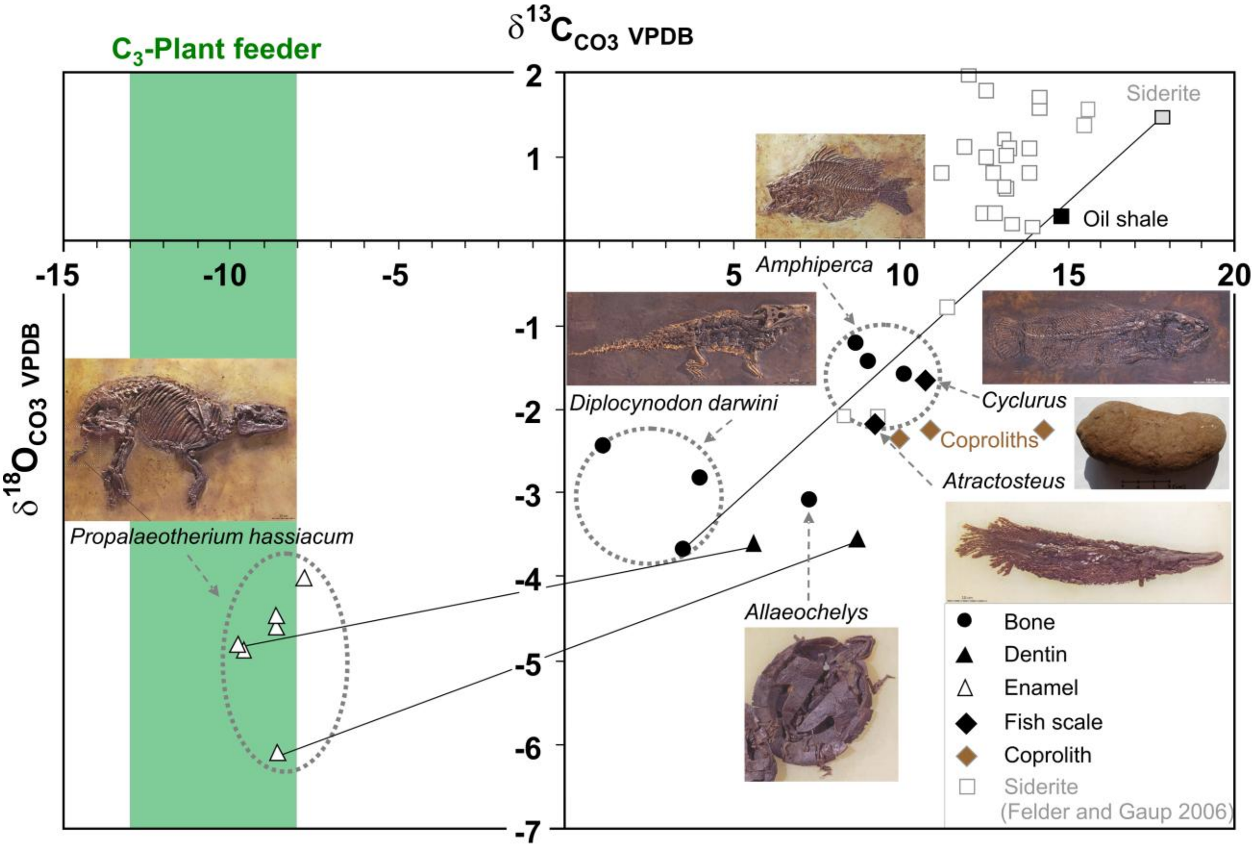

Figure 1. $\delta^{13}C$ and $\delta^{18}O$ values of the structural carbonate in the bioapatite of fossil skeletal remains of different terrestrial and aquatic vertebrates as well as some coproliths from Messel. For comparison isotopic values of siderite from Messel after Felder and Gaupp (2006) are given. These likely represent the isotopic values of the diagenetic endmember because siderite forms during early diagenesis under anoxic bottom-water conditions. The lines connect enamel and dentin samples from the same tooth and in the other case bone, siderite crust, and embedding oil shale of the crocodile specimen. In green the range of bioapatite $\delta^{13}C$ values typical for mammals feeding on C_3 plants is highlighted.

values from 1.1 up to 10.8‰ (Fig. 1). These are among the highest $\delta^{13}C$ values reported for skeletal apatite so far, and likely result from diagenetic alteration and/or indicate high $\delta^{13}C$ values of dissolved inorganic carbon in the lake water.

However, the enamel still contains *in vivo* values and seems geochemically well preserved. This is further supported by a high enamel $^{87}Sr/^{86}Sr$ value of 0.7114, reflecting the feeding habits of *Propalaeotherium* on Permian sedimentary and granitoid bedrocks in the area surrounding Messel Lake. Furthermore, the dentin of the same tooth has a much lower $^{87}Sr/^{86}Sr$ value of 0.7057, clearly indicating diagenetic Sr uptake from the volcanically influenced lake/pore water of the Messel maar lake. This is further supported by the low bone $^{87}Sr/^{86}Sr$ value of 0.7047 of the aquatic crocodile *Diplocynodon darwini.*

Enamel $\delta^{18}O_{PO4}$ values of the *Propalaeotherium* teeth are systematically lower than those of the dentin from the same teeth as well as the bones and scales of most aquatic vertebrates. This further corroborates the preservation of biogenic values in enamel. Hence, enamel $\delta^{18}O_{PO4}$ values (18.1±0.6‰, n=6) can be used to infer the $\delta^{18}O$ value of water ingested by *Propalaeotherium* by using a transfer function for modern mammals (Amiot *et al.*, 2004). The calculated drinking water $\delta^{18}O_{H2O}$ value is –6.4±0.7‰, which is about 2‰ higher than that of the modern precipitation number in the Messel area, reflecting significantly warmer climate conditions during the middle Eocene. Using a global modern-day $\delta^{18}O_{H2O}$-air-temperature relation (Amiot *et al.*, 2004) a mean annual temperature (MAT) of around 18±2°C can be determined. This value is similar to but somewhat lower than the MAT of approximately 22°C inferred for Messel from paleobotanical proxies (Grein *et al.*, 2011). Using the $\delta^{18}O_{PO4}$ value of a single turtle bone, the $\delta^{18}O_{H2O}$ of Lake Messel can be tentatively estimated to be –0.5‰, hence the lake water was ^{18}O-enriched compared to meteoric water, which is not uncommon for longterm lakes (Tütken *et al.*, 2006). Using this $\delta^{18}O_{H2O}$ and the fish scale $\delta^{18}O_{PO4}$ values, the phosphate–water fractionation equation of Longinelli and Nuti (1973) yields a water temperature of around 22°±3°C, which is in good agreement with the MAT inferred from paleobotanical data by Grein *et al.* (2011).

In conclusion, not only are the vertebrate carcasses of Messel exceptionally well preserved but also the geochemical composition of their tooth enamel. Enamel of *Propalaeotherium* still contains original C, O, and Sr isotope compositions, while bone and dentin samples appear clearly diagenetically altered. Isotope analysis of enamel from Messel vertebrates can thus be used to recontruct their diet, habitat use and mobility, yielding new insights into the paleoenvironment and the paleoecology of the Messel ecosystem.

Amiot, R., Lécuyer, C., Buffetaut, E., Fluteau, F., Legendre, S., Martineau, F. (2004). Latitudinal temperature gradient during the Cretaceous Upper Campanian–Middle Maastrichtian: $\delta^{18}O$ record of continental vertebrates. Earth and Planetary Science Letters 226: 255-272.

Felder, M., Gaupp, R. (2006). The $\delta^{13}C$ and $\delta^{18}O$ signatures of siderite – A tool to discriminate mixis patterns in ancient lakes. Zeitschrift der Deutschen Gesellschaft für Geowissenschaften 157/3: 387-410.

Grein, M., Utescher, T., Wilde, V., Roth-Nebelsick, A. (2011). Reconstruction of the middle Eocene climate of Messel using palaeobotanical data. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 260: 305-318.

Longinelli, A., Nuti, S. (1973). Revised phosphate–water isotopic temperature scale. Earth and Planetary Science Letters 19: 373-376.

Mertz, D.F., Renne, P.R. (2005). A numerical age for the Messel fossil deposit (Unesco World Natural Heritage Site) from $^{40}Ar/^{39}Ar$ dating. Courier Forschungsinstitut Senckenberg 255: 67-75.

Tütken, T., Vennemann, T.W, Janz, H., Heizmann, H.E.P (2006). Palaeoenvironment and palaeoclimate of the Middle Miocene lake in the Steinheim basin, SW Germany, a reconstruction from C, O, and Sr isotopes of fossil remains. Palaeogeography, Palaeoclimatology, Palaeoecology 241: 457-491.

Eocene mammal record in the Erlian Basin, Inner Mongolia, China

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The Erlian Basin, Inner Mongolia, China, has well-exposed Paleogene strata that are rich in fossil mammals. Many mammalian specimens have been collected from a number of localities (Fig. 1) (Russell and Zhai, 1987). Four Asian Land Mammal ages (ALMA) – the Arshantan, Irdinmanhan, Sharamurunian, and Ulangochuan – were proposed on the basis of the mammalian faunas from the Erlian Basin (Luterbacher *et al.*, 2004). The Paleogene lacustrine and alluvial deposits of the Erlian Basin are represented, in the eastern part, by four formations: the Nomogen Fm., the Arshanto Fm., the Irdin Manha Fm., and the Houldjin Fm. In the western part, the deposits are subdivided into seven formations: the Nomogen Fm., the Ulan Shireh Fm., the Tuhkum Fm., the Shara Murun Fm., the Ulan Gochu Fm., the Baron Sog Fm., and the Upper Naogangdai Fm. (Berkey *et al.*, 1929; Berkey and Morris, 1927; Jiang, 1983) (Tab. 1).

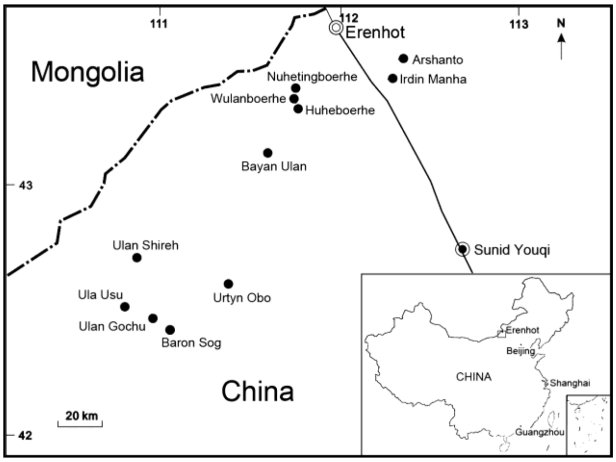

Figure 1. Sketch map showing the Eocene mammal localities in the Erlian Basin, Inner Mongolia, China.

The Eocene mammals found in the Erlian Basin are identified as being from five ALMAs. Recent investigations have clarified a number of long-standing stratigraphic problems (Meng *et al.*, 2007; Wang *et al.*, 2010), which allows the fauna lists to be annotated. The Bumbanian mammals of the Erlian Basin were recently reported from the upper Nomogen Fm. in the Huhebuerhe area (Meng *et al.*, 2004). They include *Gomphos elkema* (Mimotonida), *Yuanomys zhoui* (Rodentia), *Baataromomys ulaanus* (Primates), *Anatolostylops zhaii* (Arctostylopida), *Minchenoletes erlianensis*, and *Pataecops parvus* (Perissodactyla).

The Arshantan fauna was found in the eastern part of the basin and consists of 27 species: *Uintatherium* sp. and *Gobiatherium mirificum* (Dinocerata), *Sinosinopa sinensis* (Micropternodontidae), *Breviodon minutes*, *Schlosseria magister*, *Homogalax reliquius*, *Helaletes medius*, *Heptodon minimus*, *Hyrachyus neimongoliensis*, cf. *H. eximius*, *Teleolophus primaries*, *T.*? *rectus*, *Telmatherium cristatum*, *Desmatotitan* sp., *Microtitan* sp., *Fostercooperia huhebulakensis*, *F.*? *grandis* (Perissodactyla), *Pantolambdodon fortis* and *P.*? *minor*, *Eudinoceras mongoliensis* (Pantodonta), *Mesonyx* cf. *obtusidens*, *Hapalodectes serus*, and *Mongolonyx dolichognathus* (Mesonychia), *Dawsonolagus antiquus* (Lagomorpha), *Tamquammys wilsoni*, *Asiomys dawsoni*, *Archetypomys erlianensis*, and *Erlianomys combinatus* (Rodentia).

The Irdinmanhan fauna were represented by fossils from the Irdin Manha Fm. in the eastern part and from the Ulan Shireh and the Tuhkum formations in the western part of the basin. Mammals from the Irdin Manha Fm. include cf. *Archaeomeryx* sp., *Gobiohyus orientalis*, *G. pressidens*, *G. robustus* (Artiodactyla), *Protitan grangeri*, *P. robustus*, *P. obliquidens*, *Microtitan mongoliensis*, *Gnathotitan berkeyi*, *Metatelmatherium parvum*, *Forstercooperia totadentata*, *Triplopus*? *proficiens*, *Helaletes mongoliensis*, *Lophialetes expeditus*, *Teleolophus medius* (Perissodactyla), *Sarkastodon mongoliensis*, *Paracynohyaenodon morrisi*, *Propterodon irdinensis* (Creodonta), *Miacis invictus* (Carnivora), *Pachyaena* sp., *Andrewsarchus mongoliensis* (Mesonychia), the didymoconid *Mongoloryctes auctus*, the pantolestid ?*Pantolestes* sp., the tarkadectine primate *Tarkops mckennai*, and the mimotonid *Gomphos shevyrevae*.

Fossil mammals from the Ulan Shireh Fm. are *Sarkastodon mongoliensis*, cf. *Propterodon morrisi* (Creodonta), *Hapalodectes*? *serus*, *Harpagolestes*? *orientalis* (Mesonychia), *Eudinoceras mongoliensis*, *Pantolambdodon inermis*, *P. fortis* (Pantodonta), *Gobiohyus orientalis*? (Artiodactyla), *Desmatotitan tukhumensis*, *Microtitan mongoliensis*, *Acrotitan ulanshirehensis*, *Protitan grangeri*, *Epimanteoceras formosus*, *Lophialetes expeditus*?, *Breviodon acares*, *Zhongjianoletes chowi*, *Simplaletes ulanshirehensis*, *Teleolophus medius*?, *Forstercooperia* cf. *F. grandis*, *Lushiamynodon sharamurenensis, Triplopus*? *proficiens*, *Rhodopagus pygmaeus* (Perissodactyla), *Advenimus bohlini*, *Yuomys weijingensis* (Rodentia), *Shamolagus grangeri* (Lagomorpha), a didymoconid *Kennatherium shirensis*. Only the hyracodontid perissodactyl *Teilhardia pretiosa* was reported from the Tuhkum Fm.

The Sharamurunian fauna was found from the Shara Murun Fm. only in the western part of the Erlian Basin. It consists of *Shamolagus medius* and *Gobiolagus tolmachovi* (Lagomorpha), *Yuomys*

Epoch		ALMA	Lithostratigraphic Units	
			Western Erlian Basin	Eastern Erlian Basin
Early Oligocene		Hsandagolian	Upper Naogangdai Fm.	
Eocene	Late	Ulangochuan	Baron Sog Fm.	Houldjin Fm.
			Ulan Gochu Fm.	
	Middle	Sharamurunian	Shara Murun Fm.	
		Irdinmanhan	Tuhkum Fm. Ulan Shireh Fm.	Irdin Manha Fm.
	Early	Arshantan		Arshanto Fm.
		Bumbanian	Nomogen Fm.	
Late Paleocene		Gashatan		

Table 1. General scheme of Paleogene stratigraphy in the Erlian Basin.

cavioides (Rodentia), *Pterodon hyaenoides* (Creodonta), *Ulausuodon parvus*, *Archaeomeryx optatus* (Artiodactyla), *Rhinotitan mongoliensis*, *R. kaiseni*, *R. andrewsi*, *Pachytitan ajax*, *Embolotherim grangeri*, *Lushiamynodon sharamurenensis*, *Gigantamynodon promisus*, *Caenolophus promissus*, *C. obliquus*, *Juxia sharamurenense*, *Triplopus*? *progressus*, *Sianodon ulausuensis*, *Deperetella cristata*, *Rhodopagus*? *minimus*, *Amynodon mongoliensis*, (Perissodactyla), *Olsenia mira* (Mesonychia).

The Ulangochuan fauna include Embolotherium *andrewsi*, *Zaisanamynodon borisovi* (Perissodactyla), and *Lophiomeryx anagare* (Artiodactyla) from the Baron Sog Fm. and a brontotheriid perissodactyl *Embolotherium grangeri* from the Ulan Gochu Fm.

The Eocene mammalian faunas of the Erlian Basin did not have age constraints until recently, when the paleomagnetic work was done on some sections (Bowen *et al.*, 2005; Sun *et al.*, 2009). The paleomagnetic results show that the Bumbanian ALMA is equivalent to the middle part of the Chron C24r (55.8–54.8 Ma) and the Arshantan ALMA correlates with the upper part of the Chron C24r to the Chron C21r (54.8–47.6 Ma) (Wang *et al.*, 2010). Given this result, at least part of the Irdinmanhan fauna could be correlated with the Messel Eocene mammal fauna. However, no species and few genera have been reported from both faunas (Morlo *et al.*, 2004), which may support the existence of an obstacle to the faunal interchange during the early Middle Eocene.

Berkey, C.P., Granger, W., Morris, F.K. (1929). Additional new formations in the later sediments of Mongolia. American Museum Novitates (385): 1–12.

Berkey, C.P., Morris, F.K. (1927). Geology of Mongolia—A Reconnaissance Report Based on the Investigations of the Years 1922–1923, Natural History of Central Asia, Volume II, 475pp.

Bowen, G.J., Koch, P.L., Meng, J., Ye, J., Ting, S-Y. (2005). Age and correlation of fossiliferous late Paleocene-early Eocene strata of the Erlian Basin, Inner Mongolia, China. American Museum Novitates (3474): 1–26.

Jiang, H-X. (1983). Division of the Paleogene in the Erlian Basin of Nei Mongol. Geology of Nei Mongol: 18–36.

Luterbacher, H.P., Ali, J.R., Brinkhuis, H., Gradstein, F.M., Hooker, J.J., Monechi, S., Ogg, J.G., Powell, J., Röhl, U., Sanfilippo, A., Schmitz, B., Gradstein, F.M., Ogg, J.G., Smith, A.G. (2004). The Paleogene Period. In: Gradstein, F.M., Ogg, J.G., Smith, A. (eds) A Geological Time Scale. Cambridge University Press, Cambridge, pp 384–408.

Meng, J., Bowen, G.J., Ye, J., Koch, P.L., Ting, S-Y., Li, Q., Jin, X. (2004). *Gomphos elkema* (Glires, Mammalia) from the Erlian Basin: Evidence for the early Tertiary Bumbanian Land Mammal Age in Nei-Mongol, China. American Museum Novitates (3245): 1–24.

Meng, J., Wang, Y-Q., Ni, X-J., Beard, K.C., Sun, C., Li., Q., Jin, X., Bai, B. (2007). New stratigraphic data from the Erlian Basin: Implications for the division, correlation, and definition of Paleogene lithological units in Nei Mongol (Inner Mongolia). American Museum Novitates (3570): 1–31.

Morlo, M., Schaal, S., Mayr, G., Seiffert, C. (2004). An annotated taxonomic list of Middle Eocene (MP 11) Vertebrata of Messel. Courier Forschungsinstitut Senckenberg 252: 95–108.

Russell, D.E., Zhai, R-J. (1987). The Paleogene of Asia: Mammals and Stratigraphy. Mémoires du Muséum National d'Histoire Naturelle, Série C, Sciences de la Terre 52: 448pp.

Sun, B., Yue, L-P., Wang, Y-Q., Meng, J., Wang, J-Q., Xu, Y. (2009). Magnetostratigraphy of the early Paleogene in the Erlian Basin. Journal of Stratigraphy 33: 62–68.

Wang, Y-Q., Meng, J., Beard, K.C., Li, Q., Ni, X-J., Gebo, D.L., Bai, B., Jin, X., Li, P. (2010). Early Paleogene stratigraphic sequence, mammalian evolution and its response to the environmental change in Erlian Basin, Inner Mongolia, China. Science China: Earth Sciences 53: 1918–1926.

Testing for the effects and consequences of mid-Paleogene climate change on insect herbivory

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The Eocene appears to have been one of the most biodiverse intervals in Earth's history (Jaramillo *et al.*, 2006), and is associated with the most extensive recent migration of the subtropical rainforest biome into the midlatitudinal region (Willis *et al.*, 2010). This trend began at the Paleocene-Eocene Thermal Maximum (54.8 Ma), an event defined by a global spike in elevated temperature and a dramatic carbon isotope excursion, as recorded in benthic foraminifera (Zachos *et al.*, 2001), and an association with increased atmospheric CO_2. Palaeoclimate calculations for the middle Eocene indicate that the era was also characterized by a subtropical-style climate regime (e.g., Grein *et al.*, 2011). We propose a framework to evaluate how terrestrial food webs evolved approximately 48–44 million years ago, close to the atmospheric CO_2 peak (Pearson, 2010), as well as to the thermal and mammalian species-diversity maxima of the early middle Eocene (Blondel, 2001). The Messel and Eckfeld Maar localities are well known for their great variety of remains, ranging from organic molecules, and plants and insects and their associations, to articulated mammals exhibiting soft-tissue preservation and stomach contents (Lutz *et al.*, 2010; Micklich and Gruber, 2007).

The ecology of plant-insect associations is currently a significant aspect of modern ecological research. Consequently, studies of insect herbivory on fossil leaves provide crucial information on the ecology of feeding associations and the association of plants and their insect herbivores that cannot otherwise be obtained separately from fossil record of plant macrofossils and insect body fossils.

We analyzed insect-feeding damage on 19,868 angiosperm leaves and scored each specimen for the presence or absence of 89 distinctive and diagnosable insect damage types (DTs) found in the total data set, allocated to five main functional feeding groups of external foliage feeding, galling, mining, oviposition, and piercing-and-sucking (Labandeira *et al.*, 2007). At both localities the spectrum of interactions included varied scale leaf scars indicating piercing-and-sucking, midrib and foliar galls, and serpentine to blotch mines. Additionally, margin feeding, hole feeding, skeletonization, bud feeding, and ovipositional damage were present (Fig. 1).

The inventory of insect damage occurring on plant hosts indicates an impressive spectrum of plant-insect associations (e.g., Wappler *et al.*, 2010; Winkler *et al.*, 2010; Hughes *et al.*, 2011). Interestingly, the work on the European flora from Messel and Eckfeld shows a much greater diversity of insect feeding than comparable, contemporaneous floras from North America, revealing another important, previously unknown component of the plant-host and insect-herbivore diversification event during the European Eocene. For the entire dataset, and considering five possible major functional feeding groups, there is a highly significant departure from the null expectation (χ^2= 86.5, DF = 4, p<0.001). These results further indicate a high diversity of damage types (DTs), particularly for highly specialized interactions such as mining or galling (χ^2_{Galls} = 28.5, DF = 2, p<0.001). This may be associated with the observation that high host specificity characterizes most known lineages of gallers and miners, and the presence of sclerophyllous, evergreen-dominated plant communities dominated much of the central European midlatitudinal region during the middle Eocene.

As well, in the relatively narrow time interval associated with Messel and Eckfeld, there are indications of a change in the composition of the herbivore fauna. If specialized DTs are counted, only 45% of the DTs present at Messel are recorded from the Eckfeld sample.

In summary, the European middle Eocene previously has not been subjected to such a detailed analysis of plant-insect associations, and the proposed project would present a significant, new and extended understanding of Eocene regional climate dynamics and how they differ from those of the present day.

BLONDEL, C. (2001). The Eocene–Oligocene ungulates from Western Europe and their environment. Palaeogeography, Palaeoclimatology, Palaeoecology 168: 125-139.

GREIN, M., UTESCHER, T., WILDE, V., ROTH-NEBELSICK, A. (2011). Reconstruction of the middle Eocene climate of Messel using palaeobotanical data. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 260: 305-318.

HUGHES, D., WAPPLER, T., LABANDEIRA, C.C. (2011). Ancient death-grip leaf scars reveal ant-fungal parasitism. Biology Letters 7: 67-70.

JARAMILLO, C., RUEDA, M.J., MORA, G. (2006). Cenozoic plant diversity in the Neotropics. Science 311: 1893-1896.

LABANDEIRA, C.C., WILF, P., JOHNSON, K., MARSH. F. (2007). Guide to Insect (and Other) Damage Types on Compressed Plant Fossils (Version 3.0—Spring 2007). Smithsonian Institution, Washington, D.C., 25pp. (http://paleobiology.si.edu/pdfs/InsectDamageGuide3.01.pdf)

LUTZ, H., KAULFUß, U., WAPPLER, T., LÖHNERTZ, W., WILDE, V., MERTZ, D.F., MINGRAM, J., FRANZEN, J.L., FRANKENHÄUSER, H., KOZIOL, M. (2010). Eckfeld Maar: Window into an Eocene terrestrial habitat in Central Europe. Acta Geologica Sinica 84: 984-1009.

MICKLICH, N., GRUBER, G. (2007). Messel – Treasures of the Eocene. Hessian State Museum, Darmstadt. 158 pp.

PEARSON, P.N. (2010). Increased atmospheric CO_2 during the middle Eocene. Science 330: 763-764.

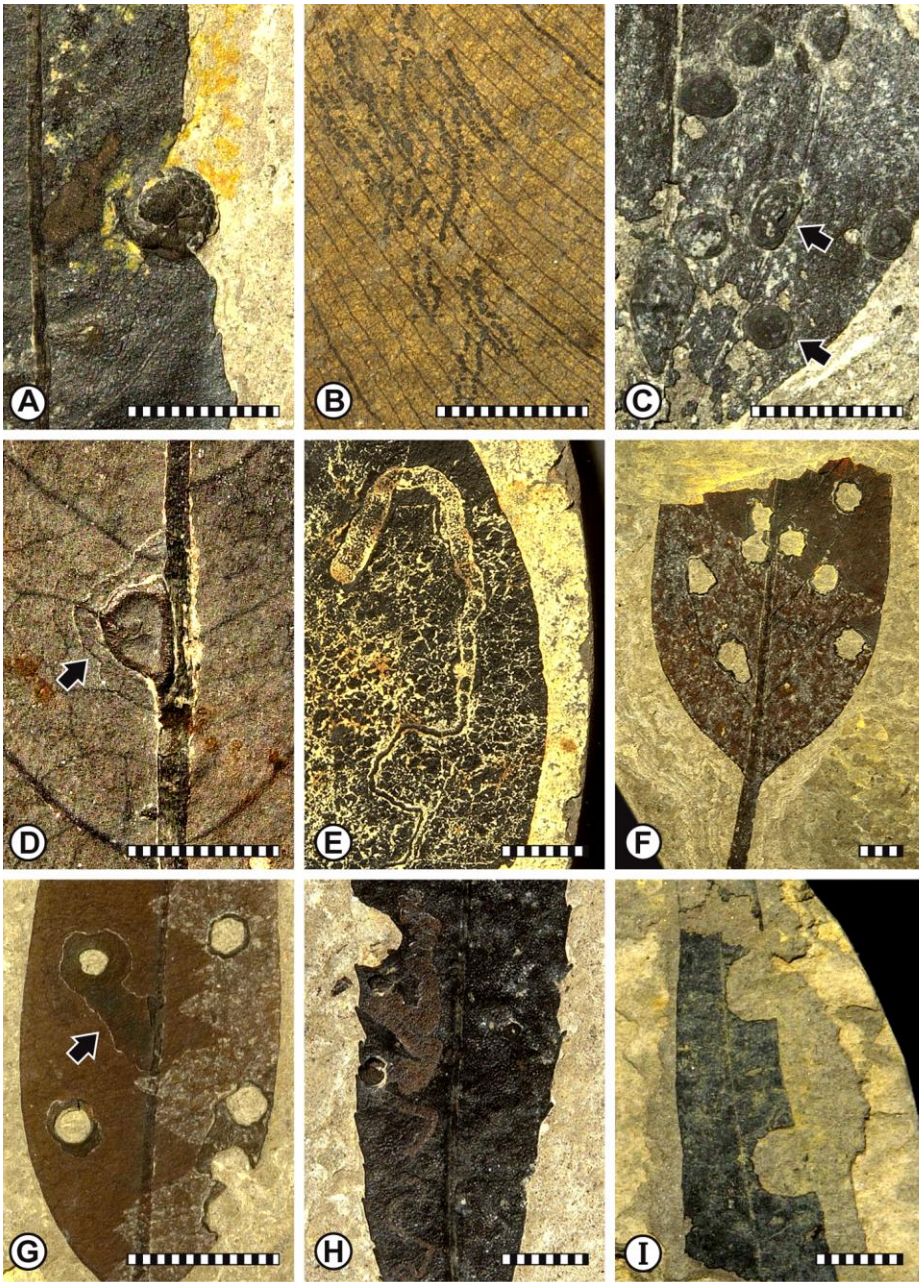

Figure 1. Examples of plant damage from a broad spectrum of insects known from the Messel and Eckfeld maar fossil sites. A. Well-preserved gall with delineation of concentric regions [DT163] (SMF Me 3591); B. Paired mandible chew marks on *Araciphyllites tertiarius* [DT219] (SMF Me 1396); C. Elongate and round scales of scale insects preserved in situ on a leaf blade (arrows) [DT191] (PB 2005-140, LS, NHMM) (Wappler and Ben-Dov, 2008); D. A broad zone of gall necrosis on surrounding plant tissue [DT163] (SMF Me 3198); E. Mine with and distinctively quadrangular terminal chamber [DT171] (SMF Me 3582); F. Gall attachment scars on a lauraceous leaf fragment [DT206] (SMF Me 21180); G. Circular holes with a broad flange of reaction tissue (arrow) [DT206] (SMF Me 21184); H. Strongly folded, serpentine mine consisting of modest width increases and containing particulate frass, on a walnut leaf [DT92] (SMF Me 13228); I. An unidentified dicot exhibiting typical margin excisions, most likely produced by megachilid bees [DT82] (PB 1990-527, LS, NHMM) (Wedmann *et al.*, 2009). Scale bar = 1 cm.

Wappler, T., Ben-Dov, Y. (2008). Preservation of armoured scale insects on angiosperm leaves from the Eocene of Germany. Acta Palaeontologica Polonica 53: 627-634.

Wappler, T., Tokuda, M., Yukawa, J., Wilde, V. (2010). Insect herbivores on *Laurophyllum lanigeroides* (Engelhardt 1992) Wilde: A role of a distinct plant-insect associational suite in host taxonomic assignment. Palaeontographica Abt. B 283: 137-155.

Wedmann, S., Wappler, T., Engel, M.S. (2009). Direct and indirect fossil records of megachilid bees from the Paleogene of Central Europe (Hymenoptera: Megachilidae). Naturwissenschaften 96: 703-712.

Willis, K.J., Bailey, R.M., Bhagwat, S.A., Birks, H.J.B. (2010). Biodiversity baselines, thresholds and resilience: Testing predictions and assumptions using palaeoecological data. Trends in Ecology & Evolution 25: 583-591.

Winkler, I.S., Labandeira, C.C., Wappler, T., Wilf, P. (2010). Distinguishing fossil Agromyzidae (Diptera) leaf mines in the fossil record: New taxa from the Paleogene of North America and Germany and their evolutionary implications. Journal of Paleontology 84: 935-954.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K. (2001). Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292: 686-693.

Insects from the Eocene of Messel and their biogeographical implications

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For insects, the Eocene is one of the best-documented geological periods. Eocene fossil deposits in which insects are very frequently found include the Green River Formation and Florissant in North America, and the Baltic amber and the former maar lakes of Eckfeld and Messel of Europe.

For Messel, ongoing excavations have yielded a multitude of insect fossils (e.g., Wedmann, 2005), which offer unique insights into the terrestrial and lacustrine paleoecosystems from about 47 million years ago.

Various studies of insects from Messel show a wide range of biogeographic relationships. Among beetles, the jewel beetles (Buprestidae) (Fig. 1A) belonging to extant genera show quite strong neotropical affinities, but there are also groups that are now distributed in the African, Oriental and Palaearctic regions. Click beetles (Elateridae) from Messel that can be assigned to extant genera show relationships to the Neotropical, Palaearctic, Australian and Oriental regions. Extant relatives of the tenebrionid beetle *Ceropria? messelense* are distributed in the African, Oriental and Australian regions.

Among other insect groups the wide range of biogeographical relationships is as impressive as among beetles. Most of the lace bugs (Tingidae) from Messel show relationships to those from the Oriental and African regions as well as from the Palaearctic region (Wappler, 2003). The closest extant relatives of the extinct mantidfly *Symphrasites eocenicus* (Neuroptera: Mantispidae) are distributed in the southernmost Nearctical and in the Neotropical region. Weaver ants (Formicidae) from Messel are the oldest fossil representatives of the extant genus *Oecophylla* (Fig. 1B), which today is distributed only in the Oriental, Australian and African regions. The species of the ant genus *Gesomyrmex* from Messel also are the oldest fossil representatives of this extant genus, which today occurs only in the Oriental region. Closely related to the extinct giant ant species *Titanomyrma simillimum* and *T. giganteum* from Messel (Hymenoptera: Formicidae) is a newly described species of the same genus from the 49.5-million-year-old Laney Member of the Green River Formation, North America (Archibald *et al.*, 2011). Giant ants were also recorded from the middle Eocene of southern England and from the lower Eocene of Tennessee, North America. Therefore, giant ants are an example for a former trans-Atlantic distribution.

The fossil record of a leaf insect (Phasmatodea: Phylliinae) from Messel shows that the former geographic range of this taxon was distinctly different from its recent distribution. At present, all species of leaf insects are distributed primarily in south-east Asia and adjacent regions, stressing the Oriental and Australian affinities.

A bombyliid fly of the genus *Comptosia* recorded from Messel is the oldest representative of this genus in the Holarctic region. Today the genus *Comptosia* is distributed only in the Australian region. Its closest related extant genera are known from southern South America, and this group of genera was previously given as a classical example for a Gondwana distribution (Hennig, 1966). Together with another, more completely preserved fossil record from the late Eocene of Florissant, North America, the Messel fossils argue against this interpretation (Wedmann and Yeates, 2008). These findings suggest that the genus *Comptosia* and its relatives were more widespread in both Northern and Southern hemispheres during the Paleogene. The very restricted distribution of

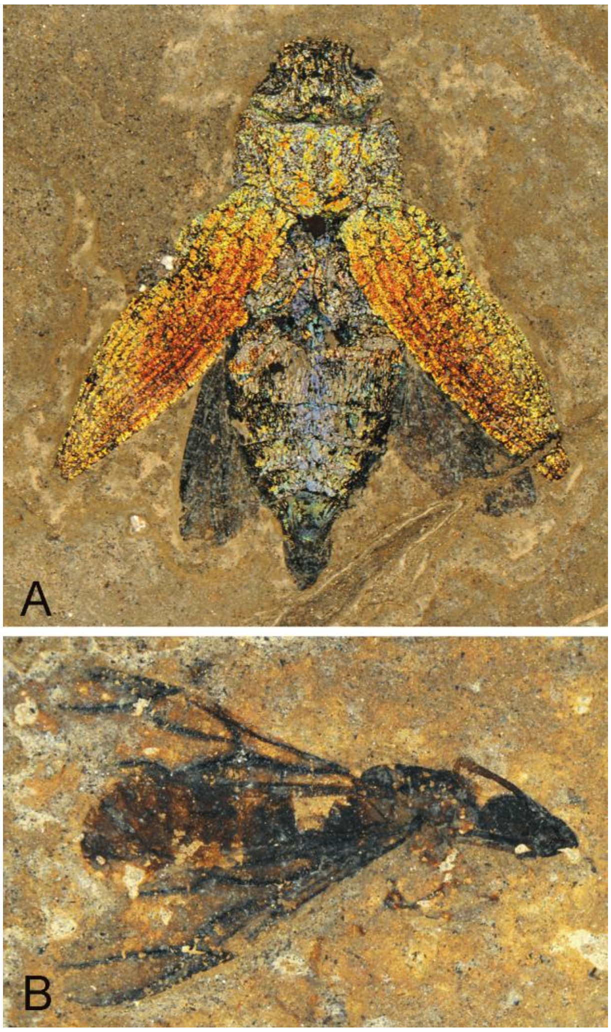

Figure 1. Insects from Messel. **A.** Jewel beetle *Lampetis weigelti* (Pongracz, 1935), Mel 6801, body length 19 mm, coll. Senckenberg. This genus today has its main biodiversity in the Neotropics, but also occurs in other warm regions worldwide. **B.** weaver ant *Oecophylla longiceps* Dlussky, 2008, Mel 13572, body length 15 mm, coll. Senckenberg. This genus is today distributed in the African, Oriental and Australian regions.

Comptosia in the Australian region seems to be a relict distribution which probably had its origin in the post-Eocene climate development.

As outlined above and detected in different studies of insects from other localities, fossil records of many insect groups are located far outside their extant distribution (e.g., Eskov, 2002; Grimaldi and Engel, 2005). For the Eocene insect fauna of Messel, there seems to be no favoured connection to a specific biogeographic region. The varying connections support the assumption that the warm and much more equable Eocene climate allowed a much wider distribution of many insect groups. For many insects the present distribution seems to be relict compared to their Eocene distribution.

The varying biogeographic connections of the insects from Messel also show that during the Eocene, faunal associations existed in higher latitudes for which no analogies exist today. This means that ecological relationships cannot be reconstructed on the basis of the extant faunas only, and that they were very different from today. It seems that during the Eocene, Europe was a hotspot of insect biodiversity.

Archibald, S.B., Johnson, K.R., Mathewes, R.W., Greenwood, D.R. (2011). Intercontinental dispersal of giant thermophilic ants across the Arctic during early Eocene hyperthermals. Proceedings of the Royal Society B: doi 10.1098/rspb.2011.0729.

Eskov, K.Y. (2002). Geographical history of insects. In: Rasnitsyn A.P., Quicke D.L.J. (eds) History of Insects. Kluwer Academic Publishers, Dordrecht, pp 427–435.

Grimaldi, D.A., Engel, M.S. (2005). Evolution of the insects. Cambridge University Press, Cambridge. 755pp.

Hennig, W. (1966). The Diptera fauna of New Zealand as a problem in systematics and zoogeography. Pacific Insects Monograph 9: 1-81.

Wappler, T. (2003). New fossil lace bugs (Heteroptera: Tingidae) from the Middle Eocene of the Grube Messel (Germany), with a catalog of fossil lace bugs. Zootaxa 374: 1-26.

Wedmann, S. (2005). Annotated taxon-list of the invertebrate animals from the Eocene fossil site Grube Messel near Darmstadt, Germany. Courier Forschungsinstitut Senckenberg 255: 103-110.

Wedmann, S., Yeates, D. (2008). Eocene records of bee flies (Insecta, Diptera, Bombyliidae, *Comptosia*): Their paleobiogeographic implications and remarks on the evolutionary history of bombyliids. Palaeontology 51: 231-240.

Paleoecology of a primate-friendly, late middle Eocene (late Uintan), tropical rain forest/mangrove swamp community from Laredo, Texas, USA

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The Casa Blanca fossil community inhabited a tropical rain forest/estuarine mangrove swamp which supported both cercomoniine and omomyid primates (Fig. 1). The fauna was recovered from the late middle Eocene (late Uintan North American Land Mammal Age), Laredo Formation (Claiborne Group) in Lake Casa Blanca International State Park in Laredo, Texas. The presence of *Mahgarita* cf. *M. stevensi* at Lake Casa Blanca marks the oldest record of the subfamily Cercomoniinae in the New World (Westgate *et al.*, 2010). It is significant that two skulls and a mandible of the cercomoniine *Mahgarita stevensi* from the upper Devil's Graveyard Formation (DGF) are the only records of early Duchesnean primates in Texas. Similarly, the skull of the questionable omomyid, *Rooneyia viejaensis*, from the Vieja region of Trans-Pecos, TX, is the sole record of a late Duchesnean primate in Texas.

Casa Blanca omomyids are represented by about 50 isolated teeth from a small *Mytonius* (new species description in progress) and a large undetermined genus. A fourth primate species is represented by an unidentified upper molar and probably represents a third omomyid species. This level of omomyid diversity equals that of the Uinta C portion of the Uinta Formation in the Uinta Basin of Uintah County, Utah, where *Mytonius*, *Ourayia*, and an *Omomys*-sized omomyid have been recovered (Walsh, 1996; Westgate *et al.* 2008). However, no adapids are known from the Uinta Formation (Williams and Kirk, 2008). The Casa Blanca primate diversity mirrors that of the Uinta C correlate, the middle portion of the DGF in Trans-Pecos, TX. Williams and Kirk (2008) listed the occurrence of three Uinta C omomyids and an adapiform in the DGF. The omomyids are *Diablomomys dalquesti, Omomys carteri* and *Mytonius hopsoni.*

Evidence for the paleoecologic conditions in the forest and estuary comes from plants, estuarine invertebrates, and vertebrates. Plant remains include pollen, spores, fruits, leaves, and wood. Three main plant communities comprised *Nypa* mangrove swamps; a back mangrove swamp with trees and *Acrostichum* ferns; and a lowland tropical rain forest with woody dicots, palms, ferns, and epiphytes (Gee, 2007). *Nypa* mangroves suggest water temperatures were 24°C or greater (Gee, 2007).

The invertebrate assemblage is dominated by the estuarine oyster *Crassostrea amichel* in association with mussels preserved as molds. Nearly all molluscan shells having aragonitic composition were destroyed by post-depositional diagenesis. Modern

Figure. 1. Artistic reconstruction of the Casa Blanca community by Abby Salazar (Westgate, 1999).

Crassostrea prefer salinities of 10–30 ppt, with most productive reefs growing in salinities averaging about 20 ppt. In Laredo Formation outcrops near Lake Casa Blanca, mud lobster burrows may be found below *Crassostrea* reefs, and callianassid ghost shrimp burrows are common in laminated sandstone facies.

The fish and reptilian assemblage provides environmental clues based on modern habitat preferences and geographic distributions of the closest living relatives of the fossil taxa. The rays *Myliobatis*, *Dasyatis*, and *Rhinoptera* prefer water depths of 1–10 m. Both those rays and the sharks, *Galeocerdo* and *Carcharinus*, are found in normal salinity and hyposaline estuarine waters today. However, the low diversity of the shark fauna (*Striatolamia macrota* is the only other selachian present) and a large sample exceeding 1000 teeth suggest salinities averaged in the 10 ppt range (Westgate, 2001; Gee, 2007).

The presence of a diverse crocodilian suite of genera including *Allognathosuchus*, *Pristichampsus*, a caiman and a much larger, unidentified crocodylian, along with the tortoise *Hadrianus*, indicates the climate was frost-free and either tropical or subtropical. Additionally, the presence of the aquatic turtles cf. *Allaeochelys*, cf. *Baptemys* and *Xenochelys* suggest the climate was fully tropical, based on the distribution of their modern relatives. The extant carettochelyid, *Carettochelys insculpta*, is restricted to tropical rivers of southern New Guinea and northern Australia. Modern dermatemyds and staurotypine turtles inhabit tropical streams from southern Mexico to northern Central America. An interesting note is that the middle Eocene Lake Messel area and the Casa Blanca estuary shared the taxa *Lepisosteus,* cf. *Allognathosuchus, Pristichampsus*, *Allaeochelys, Trionyx,* and *Microparamys*, suggesting that a similar climatic regime existed in both regions.

The diverse suite of 32 mammalian species in the Casa Blanca fauna offers a rare chance for biostratigraphic correlation between the mammal-rich deposits of the North American interior and those of marine-invertebrate-rich coastal plain deposits. The Red Hot fauna from the earliest Wasatchian Tuscahoma Formation at Meridian, Mississippi, is the only other diverse land mammal community associated with marine Paleogene deposits on the North American Coastal Plain (Beard and Dawson, 2009). These two faunas provide a means to better synchronize the NALMA time scale with marine time scales which are used for intra-Coastal Plain and trans-oceanic correlation.

The following non-primate mammals have been recognized in the Casa Blanca community – marsupials: *Peratherium comstocki and P. marsupium*; insectivores: cf. *Simidectes magnus* and *Centetodon pulcher*; Chiroptera: sp. undet.; mesonychids: *Mesonyx uintensis*; carnivores: cf. *Uintacyon* and *Procynodictis* cf. *P. vulpiceps*; Sirenia: sp. undet.; perissodactyls: *Epihippus gracilis, Amynodon advenus*, cf. *Triplopus*, and *Notiotitanops mississippiensis*; artiodactyls: *Laredochoerus edwardsi, Protoreodon petersoni, P. edwardsi, Leptoreodon pusillus, L. leptolophus,* and *Toromeryx marginensis*; rodents: *Mytonomys* nov. sp., *Microparamys* sp.*, Pauromys simplex, Lareodomys riograndensis, Microeutypomys karenae, Nonomys* sp., and cylindrodontid undet. (Westgate, 2001, 2009). Remains of *Epihippus gracilis* (horse), *Amynodon advenus* (rhino), and *Mytonomys* nov. sp. (rodent) indicate that the middle Laredo Formation is Uintan in age. *Procynodictis* cf. *P. vulpiceps* and *Protoreodon petersoni* suggest it is a Uinta C correlate. The presence of *Notiotitanops mississippiensis* provides a westward range extension of this coastal brontothere which formerly was known only from the marine Cook Mountain Formation of Mississippi.

The gastropod *Turritella cortezi* allows correlation of the paralic middle Laredo Formation with the open marine Hurricane Lentil in the Cook Mountain Formation of east Texas. Cook Mountain Formation plankton are placed in the upper half of zone NP16 and have been broadly correlated with lower Bartonian and upper Lutetian strata.

Beard, C., Dawson, M. (2009). Early Wasatchian mammals of the Red Hot local fauna, uppermost Tuscahoma Formation, Lauderdale County, Mississippi. Annals of the Carnegie Museum, v. 78 (3): 193-243.

Gee, C. (2007). The mangrove palm *Nypa* and its paleoecological implications for a middle Eocene community from Laredo, Texas, USA. Quaternary International, 167-168 supp.: 446-447.

Walsh, S. (1996). Middle Eocene mammal faunas of San Diego County, California. In: Prothero, D., R. Emry (eds) The Terrestrial Eocene-Oligocene Transition in North America. Cambridge University Press, New York, pp 75-119.

Westgate, J.W. (1999). After the dinosaurs: A Texas tropical paradise recovered at Lake Casa Blanca. Texas Parks & Wildlife Press, Austin, 69 p.

Westgate, J.W. (2001). Paleoecology and biostratigraphy of marginal marine Gulf Coast Eocene vertebrate localities. In: Gunnel, G. (ed) Eocene Biodiversity: Unusual Occurrences and Rarely Sampled Habitats. Kluwer Academic/ Plenum, New York, pp 263-297.

Westgate, J.W., Cope, D., Beard, C. (2010). First occurrence and significance of *Mahgarita stevensi* in a late middle Eocene (late Uintan) Tethyan-influenced Gulf coast community. Journal of Vertebrate Paleontology, SVP Program & Abstracts Book, pp 186A.

Westgate, J.W., Townsend, B. Cope, D., Friscia, A. (2008). Snapshot from the past: A Uintan vertebrate assemblage preserving community structure. Journal of Vertebrate Paleontology 28(3) sup.:159A.

Williams, B., Kirk, C. (2008). New Uintan primates from Texas and their implications for North American patterns of species richness during the Eocene. Journal of Human Evolution 55: 927-941.

Morphometric analysis of Eocene adapiform lower molar shape variation: Inferring function and ecological adaptation from the fossil record

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As discoveries like *Darwinius masillae* (Franzen et *al*., 2009) add to our knowledge of the European Eocene fossil record, they expand our understanding of primate phylogeny during the Eocene and broaden our perspective on patterns of ecological adaptation and behavior. Geometric morphometric analysis of nine landmarks located on the first lower molar in a sample of North American, European, and Asian adapiform (*Adapis parisiensis*, *Cantius mckennai*, *Cantius ralstoni, Leptadapis magnus, Notharctus robustior, Notharctus tenebrosus*, *Sivaladapis nagrii*, *Smilodectes gracilis*), extant (*Propithecus diadema, Propithecus verreauxi*), and outgroup (*Plesiadapis anceps*) taxa indicate that the relative orientation of molar landmarks and crest curvature can be used to discriminate between generic categories, and, to a lesser extent, specific designations.

Materials and Methods

Two-dimensional images of the occlusal surface of the first lower molar were collected using a digital microscope (Intel), and nine landmarks were digitized using the TPSDIG2 software package (following the methodology described in White (2009) and including the paraconid) (see Fig. 1a). Specimens were examined and chosen from vertebrate collections at the University of Michigan Museum of Paleontology, the Field Museum of Natural History, the American Museum of Natural History, the Smithsonian Institution National Museum of Natural History, Muséum National d'Histoire Naturelle (Paris), Panjab University (India), and the University of Washington Burke Museum of Natural History and Culture. Partial warp scores were calculated for the sample (N=97) using the TPSRELW package and exported into SPSS 19.0 for statistical analysis (Principal Components Analysis and Discriminant Function Analysis). The sample consisted of the following genera and species: *Adapis* (*A. parisiensis* [N=24]), *Cantius* (*C. mckennai* [N=5], *C. ralstoni* [N=21]), *Leptadapis* (*L. magnus* [N=5]), *Notharctus* (*N. robustior* [N=6], *N. tenebrosus* [N=7]), *Plesiadapis* (*P. anceps* [N=5]), *Propithecus* (*P. diadema* [N=6], *P. verreauxi* [N=9]), *Sivaladapis* (*S. nagrii* [N=3]), *Smilodectes* (*S. gracilis* [N=6]). While the sample sizes of some groups are small (fewer than the number of landmarks used in the analysis),

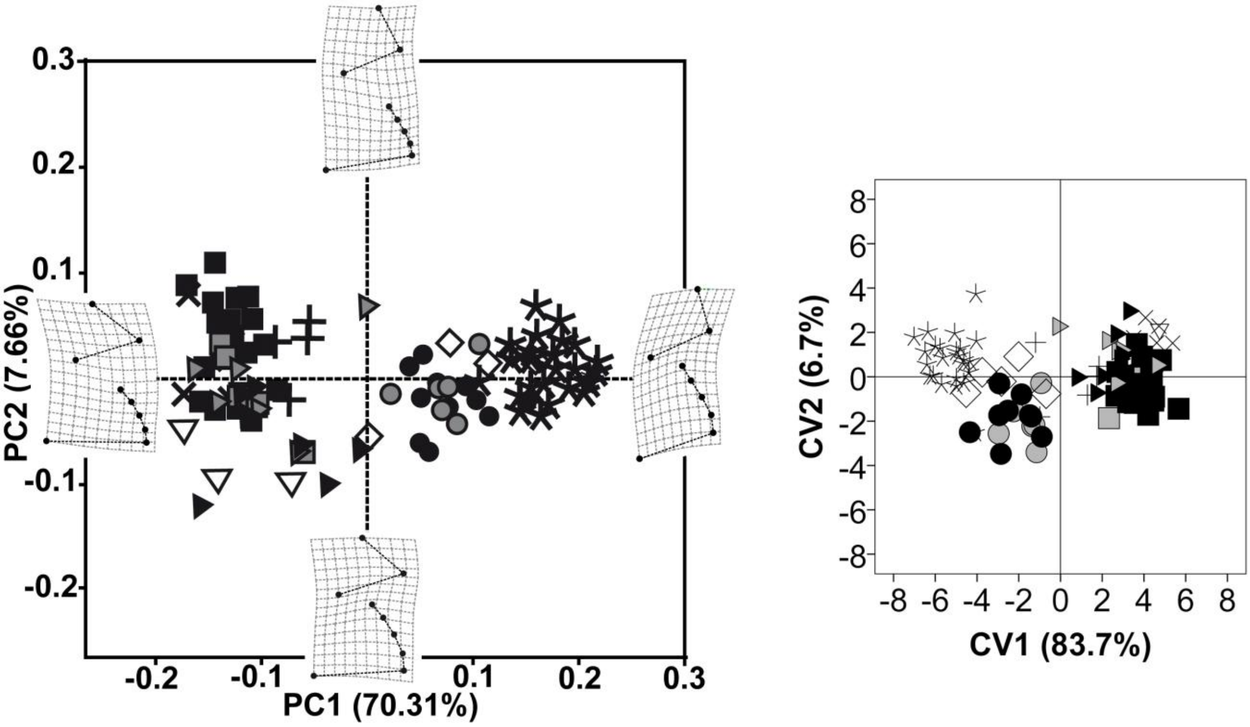

Figure 1. Bivariate plot of (a) Principal Component 1 (PC1) and Principal Component 2 (PC2), and (b) Canonical Variate 1 (CV1) and Canonical Variate 2 (CV2). Symbols represent – ○: *Propithecus* (black, *P. verreauxi*, gray, *P. diadema*), □: *Cantius* (black, *C. ralstoni*, gray, *C. mckennai*), ▷: *Notharctus* (black, *N. tenebrosus*, gray, *N. robustior*), ×: *Plesiadapis anceps*, ▽: *Sivaladapis nagrii*, ✶: *Adapis parisiensis*, +: *Smilodectes gracilis*, ◇: *Leptadapis magnus*. Percentages accompanying axis titles represent percentage of total variance. Shape deformation grids are included in (a) to illustrate shape change along the first principal axes.

preliminary results were anticipated to provide an assessment as to whether landmark-based shape data could be used to investigate shape variation among a sample of fossil primate taxa, or be used to discriminate reliably between groups classified at the generic and specific level. Additionally, extant material (*Propithecus*) was intentionally chosen to compare with fossil specimens to strengthen the investigation of variation between species classified within one genus.

RESULTS AND DISCUSSION

Results of the statistical analyses suggest species within each of the eight individual genera demonstrate an overall pattern of intra-generic shape similarity, indicating that molar shape can be used to discriminate between genera. Scrutiny of the PCA results reveals that variation along the first principal component accounts for approximately 70% of the shape variance in the sample. DFA results show that the overall accuracy of prediction based on landmark data (using a cross-validated approach) exceeds 70% accuracy at the generic level, but only approximately 60% at the specific level, suggesting that the use of shape variation in assessing group distinction at the specific level may require additional specimens, as well as further understanding of the functional and phylogenetic influences on first lower molar shape. At the generic level, cross-validated results demonstrate a prediction rate greater than 80% for the following genera: *Adapis*, *Cantius*, and *Propithecus*. The lowest rate of correct group prediction was exhibited by *Smilodectes*, with the majority of the specimens being classified as *Cantius*, *Leptadapis*, *Notharctus*, or *Propithecus*. Along the first principal component axis (accounting for approximately 70% of the variance), shape variation appears to be correlated with differences in the relative location of the paraconid, the relative dimensions of the talonid basin, and the curvature and orientation of the cristid obliqua.

Overall, shape trends suggest a similarity in shape between adapines (*Adapis*, *Leptadapis*) in contrast to that shared by notharctines, *Sivaladapis*, and *Plesiadapis*. Analysis of the Principal Components Analysis results suggests the shape of *Propithecus* is most similar to that of the European adapines – this result is intriguing, given the similarity in the observed folivorous and granivorous (seed-eating) diet of the modern Malagasy genus and the inferred folivorous diet of the extinct adapines. When employed to analyze shape and function, geometric morphometrics provides a great potential for investigating the paleobiology of extinct forms. Future expansion of this dataset should include not only additional fossil material, but also representatives of additional extant prosimian genera that consist of several species (*Eulemur* or *Hapalemur*, for example). Potential functional and phylogenetic implications of shape trend data will be discussed, including a comparison of behavioral inferences using other techniques. The morphometric trends of *Darwinius* will also be discussed in comparison with the Eocene adapiform sample.

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WHITE, J. (2009). Geometric morphometric investigation of molar shape diversity in modern lemurs and lorises. The Anatomical Record 292: 701-719.

Taphonomic phenomena of the Messel Equoidea

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The World Heritage Site Grube Messel is particularly famous for its excellent preservation of articulated skeletons of many classes of vertebrates. Skeletons and, at times, associated soft-part preservation by replicating, fossilized bacteria (Wuttke, 1983; Ernst, 1998) of keratinaceous scales of iguanid reptiles (Smith, 2009) and notably of melanosomes from feathers (Vinther *et al.*, 2010) provide a deep insight into taphonomic processes and the depositional environment of middle Eocene Lake Messel.

More than 50 specimens of Equoidea (Franzen, 2007) in finely laminated black pelites from the former Lake Messel represent a well-defined taphonomic size range for larger corpses of terrestrial vertebrates. Bodies of equids entering the Messel Lake theoretically may have initially floated or sunk. They possibly came back to surface later or remained submerged, potentially influenced by turbidity or other currents. Such hydraulic factors, therefore, may have played a significant role in transport, modification, and burial of the carcasses.

The key to understanding the taphonomy of an organism is to reconstruct the environmental and decompositional context. Documentation and analysis of the sedimentological context and, furthermore, palaeoclimatological and -geographic deductions are necessary to get insights into the depositional scene. The fate of a cadaver is conditioned by a large number of factors. The only possibility for reconstructing the rate and pattern of the decomposing carcasses is by deducing them from the relative position of the skeletal elements on the artificial slab (in Messel it is made of epoxy resin, onto which the Messel vertebrates have to be transferred from the black pelites, but its surface still displays sedimentological information, which is transferred as well).

Decomposition is a general term, and it is used by us to refer to its two major processes: autolysis (involving enzymes), and putrefaction (involving bacteria). Disarticulation is defined as complete reduction of the soft tissues that hold bones together within a joint in recent organisms, and, in paleontology, this definition includes the movement of bone(s).

Intrinsic factors of a carcass include the cause of death, state of the body at death, age, body mass, and functional anatomy. Extrinsic factors, such as the time passed between death and deposition at the bottom of the Messel Lake and the burial environ

Figure 1. *Propalaeotherium hassiacum* Haupt 1925, © Senckenberg Forschungsinstitut und Naturmuseum Frankfurt.

ment, are all primarily physical and have to be deduced from the skeleton and the known sedimentological factors.

From the perspective of understanding depositional and decompositional patterns, taphonomic factors need to be identified and understood in the way that a forensic expert works. Post-depositional movements of bones can be understood from a forensic taphonomical perspective by investigating a) the effects of soft-tissue decomposition, b) the sequences of disarticulation or disintegration of connective tissue between bones, and c) the potential amplitude of movement of skeletal elements as triggered by gravity, putrefaction gases, and the collapse of joint connections.

Examination of the 50 Equoidea carcasses shows that every cadaver settled to the lake bed within a short time after death. Although in some carcasses buoyancy may have increased from the buildup of decomposition gases, none of them came back to surface. The sediment was stabilized by microbial mats. Normally, the sedimentation rate was below 0.2 mm/a (Goth, 1990). Carcasses, being nearly buoyant, therefore settled to the floor of the lake without signs of penetration of the sediment (e.g., disturbance of the lamination). There is no evidence of postdepositional transport of the Equoidea carcasses. Only one skeleton seems to have been splayed by a turbidity current and loaded with coarser sediment from the shoreline. Disarticulation and dislocation patterns of the Messel Equoidea can be deduced from intrinsic factors of the decomposing carcass, from displacement of bones due to the floating of soft parts of the corpse with connected bones, and from the collapse of joint connections.

Ernst, K. (1998). Fossil microorganisms from the Eocene Messel oil shale of Southern Hesse, Germany. Kaupia Darmstädter Beiträge zur Naturgeschichte 7: 1-95.

Franzen, J.L. (2007). Eozäne Equoidea (Mammalia, Perissodactyla) aus der Grube Messel bei Darmstadt (Deutschland). Funde der Jahre 1969–2000. – Schweizerische Paläontologische Abhandlungen. 127: 1-245.

Goth, K. (1990). Der Messeler Ölschiefer – Ein Algenlaminit. Cour. Forsch.-Inst. Senckenberg 131:1-143.

Smith, K.T. (2009). Eocene lizards of the clade *Geiseltaliellus* from Messel and Geiseltal, Germany, and the early radiation of Iguanidae (Squamata: Iguania). Bulletin of the Peabody Museum of Natural History, 50(2): 219-306.

Vinther, J. Briggs, D.E.G., Clarke, J., Mayr, G., Prum, R.O. (2010). Structural coloration in a fossil feather Biol. Lett. 2010: 128-131.

Wuttke, M. (1983). "Weichteil-Erhaltung" durch lithifizierte Mikroorganismen bei mittel-eozänen Vertebraten aus den Ölschiefern der "Grube Messel" bei Darmstadt. Senckenbergiana lethaea 64: 509-527.

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