Palaeobio Palaeoenv (2012) 92:397–402
DOI 10.1007/s12549-012-0107-3

SENCKENBERG

PREFACE

"Messel and the terrestrial Eocene" – Proceedings of the 22nd Senckenberg Conference

Thomas Lehmann · Stephan F. K. Schaal

Received: 28 August 2012 / Accepted: 29 August 2012 / Published online: 25 October 2012

Ida, …

In May 2009, a new fossil entered the history books: "Ida", a.k.a. *Darwinius masillae*, the most complete fossil primate ever found (Franzen et al. 2009). All around the world, from secluded palaeontology laboratories to the mass-frequented internet, this little female had tongues wagging vehemently about our own origin. Indeed, whereas everybody agrees that "Ida" belongs to the adapiforms (an extinct group of primates traditionally allied with lemurs), Franzen et al. (2009) claim that, based on features displayed by "Ida", the whole Adapiform clade should be allied with Haplorhini (tarsiiforms, monkeys and apes). Detractors of this hypothesis would question the significance of the characters chosen by Franzen et al. (2009), or even their interpretation, and put forth other morphological characters as well as other fossil primates as arguments against a relationship between haplorhines and adapiforms. Determinedly, these critics argue that more features support the widely held hypothesis that adapiforms and lemurs (Lemuriformes) are sister taxa in the clade Strepsirrhini. In any case, "Ida" is a wonderful fossil, which also advertises—thanks to her name *"masillae"*—the site of Messel that bore her remains for over 47 million years. Masilla is the Latin name for Messel used in the Lorsch monastery Codex, 800 AD.

This article is a contribution to the special issue "Messel and the terrestrial Eocene - Proceedings of the 22nd Senckenberg Conference"

T. Lehmann (✉) · S. F. K. Schaal
Palaeoanthropology and Messel Research Department,
Senckenberg Research Institute
and Natural History Museum Frankfurt,
Senckenberganlage 25,
60325 Frankfurt am Main, Germany
e-mail: thomas.lehmann@senckenberg.de

S. F. K. Schaal
e-mail: Stephan.Schaal@senckenberg.de

… Messel, …

The Messel Pit Fossil Site, the first World Natural Heritage Site in Germany (since 1995), was already renowned in the field of palaeontology before the publication of "Ida". The Messel Pit is arguably one of the best and most productive examples of Eocene fossil localities so far discovered. 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 (see Habersetzer and Schaal 2004; von Koenigswald et al. 1998; Schaal and Ziegler 1992; Smith and Wuttke 2012; and references herein). As a result, an outstanding vertebrate fauna of more than 130 species, including at least 44 species of mammals in 31 genera, has so far been described from the Messel Pit (Morlo et al. 2004).

Therefore, the mammalian species from the Messel Pit provide a unique window on the anatomical structure and palaeobiology of fossil mammals. No other site in the world has provided such an extensive and diverse database of Eocene mammal skeletons. This period is particularly important for them, as it represents an early stage in their evolution, when many of the basic steps in diversification were being achieved. Hence, the fossils from the Messel Pit are internationally regarded as a reference fauna, used for comparison in studies dealing with terrestrial Eocene organisms (e.g. Franzen 2005; Rose 2012, this issue). For many Eocene taxa, the Messel fossils provide the best or only view of the complete skeleton.

Most studies of Eocene terrestrial faunas have focused on mammals. But in Messel, like elsewhere, mammals were not the only component of the fossil fauna. Birds, reptiles, fish, insects and plant remains have also been found in the Messel Pit's extraordinary fossil assemblage (Schaal 2005). Similar to the mammals, the Eocene is a crucial

period in the development of the modern herpetofauna. Both "old" and "modern" reptile and amphibian groups coexisted at this time: those inherited from the Cretaceous and those which are part of the present fauna (Rage 2012, this issue; Rage and Augé 1993). This faunal mixture is well represented at the middle Eocene Messel Pit. Quite a few of the known Eocene reptile and amphibian genera from Europe are represented by well-preserved, articulated specimens from Messel (Schaal and Ziegler 1992). These specimens are of great interest for precise phylogenetic studies (e.g. Smith 2009). Still, the lower vertebrates have received far less attention than the mammals. Given their biology (e.g. limited thermoregulation capabilities), 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. The Eocene was a time when many major modern insect lineages were already in existence and still radiating (Grimaldi and Engel 2005). In comparison, insects from Messel represent a mix from different modern biogeographic regions, ranging from the Neotropical to the Australian and Oriental region (e.g. Wedmann et al. 2007). Mixed geographic affinities are also observed in the plant taphocoenosis, which is one of the richest and most diverse of the Paleogene worldwide. Indeed, so far, plants are represented by 75 families and 203 species (Collinson et al. 2012). Finally, the Research Core Messel 2001 not only clarified the genesis of the Messel fossil site as a maar lake (see Felder and Harms 2004) 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 (Lenz et al. 2010).

… and the Eocene world

The formation of the Messel maar and the subsequent deposition of the Messel oil shale in the maar lake took place during the middle Eocene. Therefore, the wealth of terrestrial fossils provided by the Messel Pit greatly increased our understanding of this period—and still does—propelling it to being the emblematic fossil site for the middle part of the Eocene. Around the Paleocene–Eocene boundary, mammals experienced a major turnover and modern groups became firmly established in all principal land ecosystems (e.g. Maas et al. 1995; Gingerich 2003). They also reinvaded the seas (e.g. whales) and took to the sky (e.g. bats), which is particularly well documented from the Messel Pit (e.g. Simmons and Geisler 1998; Storch et al. 2002).

This epoch was also a remarkable time in the Earth's climatic history. The Eocene was characterised by a warm and worldwide little-differentiated climate, noticeably higher-than-present concentrations of carbon dioxide, as well as poles with little or no ice (e.g. Zachos et al. 2008). In fact, the temperature on the Earth's surface reached its maximum for the whole Cenozoic in the Eocene. Several rapid global warming events connected with massive carbon input to the ocean and atmosphere ("hyperthermals") happened during this time. One of the most important hyperthermals was the Paleocene–Eocene Thermal Maximum (PETM), which marks the beginning of the Eocene. During this event, surface temperatures rose by 5–9 °C (Zachos et al. 2008). Moreover, the Eocene global climate was quite homogeneous: the Polar Regions were warm and covered with temperate forests, while rainy "tropical" climates extended as far north as 45 ° (e.g. McIver and Basinger 1999; Eberle and Greenwood 2012).

During the Eocene, the continents continued to drift towards their present positions (Scotese 2001; Blakey 2006). After the northern supercontinent of Laurasia started to break up, land contact between North America, Europe, and Asia was intermittent. Similarities between North American and European early Eocene faunas show that land connections (probably through Greenland) were still possible, until the North Atlantic Ocean opened completely (Clyde and Gingerich 1998; Gingerich 1989). While the Tethys still separated Europe from Africa, the uplift of the Alps created a shallow sea with island archipelagos in what is now southeastern Europe. Asia and Europe were long separated by the Obik Sea and the Turgai Strait, which probably also represented a marine barrier to faunal exchange (e.g. Hooker and Dashzeveg 2003). India began its collision with Asia, folding the Himalayas into existence. After a long period of contact, Australia split from Antarctica during the Eocene, which in turn led to the development of the cold circumpolar current around Antarctica (e.g. Barker and Thomas 2004).

Finally, the end of the Eocene is marked by a major climatic deterioration in combination with the "*Grande Coupure*" (Stehlin 1910), 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.

22nd Senckenberg Conference "The world at the time of Messel"

These are the reasons that prompted the organisation of a conference, which gathered prominent international specialists from different disciplines in order to, through their respective fields of interest, develop a synthetic perspective on continental life on earth during the Eocene. Naturally, as

it represents a peerless window through which we can study life on earth during the Eocene, the site of Messel was chosen to be the focus of the discussions. Nonetheless, Messel is only one motif in a much larger tapestry, one piece of the puzzle that is the world during the Eocene. Other fossil sites in Australia, China, Egypt, France, and USA contribute to complete this patchy picture. The study and comparison of the terrestrial fauna and flora from these different sites were at the core of the conference discussions, and provided insights into different evolutionary aspects of Palaeobiology (e.g. phylogeny, biodiversity) and Palaeoenvironment (e.g. ecosystems, climates, palaeogeography) during the Eocene (see Lehmann and Schaal 2011 for the detailed programme).

This special issue contains 16 papers that were presented last year during the 22nd Senckenberg Conference "***The world at the time of Messel: Puzzles in Palaeobiology, Palaeoenvironment and the History of early Primates***" held at the Senckenberg Natural History Museum, in Frankfurt, Germany from 15 to 19 November 2011. The meeting was organised by the Senckenberg Research Institute and Natural History Museum Frankfurt. The conveners of this conference were Thomas Lehmann and Stephan F.K. Schaal. The organising committee consisted of Jörg Habersetzer, Ottmar Kullmer, Krister T. Smith, Friedemann Schrenk, Virginie Volpato, Sonja Wedmann and Volker Wilde. Over 100 palaeontologists from 14 countries and five continents attended the conference. The participation of numerous American, but also African, Australian, Chinese, and Japanese colleagues manifested the international significance of the Messel site and its outstanding fossils, and contributed to the success of the meeting. During this conference, and through 52 oral and 28 poster presentations, we tried 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 presentations covered multiple aspects of life on earth during the Eocene, from the colour 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. At the end of the conference, about 20 renowned primate specialists were able to debate the evolutionary history of early primates during a unique workshop organised on site, at the Senckenberg Messel Research Station. For the purpose of this one-off event, the original specimen of "Ida" as well as rare original and high quality casts of Palaeogene primates from all over the world were even brought together. Through the fruitful discussions that followed each talk and the workshop, all presentations complemented each other and helped to fill in the gaps in our understanding of a period in earth history crucial for terrestrial fauna and flora.

In this respect, the papers brought together in this special issue provide a good overview of the topics that were presented and discussed during the conference. Moreover, they fit perfectly within the scope of *Palaeobiodiversity and Palaeoenvironments* as they all focus on "biodiversity of fossil organisms and their palaeoenvironment, palaeoecology, and palaeobiogeography".

Collinson, Smith, Manchester, Wilde, Howard, Robson, Ford, Marone, Fife and Stampanoni evaluate X-ray tomographic methods for their suitability to visualise morphology and anatomy of fossil fruits and seeds preserved in the oil shale of Messel. Their investigations show that X-ray data also permit the visualisation of fine structures, giving additional features for comparison with other extinct and extant taxa. With this method they revealed important features for 30 taxa from Messel, such as soft tissue in fruits. This exceptional preservation was previously only revealed for famous vertebrate remains. (Palaeobio Palaeoenv 92(4). doi:10.1007/s12549-012-0091-7).

Gaudant, Schaal and Sun give an account on isolated fish bones from the Middle Eocene oilshales from Huadian, China. These remains were found, together with several mammalian remains, during previous field campaigns. They are indicative of freshwater lacustrine conditions, although the fact that all the fish remains were found disarticulated results from a transportation of the bones from the living place of the fishes to the spot where the fossilisation took place. (Palaeobio Palaeoenv 92(4). doi:10.1007/s12549-012-0094-4).

Augé revises a part of the amphisbaenian fossil record from the European Eocene. European fossil taxa previously assigned to the amphisbaenians are briefly reviewed and a description of some representative specimens from the Eocene fossil record is presented. Global distribution of fossil amphisbaenians is discussed and some explanations are suggested for the absence of crown amphisbaenians at Messel and in the European middle Eocene. (Palaeobio Palaeoenv 92(4). doi:10.1007/s12549-012-0104-6).

Rage discusses the development of the amphibian and squamate fauna during biochronologic intervals MP 8 to 20 (Eocene) in Western Europe. It reflects initially the addition of an old, pre-Eocene fauna, and of a new fauna that arrived as a big wave of dispersals at the beginning of the Eocene. These dispersals were likely favoured by the warm climate. Latest middle and late Eocene is characterised by its richness and diversity resulting from dispersals and local radiations. (Palaeobio Palaeoenv 92(4). doi:10.1007/s12549-012-0087-3).

Rose gives a wide-ranging and compelling review about the importance of Messel in the actual state of our

knowledge on the palaeobiology of Eocene mammals. In particular, the fantastic preservation of Messel´s mammals (from entire skeletons to outlines of fur and gut contents) provide unique insights for interpreting the functional anatomy, and study the phylogeny and evolution of many taxa known elsewhere only from fragmentary remains. The comparison of the inhabitants of the Messel Lake in Europe with their close relatives from North America and Asia further documents the palaeobiogeographical relationships between these continents during the Eocene. (Palaeobio Palaeoenv 92(4). doi:10.1007/s12549-012-0090-8).

Preuschoft and Franzen present a biomechanical study of some inhabitants of the Eocene Messel Lake. To do so, they categorise fossil terrestrial mammals into 2D- (ground dwellers) and 3D-mammals (arboreal) based on the biotope on which they lived. Between running equids and jumping leptictids on the one hand, and climbing primates on the other hand, differences are mostly seen in the anatomy of their hands and feet (autopodes). In the 2D-mammals, these are more compression-transmitting organs, with energy-saving adaptations, whereas in the 3D-mammals, they are part of a versatile prehensile organ and present a complex musculature system, which requires more energy. (Palaeobio Palaeoenv 92(4). doi:10.1007/s12549-012-0103-7).

Métais, Gheerbrant and Şen offer a revision of the poorly known taxon *Parabunodon anatolicum* from Turkey. Based on a new analysis of the type specimen, additional new characters have been proposed and their state has been compared with that in Choeropotamidae (extinct artiodactyl and initial affiliation) and Pleuraspidotheriidae (European "Condylarthra"). Their cladistic analysis refutes affinities with choeropotamid artiodactyls and suggests that *Parabunodon* belongs to the pleuraspidotheriids. Along with the closely related Turkish genus *Hilalia*, *Parabunodon* would represent an Anatolian lineage of pleuraspidotheriid "Condylarthra", which was long restricted to the late Paleogene of the Paris basin. (Palaeobio Palaeoenv 92(4). doi:10.1007/s12549-012-0095-3).

Jehle, Godinot, Delsate, Phélizon and Pellouin report the discovery of a new late Paleocene locality in Montchenot (France). The preliminary investigations led to the recovery of numerous teeth belonging to different taxa of micromammals ranging from multituberculates, and pleuraspidotheriid "condylarthrans", to pantolestids, lipotyphlans, adapisoriculids, plesiadapids, and perhaps stem macroscelids. This mammal community shows similarities with those found at Cernay-les-Reims and Berru (France), so that a Thanetian age is assumed for the Montchenot fauna. The assemblage seems, however, to be palaeoenvironmentally and taphonomically biased toward small mammals. (Palaeobio Palaeoenv 92(4). doi:10.1007/s12549-012-0100-x).

Westgate provides an overview of the Paleogene land mammal fauna known from Gulf Coastal deposits (North America) and highlights the primate-rich middle Eocene Casa Blanca fauna. The latter fossil community, which certainly inhabited a tropical rain forest/estuarine mangrove swamp, bears no less than three omomyid taxa and the oldest New World record of a Cercamoniinae. Along with the Red Hot fauna (latest Paleocene, Mississippi), it is the only Palaeogene land mammal community known from Gulf Coastal plain associated with marine Palaeogene deposits. Therefore, it represents a rare key for the correlation of the NALMA (North American Land Mammal Age) time scale and the marine time scales. (Palaeobio Palaeoenv 92(4). doi:10.1007/s12549-012-0084-6).

Gingerich reviews our current knowledge on the Eocene primates. This period is important for that order, as it made its first appearance during the Paleocene–Eocene Thermal Maximum (PETM). Moreover, the dominating primate taxa of the Eocene, Tarsioidea and Adapoidea, waned at the end of the period in response to the "Grande Coupure", and preceded the rise of the anthropoids. The globally warm Eocene enabled Tarsioidea and Adapoidea to thrive and even to expand their geographic range to the Arctic Circle. Further discussion focuses on the position of adapoids in relationship to extant Strepsirrhini (lemurs, lorises) and Haplorhini (tarsioids, monkeys, apes). Based on the reassessment of morphological characters and in contrast with mainstream classifications, the adapoid genera *Darwinius* ("Ida") and *Notharctus* fall into haplorhines. (Palaeobio Palaeoenv 92(4). doi:10.1007/s12549-012-0093-5).

Rosenberger and Preuschoft study the orbital morphology in *Tarsius* in order to establish its phylogenetic position. This genus is important for the debates about the origin of Anthropoidea (monkey and apes) as they might be sister taxa. There are disagreements whether the postorbital septum observed in *Tarsius* and Anthropoidea represents a synapomorphy of a [tarsier-anthropoid] clade, or if it is a convergence in which case *Tarsius* would be rather nested among fossil omomyids. Based on a morpho-functional and biomechanical examination of this septum, it seems that this feature had another function in *Tarsius* than in anthropoids, and represents a form–function convergence. Consequently, *Tarsius* would be more closely related to Eocene omomyids than it is to Anthropoidea. (Palaeobio Palaeoenv 92(4). doi:10.1007/s12549-012-0098-0).

Lebrun, Godinot, Couette, Tafforeau and Zollikofer explore the morphology of the bony labyrinth in selected primates in order to extract a phylogenetic signal. In particular, the ear of *Pronycticebus gaudryi*, an adapiform belonging to the same sub-family Cercamoniinae as "Ida", is investigated using microcomputer tomographic technics (μCT). No synapomorphy could be found between the labyrinths of *Pronycticebus* and those of modern

anthropoids. *Pronycticebus* exhibits rather a morphology close to that of extant strepsirrhines. This in turn further supports the traditional hypothesis that Cercamoniinae (including "Ida") and the adapoids in general are the sister taxon of lemuriforms and do not belong to Haplorhini. (Palaeobio Palaeoenv 92(4). doi:10.1007/s12549-012-0099-z).

Koenigswald, Habersetzer and Gingerich present a thorough morphological analysis of the pedal distal phalanges in Eocene and extant primates. Most anthropoids have nails, whereas extant lemuriforms present a grooming claw on the second toe, and in *Tarsius* both second and third toes are modified. Distal phalanges might thus bear a phylogenetic signal for distinguishing strepsirrhines and haplorhines. Articulated fossil primate feet are rare, but study of three adapoids, *Europolemur* and *Darwinius* from Messel, and *Notharctus* from Wyoming, was possible. Their analysis produced a complex signal, and substantial variability in the morphology of the distal phalanges within adapoids must be assumed. Therefore, although close in morphology, the authors hesitate to classify Adapoidea next to Lemuriforms within Strepsirrhini solely on the anatomy of their pedal distal phalanges. (Palaeobio Palaeoenv 92(4). doi:10.1007/s12549-012-0096-2).

Franzen, J.L., Habersetzer, Schlosser-Sturm and Franzen, E.L. open a singular window into the life history of the type individual of *Darwinius masillae*, known as "Ida", from the Eocene of Messel. Microcomputer tomographic images (μCT) of its right wrist reveal an amorphous structure interpreted as a bone callus. Calluses are hard bony tissue that develops around the ends of broken bones during the healing process. Accordingly, a fall from a tree is hypothesised to have led to the fracture of the wrist and obliged "Ida" to live on the ground. There, the usually arboreal primate was exposed to other dangers that eventually led to her death and subsequent fossilisation in the Messel Lake. (Palaeobio Palaeoenv 92(4). doi:10.1007/s12549-012-0102-8)

Sauther and Cuozzo propose a morphological and ecological comparison of Eocene primates and extant lemurs from Madagascar. In particular, gross tooth wear pattern was recorded in extant lemurs and linked to their feeding ecology and food properties. For instance, post-canine tooth wear laterality is significantly higher in the omnivorous *Lemur catta*, which feeds on large, hard and tough fruits, than in *Propithecus verreauxi*, a folivorous primate. The wear pattern in *Notharctus* species (adapoids) exhibits no dental laterality, as in *Propithecus*, and thus suggests a folivorous diet. Further interpretations of Eocene primate palaeobiology are proposed, including a comparison of injuries in extant lemurs that conflicts with the hypothesised incapacitating effect (with respect to climbing ability) of the wrist fracture seen in "Ida" from Messel. (Palaeobio Palaeoenv 92(4). doi:10.1007/s12549-012-0089-1).

Micklich discusses in his comprehensive contribution the Messel Lake fish fauna with special focus on palaeoenvironmental framework. His results suggest that the Messel Lake could not have been constantly isolated from external water bodies during the period of time that is represented by the investigated fossils. There must have been various opportunities for a renovation of the lake's fish fauna instead. (Palaeobio Palaeoenv 92(4). doi:10.1007/s12549-012-0106-4).

Acknowledgements 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 and the Goethe University, Frankfurt am Main. 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 Paleoanthropology and Messel Research Department, the Messel Research Station, and the Sektion Palaeobotanik of the Senckenberg Research Institute and Natural History Museum Frankfurt.

References

Barker PF, Thomas E (2004) Origin, signature and palaeoclimatic influence of the Antarctic Circumpolar Current. Earth Sci Rev 66:143–162

Blakey RH (2006) Mollewide plate tectonic maps. Flagstaff (AZ). Available from: http://jan.ucc.nau.edu

Clyde WC, Gingerich PD (1998) Mammalian community response to the latest Paleocene thermal maximum: An isotaphonomic study in the northern Bighorn Basin, Wyoming. Geology 26:1011–1014

Collinson ME, Manchester SR, Wilde V (2012) Fossil fruits and seeds of the Middle Eocene Messel biota, Germany. Abh Senckenberg Ges Naturforsch 570:1–251

Eberle JJ, Greenwood DR (2012) Life at the top of the greenhouse Eocene world — A review of the Eocene flora and vertebrate fauna from Canada's High Arctic. Bull Geol Soc Am 124(1/2):3–23

Felder M, Harms F-J (2004) Lithologie und genetische Interpretation der vulkano-sedimentären Ablagerungen aus der Grube Messel anhand der Forschungsbohrung Messel 2001 und weiterer Bohrungen (Eozän, Messel-Formation, Sprendlinger Horst, Südhessen). Cour Forsch-Inst Senckenberg 252:151–203

Franzen JL (2005) The implications of the numerical dating of the Messel fossil deposit (Eocene, Germany) for mammalian biochronology - Conséquences de la datation de l'âge numérique du gisement de Messel (Eocéne, Allemagne) pour la biochronologie des mammifères. Ann Paléontol 91:329–335

Franzen JL, Gingerich PD, Habersetzer J, Hurum JH, von Koenigswald W, Smith BH (2009) Complete primate skeleton from the middle Eocene of Messel in Germany: morphology and paleobiology. PLoS One 4(e5723):1–27

Gingerich PD (1989) New earliest Wasatchian mammalian fauna from the Eocene of northwestern Wyoming: Composition and diversity in a rarely sampled high-floodplain assemblage. Univ Mich Pap Paleontol 28:1–97

Gingerich PD (2003) Mammalian responses to climate change at the Paleocene-Eocene boundary: Polecat Bench record in the northern Bighorn Basin, Wyoming. In: Wing SL, Gingerich PD, Schmitz B, Thomas E (eds) Causes and consequences of globally warm climates in the early Paleogene: Boulder, Colorado. Geolog Soc Am Spec Pap 369:479–500

Grimaldi D, Engel MS (2005) Evolution of the insects. Cambridge University Press, NY, p 755

Habersetzer J, Schaal SFK (eds) (2004) Current geological and paleontological research in the Messel Formation. Cour Forsch-Inst Senckenberg 252:1–245

Hooker JJ, Dashzeveg D (2003) Evidence for direct mammalian faunal interchange between Europe and Asia near the Paleocene-Eocene boundary. In: Wing SL, Gingerich PD, Schmitz B, Thomas E (eds) Causes and consequences of globally warm climates in the early Paleogene: Boulder, Colorado. Geolog Soc Am, Spec Pap 369:479–500

Lehmann T, Schaal SFK (eds) (2011) The World at the Time of Messel: Puzzles in Palaeobiology, Palaeoenvironment, and the History of Early Primates. (22nd Int Senckenberg Conf, conference volume). Senckenberg Gesellschaft für Naturforschung, Frankfurt am Main. pp. 203

Lenz OK, Wilde V, Riegel W, Harms F-J (2010) 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 38:627–630

Maas MC, Anthony MRL, Gingerich PD, Gunnell GF, Krause DW (1995) Mammalian generic diversity and turnover in the late Paleocene and early Eocene of the Bighorn and Crazy Mountains Basins, Wyoming and Montana (USA). Palaeogeogr Palaeoclimatol Palaeoecol 115(1–4):181–207

McIver EE, Basinger JF (1999) Early Tertiary floral evolution in the Canadian High Arctic. Ann Missouri Bot Gard 86:523–545

Morlo M, Schaal S, Mayr G, Seiffert C (2004) An annotated taxonomic list of the Middle Eocene (MP 11) Vertebrata of Messel. Cour Forsch-Inst Senckenberg 252:95–108

Rage JC (2012) Amphibians and squamates in the Eocene of Europe: what do they tell us? In: Lehmann T, Schaal SFK (eds) Messel and the terrestrial Eocene - Proceedings of the 22nd Senckenberg Conference. Palaeobio Palaeoenv 92(4). doi:10.1007/s12549-012-0087-3

Rage JC, Augé M (1993) Squamates from the Cainozoic of the western part of Europe. A review. Rev Paléobiol volume spécial 7:199–216

Rose KD (2012) The importance of Messel for interpreting Eocene Holarctic mammalian faunas. In: Lehmann T, Schaal SFK (eds) Messel and the terrestrial Eocene - Proceedings of the 22nd Senckenberg Conference. Palaeobio Palaeoenv 92(4). doi:10.1007/s12549-012-0090-8

Schaal SFK (ed) (2005) Messel Pit Fossil Site: Snapshots from the Eocene. Vernissage, UNESCO World Heritage Sites ser., 21 (05), 13th year

Schaal SFK, Ziegler W (eds) (1992) Messel: An insight into the history of life and of the earth. Oxford University Press

Scotese CR (2001) Atlas of Earth History, Vol. 1 Paleogeogr. PALEOMAP Project, Arlington, Texas

Simmons NB, Geisler JH (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. Bull Am Mus Nat Hist 235:1–182

Smith KT (2009) Eocene Lizards of the clade *Geiseltaliellus* from Messel and Geiseltal, Germany, and the early radiation of Iguanidae (Reptilia: Squamata). Bull Peabody Mus Nat Hist 50 (2):219–306

Smith KT, Wuttke M (2012) From tree to shining sea: Taphonomy of the arboreal lizard *Geiseltaliellus maarius* from Messel, Germany. In: Wuttke M, Reisdorf AG (eds) Taphonomic processes in terrestrial and marine environments. Palaeobio Palaeoenv 92 (1):45–65. doi:10.1007/s12549-011-0064-2

Stehlin HG (1910) Remarques sur les faunules de mammifères des couches eocenes et oligocenes du Bassin de Paris. Bull Soc Géol France 4(9):488–520

Storch G, Sigé B, Habersetzer J (2002) *Tachypteron franzeni*, n. gen., n. sp., earliest emballonurid bat from the middle Eocene of Messel (Mammalia, Chiroptera). Paläontol Z 76:189–199

von Koenigswald W, Storch G, Habersetzer J (eds) (1998) Messel: Ein Pompeji der Paläontologie. Jan Thorbecke, Sigmaringen

Wedmann S, Bradler S, Rust J (2007) The first fossil leaf insect: 47 million years of specialized cryptic morphology and behavior. Proc Natl Acad Sci USA 104(2):565–569

Zachos JC, Dickens GR, Zeebe RE (2008) An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. Nature 451(17):279–283