MESSEL

An Ancient Greenhouse Ecosystem

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SENCKENBERG

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MESSEL – An Ancient Greenhouse Ecosystem

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Preface

This second Messel book by Senckenberg, published simultaneously in German and English, will introduce readers with an interest in nature to the results of the research conducted since the 1970s by biologists and geo-scientists on the unique fossils from the Messel oil shale deposits. Alternatively, you can simply peruse the illustrations and take pleasure from the beauty of the 48-million-year-old fossils.

Most of the illustrated fossils are part of the Senckenberg collection and thus primarily originate from our own research excavations. Additional fossils illustrated here come from the Hessian State Museum in Darmstadt as well as other museums and private collectors. We are extremely grateful to them for making their fossils and photographs available. A complete list of the institutions and collections can be found in the image captions and sources.

We would like to pay tribute to all who were involved in the campaign to permanently preserve the Messel Pit, from the cessation of the mining activities until its purchase by the State of Hesse, and who helped to unearth the traces of a buried world and make them widely available for future generations. Besides volunteers and honorary fossil hunters, this also includes hundreds of interns who supported the institutes during their annual digs. Our technical assistants and taxidermists always assured the required care and quality during the excavations and preparation. We express our heartfelt thanks to all of the authors who, with their respective chapters, contributed to the book's success. The large number of contributions adds a personal touch to each individual chapter and impressively demonstrates the international co-operation. The up-to-date, first-hand information makes the topics accessible to the discerning, interested layperson without abbreviating the scientific content. In the two editions of this book, the change of primary editor represents the competency of the respective native speaker.

Twenty-five years ago, the Department of Messel Research was established at the Senckenberg Research Institute in Frankfurt am Main. For Senckenberg, which had already been conducting scientific excavations in the pit since 1975, this solidification represented an important step and an acknowledgement of the Messel research. The research, carried out in conjunction with many German and international scientists, produces exciting results but also illustrates that the species diversity at the site has only been incompletely recorded to date. Based on extrapolations, it is likely that there are still many species of invertebrates waiting to be discovered, and that the known diversity of seed-bearing plants and several groups of vertebrates may increase significantly. Therefore, it stands to reason that several future generations will continue to be involved in exploring the fossil site.

New methods established in paleontology during the past decades, e.g., 3-D computer tomography for non-destructive analysis of bone structures, have significantly improved the examination of Messel fossils in regard to both qualitative and quantitative data. Accordingly, more exciting research findings can be expected in the future, which will further increase our understanding of the Messel ecosystem.

The inclusion of the Messel Pit Fossil Site in the UNESCO World Heritage List in 1995 represents a global acknowledgement and appreciation of the work done by many involved persons. In the year 2020, the Messel Pit will celebrate its 25-year anniversary as a World Heritage Site. This success story gives all of us a reason to be proud.

Krister T. Smith — Stephan F. K. Schaal — Jörg Habersetzer

Contents

Chapter 1
Messel – Eventful Past, Exciting Future

Stephan F. K. Schaal

About 48,270,000 years ago Volcanism in Europe causes the formation of maars – differently shaped craters of variable depth – thereby creating space for maar lakes and the deposit of lake sediments. According to the plate tectonic model by Scotese (2013), at the time of its formation, the Messel Maar was located at the current geographic latitude of the Alps. The crater quickly filled with water and sediments began to accumulate as Messel drifted northward with the European continental plate (Chapter 2).

About 47,300,000 years ago Over a period of about 1 million years, the Messel oil shale was formed. Upon filling up with sediments, the maar is silted up and from now on holds the fossilized remains of animals and plants from paratropical habitats (Chapter 3).

About 30,000,000 years ago The lifting and folding of the Alps begins. Central Europe – an island archipelago at the time – becomes dry land as the Antarctic binds significant amounts of water as ice and sea level drops. The Alpine region as well as the area including the Messel Maar located farther north are affected by tectonic uplift; this is followed by erosion (continuing to the present day). Several hundred vertical meters of material are eroded in the Messel region.

Start of modern chronology The Messel Maar has reached its current position, now located farther to the north. From the time of its origin until today it moved approximately 500 km northward, due to the shift of the European continental plate (Fig. 2.2; Chapter 2).

18th century Oil shale is discovered south of the village of Messel, located between Frankfurt am Main and Darmstadt in the state of Hesse.

19th century The first fossil crocodylian is recovered from the oil shale layer in 1875, and the discovery is described shortly afterwards (Ludwig 1877). The first paper offering an overview of the fossil site's geology and paleontology is published (Wittich 1898). Following the awarding of the Messel claim, the Messel Union is founded in 1884 for the exploitation of ironstone and lignite. In addition, a pyrolization plant is operated for the production of mineral oil and paraffin from the oil shale.

1912 A contractual agreement with the mine owner transfers the sole rights of the Messel fossils to the Grand Ducal Museum at Darmstadt (the future Hessian State Museum Darmstadt). Henceforth, until 1973, all fossils recovered in Messel find their way into the Darmstadt fossil collection.

1945–1959 The production facilities are destroyed during World War II, but are immediately rebuilt after the end of the war. The facility is seized by the American military government and, until 1953, is under the auspices of the I.G. Farbenindustrie AG, Frankfurt am Main. The facility is converted into a paraffin and mineral oil factory. A mining and extraction agreement is entered into with the state of Hesse.

1959 The YTONG concern, an aerated concrete manufacturer from Sweden, takes over the paraffin and mineral oil factory Messel GmbH (Beeger in Schaal & Schneider 1995).

Fig. 1.1: View into the Messel Pit, summer of 2017.

Chapter 3
Paleoclimate – Learning from the Past for the Future

Olaf K. Lenz, Volker Wilde, Walter Riegel

Throughout its history, the earth has been subject to steadily alternating glacial periods and greenhouse phases. In order to make reliable predictions regarding the future global climate change and its effects on our species and our environment, it is necessary to develop an understanding of the processes that took place over periods of time far beyond the instrumental record of climate data during the past decades.

With the aid of numerous deep sea drillings, scientists in recent years developed an oxygen isotope curve that reflects the development of deep sea temperatures in the past 65 million years (Zachos et al. 2001, 2008; Fig. 3.2). In the meantime, it has also been accepted as a global temperature development curve. It shows a warming trend since the middle Paleocene, which reached its high point with the "Early Eocene Climatic Optimum" (EECO) approx. 50–52 million years ago. This was followed by a gradual, initially very slow cooling, until the occurrence of a drastic drop in temperature around the turn from the Eocene to the Oligocene. This started the transition from the Paleogene greenhouse climate to the glacial climate of the Oligocene and Neogene (Zachos et al. 2001).

The long-term climate development was only interrupted by a few short-term fluctuations. The most prominent of these warming events ("hyperthermals"), the "Paleocene-Eocene Thermal Maximum" (PETM; McInerney & Wing 2011), occurred at the Paleocene-Eocene boundary, approx. 56 million years ago. The total duration of this event is estimated to have lasted about 170,000 years (Röhl et al. 2007). It was caused by a short-term massive input of greenhouse gases in the atmosphere and was accompanied by an average temperature increase of 5–6 °C. This increase was felt most noticeably in the high latitudes, where, with a rise of 7–10 °C, it far exceeded these average values.

The Eocene – the time when the Messel oil shale was deposited – thus falls into a period when the earth was dominated for the last time by a greenhouse climate not caused by man. For example, the report of the Intergovernmental Panel on Climate Change (IPCC 2014) predicts a CO_2 level for the year 2100 that is comparable to the levels in the Eocene (Parrish & Soreghan 2013). The Eocene is thus particularly well-suited as a reference period.

During the Eocene, the area around Messel was covered by a forest characterized by a subtropical to

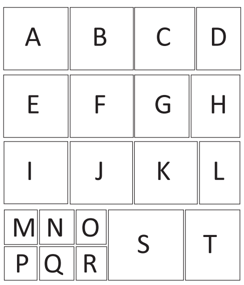


Fig. 3.1 Examples of pollen and spores from the scientific drilling at Messel in 2001.
A: spore of a climbing fern (Schizaeaceae), B and C: different types of fern spores, D and F: spores of polypod ferns (Polypodiaceae), E: spore of a club moss (Selaginellaceae), G: pollen grains of a water lily (Nymphacaea), H: pollen grain of a sapotaceous plant (Sapotaceae), I: pollen grain of a restio plant (Restionaceae), J: pollen grain of a plant from the kapok family (Bombacaceae), K: pollen grain of a witch hazel plant (Hamamelidaceae), L: pollen grain of a vine plant (Vitaceae), M, P and Q: pollen grains of extinct walnut plants (Juglandaceae), N: pollen grain of an unknown extinct plant, O: pollen grain of an oleaceous plant (Oleaceae), R: pollen grain of an heather plant (Ericacea), S: colony of the "oil alga" *Botryococcus*, T: shell of the dinoflagellate *Messelodinium* (Dinophyceae). Scales: 10 µm.

Chapter 7
Jewels in the Oil Shale – Insects and Other Invertebrates

Sonja Wedmann

In the past 20 years, our view of the relationships between different groups of animals has undergone significant changes. The traditional system of the animal kingdom was primarily based on morphological, anatomical and physiological features and on the comparison of the organisms' development (ontogeny). In the past decades, the use of genetic methods in the analysis of the phylogeny necessitated a review of the traditional system and led to changes in many areas. However, several of the traditional concepts were confirmed by the new methodology (e.g., Westheide & Rieger 2013).

The Metazoa (Fig. 7.2) encompass all of the multicellular animals. One of the most primitive groups are the sponges (Porifera), which do not yet possess any organs such as blood vessels or reproductive organs; moreover, they also lack a nervous system and a head. The head only develops in the Bilateria. As their name implies, the body of the Bilateria shows a bilaterally symmetrical design, i.e., it can be divided into a left and a right half. Large, traditionally recognized groups in the system of the Bilateria are the Protostomia (from Greek for "first mouth"), in which the blastopore ("original mouth") develops into the mouth during ontogeny, and the Deuterostomia (from Greek for "second mouth"), in which the blastopore develops into the anus during ontogeny. while the actual mouth opening is newly formed. According to the latest findings, the Protostomia can be divided into Ecdysozoa (molting or shedding animals) and the Lophotrochozoa (Spiralia) (e.g., Westheide & Rieger 2013, Dunn et al. 2014); Fig. 7.2 only illustrates the most important groups or the ones represented in Messel. The main distinction

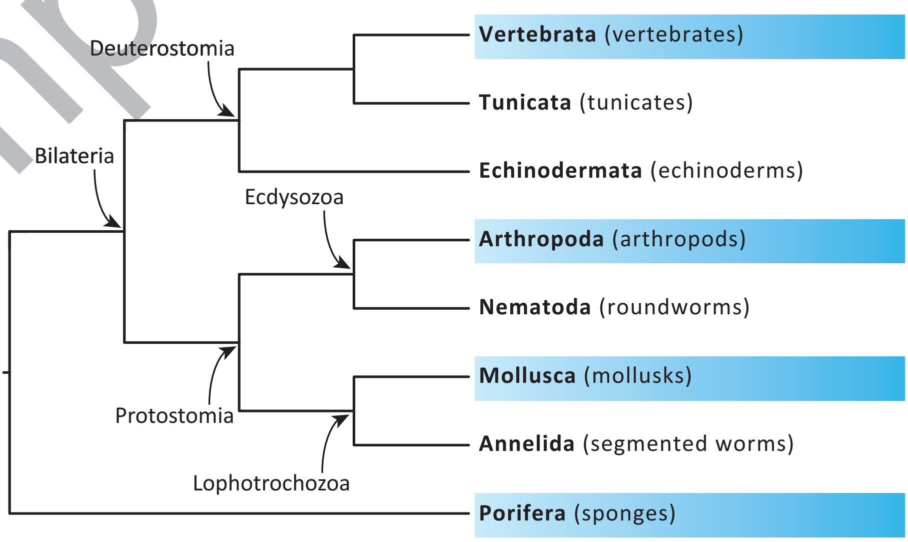


Fig. 7.2: Simplified phylogenetic tree of the animal kingdom (Metazoa). Groups recorded from Messel are marked blue.

Fig. 7.1: Fossilized male and recent female leaf insect (Phasmatodea).

beetles feed on wood; some adults do not eat at all, while others suck tree sap or feed on pollen. The intestinal contents of a longhorn beetle from Messel reveal that it had eaten pollen shortly before its death (Fig. 7.61). Insects that allow such ecological conclusions regarding food plants are rarely found. Next to the weevils, the leaf beetles (Chrysomelidae) are the most species-rich group of beetles. As their name implies, leaf beetles generally have a vegetarian diet. Their host species are almost exclusively higher plants (flowering plants), and the leaf beetles' evolution shows close connections to that of the plants. Similar to the weevils, this is a very diverse group with many species, especially in the tropics. They are often remarkably colorful, due to the presence of both pigment and structural colors. The specimens from Messel show impressive original structural colors, but they are often missing legs and antennae, which are required for a more detailed identification (Fig. 7.62). The subfamily Sagrinae, which today occurs mainly in Southeast Asia and across the Southern Hemisphere, has been documented from Messel. Its members can be recognized by their noticeably thickened hind legs (Fig. 7.63), which are not used for jumping, but rather in fights. The metallic-green body is also characteristic for this group.

Fig. 7.61: Longhorn beetle (Cerambycidae) with preserved fossil pollen remains in the intestinal tract, body length 22.5 mm.

The weevils and their relatives (Curculionoidea) comprise four families of beetles which usually have the head prolonged into a snout or beak. The mouthparts, which are often small and somewhat modified, are located at the front end of the snout. Most weevils are vegetarians and usually feed on plants, and rarely on decayed wood as well. More than 75,000 recent species have been described. With more than 57,000 species found around the globe, the true weevils (Curculionidae) are the largest family among the weevil-like beetles. Their antennae are usually geniculate (elbowed), i.e., similar to ants, a markedly elongated first segment is followed at an angle by several much shorter segments. The group can be divided into long-nosed weevils with a very long, thin, curved snout, and short-nosed weevils with a short, thick and flattened snout (Dathe 2005). Their body length can vary from less than 1 mm to about 60 mm. In addition to large species, many smaller weevils are also represented in Messel (Fig. 7.64), some of which only measure ½ mm in length. The larger specimens are up to 20 mm long. Only four species have been described from Messel, with one species distinguished by a metallic, light blue coloration (Rheinheimer 2007). Straight-snouted weevils in the narrow sense (Brentidae) are a heterogeneous group. The straight-snouted weevils are distinguished by their rather slender body. They are represented in Messel by just under 20 specimens, while the related Apionidae are found much more frequently.

There are a few additional groups of beetles in Messel, which are not covered in detail here. These include the throscid beetles (Throscidae), false click beetles (Eucnemidae), cylindrical bark beetles (Colydiidae) and hister beetles (Histeridae) as well as a single representative of the bark-gnawing beetles (Trogossitidae) described by Meunier (1921).

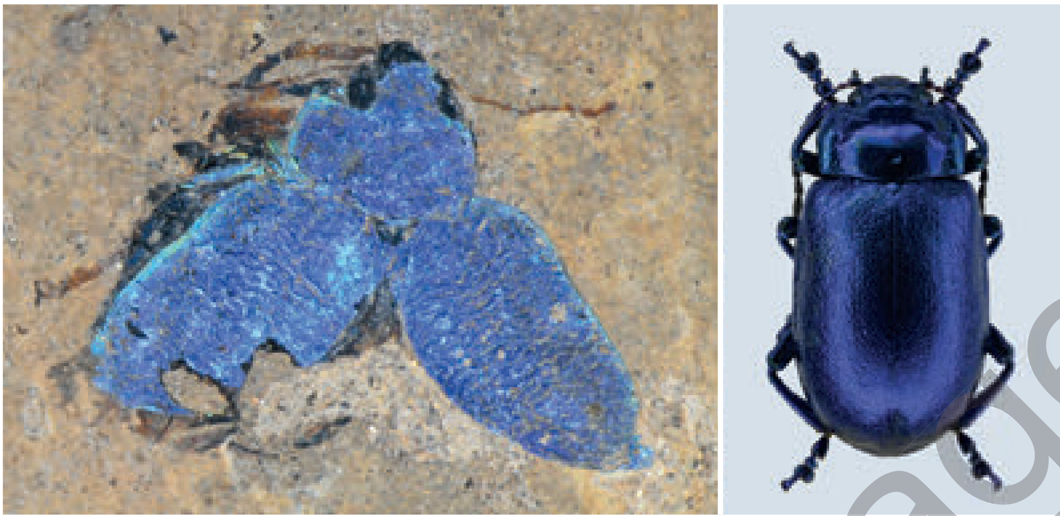


Fig. 7.62: Leaf beetle (Chrysomelidae). Left: fossil leaf beetle, body length c. 7 mm; right: the recent species *Chrysochloa tristis*, body length 11.5 mm.

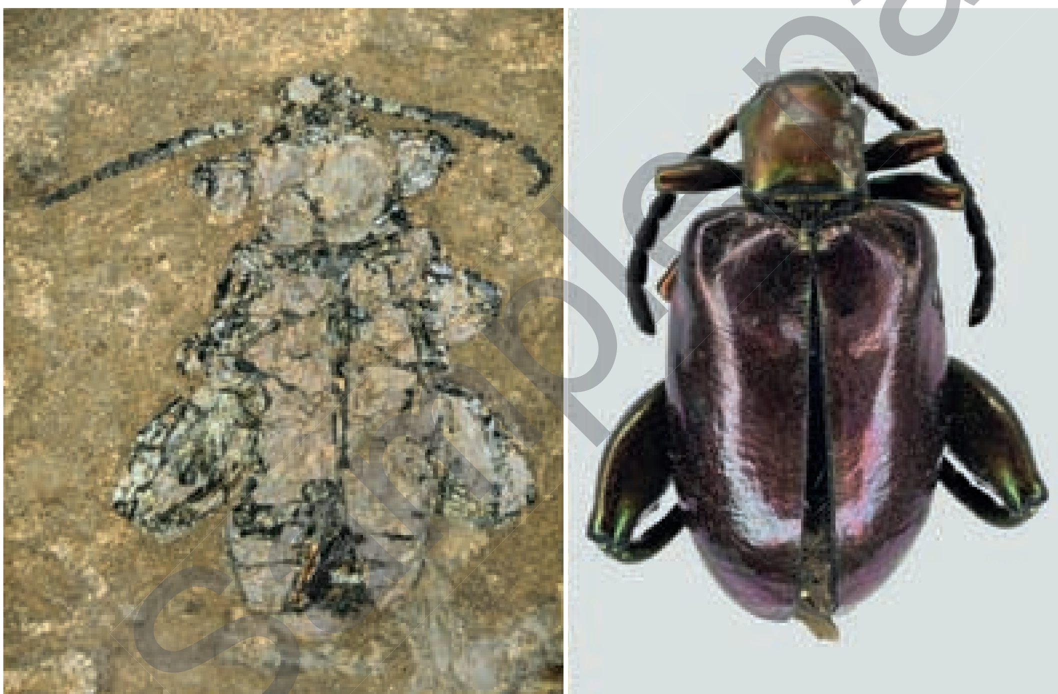


Fig. 7.63: Leaf beetle (Chrysomelidae) from the subfamily Sagrinae. Left: fossil leaf beetle, body length 17 mm; right: the recent species *Sagra mutabilis* with a body length of 20 mm.

Caddisflies (Trichoptera)

The aquatic larvae of many caddisflies build a case using grains of sand. These cases protect the delicate body of the larva. Adult caddisflies resemble small moths, have hairs on their wings and special, modified mouthparts.

Caddisflies are almost exclusively represented by larval cases in Messel, where they are among the most common fossils. Their abundance varies from one excavaction site to another, which was seen as an indication of transport via an inlet (Lutz 1990). Recently, it has become apparent that sand cases can be common not only in the northwest, but also in the eastern part of the pit, while they are entirely missing from the layers in the former center of the lake (Sonja Wedmann, *unpubl. data*).

The material used for the cases in Messel is mainly restricted to grains of sand (Fig. 7.65); in rare cases,

Chapter 10.2
Turtles – Armored Survivalists

Edwin Cadena, Walter G. Joyce, Krister T. Smith

Turtles (Testudines) are a successful group of vertebrates with nearly 350 living species. The most prominent feature of these animals is their protective shell. The shell is composed of two layers: an exterior layer of horny scales (scutes) formed by the outermost skin layer (epidermis), and an interior layer of bone (the carapace above and the plastron below), which is composed of numerous bony elements whose full evolutionary history has only recently been elucidated (Lyson et al. 2013a). The sutures between the scutes and between the bony elements of the shell generally do not correspond, such that the scutes, after they have decayed, leave a complex pattern of traces on the shell bones (Fig. 2, left). The plastron derives in part from the belly ribs (gastralia), which are ossifications of the dermis, the thick layer of the skin that underlies the epidermis, whereas most of the carapace develops in association with the ribs and vertebrae. The carapace usually has a row of marginal elements (called peripherals), which unite carapace and plastron at the bridge. Both carapace and plastron receive contributions from the shoulder girdle (Fig. 2, center, right).

Because many reptiles show ossifications of their skin in the form of osteoderms, paleontologists historically presumed that the turtle shell formed as the result of the successive accumulation and expansion of osteoderms in the thoracic region and the eventual fusion of this dermal shell with the underlying skeletal elements (e.g., Lee 1997). However, developmental biologists had long noted that this conclusion is not supported by embryology: the ossification of the dermis appears to be triggered during growth by the underlying skeletal elements (e.g., Burke 1989). The recent discovery or renewed study of fossil reptiles with intermediate morphologies – *Pappochelys* (Schoch & Sues 2015) and *Odontochelys* (Li et al. 2008) from the Triassic and *Eunotosaurus* from the Permian (Lyson et al. 2010) – contributed substantially to bridging the gap between primitive amniotes and early turtles and now corroborate the initial hypothesis by developmental biologists with paleontological data (Lyson et al. 2013a).

Although turtles have remained faithful to their shell, it is a commonly held misconception that the group underwent little change over the course of its evolutionary history. Among others, turtles have conquered a wide range of habitats, from tropical forests to subarctic oceans, evolved different ways to retract their heads and limbs within the protection of the shell, including the addition of hinges in the plastron, devised different ways to strengthen their jaws, and adapted to a wide range of diets, such as hard-shelled mollusks, terrestrial plants, and jellyfish (Ernst & Barbour 1989). Turtles rarely achieved high species-richness over the course of their evolutionary history, but fully shelled members of the stem or crown group have been persistently present since the Triassic in most tropical to temperate biomes.

Extant turtles are universally regarded to form two primary groups (Fig. 3), which are easily identified by the way they retract their necks: side-necked-turtles (Pleurodira), which double fold their elongate necks horizontally to hide below the shell, and hide-necked turtles (Cryptodira), which double fold their necks vertically to withdraw the head between the shoulder girdles inside the shell (Ernst & Barbour 1989). The ancestral crown turtle could not yet withdraw its neck in either fashion, but was nevertheless able to partially protect itself by laterally tucking its head below the shell (Werneburg et al. 2015). To strengthen their bite, turtles have evolved expanded temporal (jaw) muscles that are packed towards the back of the skull, but the ear region blocks the direct path to the mandible. The two primary groups of turtles also differ in their solution to this problem. In cryptodires, the ear capsule forms a trochlea (pulley) that allows the muscles to glide around the ear, whereas in pleurodires, a trochlea is formed instead by an expansion of the lateral process of the pterygoid (one of the palatal bones) that circumvents the ear capsule entirely (Gaffney 1975). Although this feature is useful

Fig. 10.2.1: Soft-shelled turtle, *Palaeoamyda messeliana*, seen from above. Scale: 5 cm.

Chapter 11
Birds – the Most Species-rich Vertebrate Group in Messel

Gerald Mayr

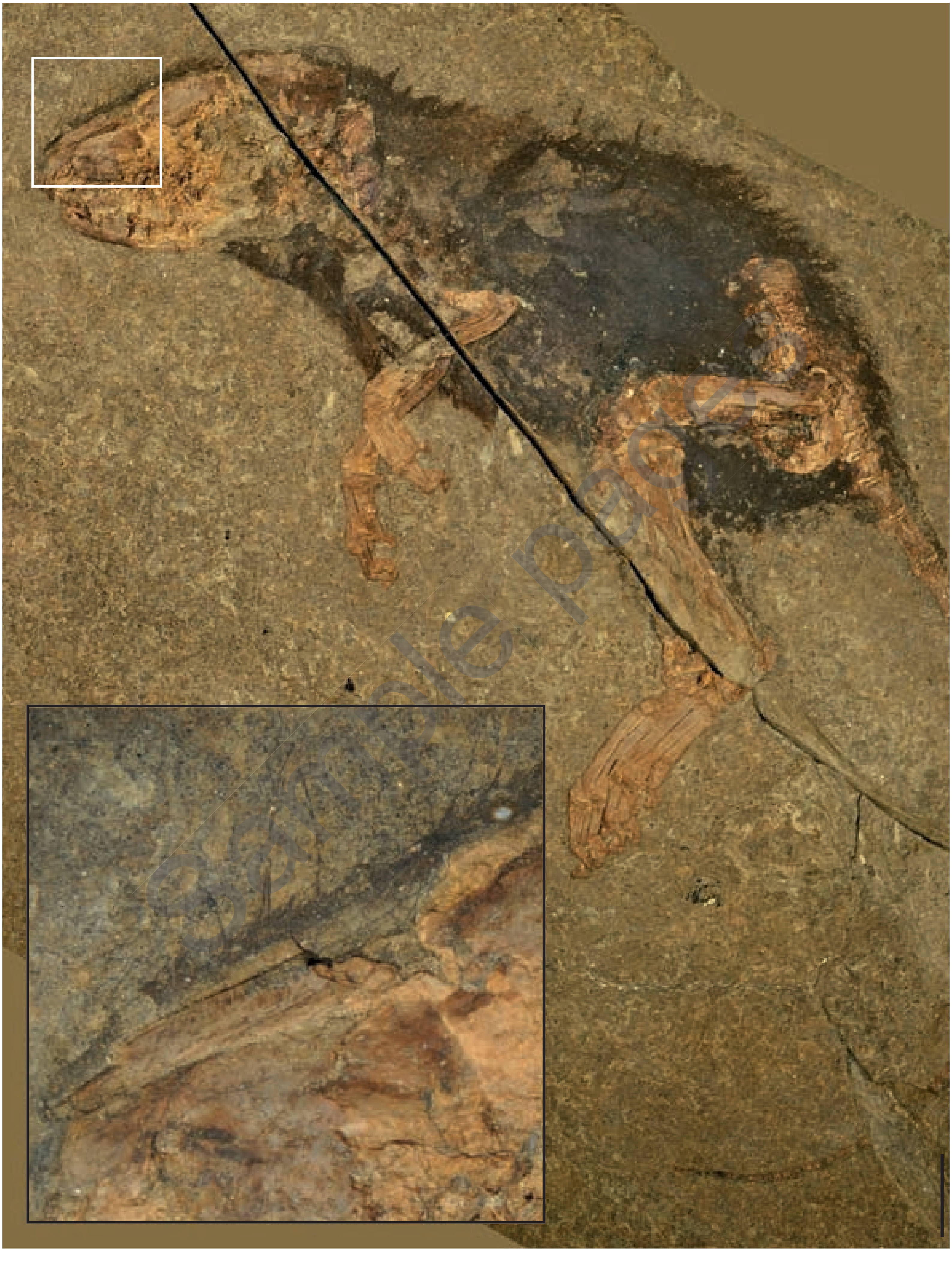
Among the terrestrial vertebrates in Messel, birds represent the majority of all fossil specimens. The collection of the Senckenberg Research Institute in Frankfurt alone comprises around 1,000 skeletal remains of birds (Mayr 2016a), and numerous additional ones are found in the other larger collections. Approximately 70 different species of birds from the oil shale deposits could be distinguished to date, although not all of them have been scientifically described yet. In regard to their species diversity, birds exceed all other vertebrate groups from Messel (Box 11.1). Therefore, a detailed knowledge of the avifauna of Messel is of great significance for our understanding of the ecosystem that encompassed Lake Messel.

In recent years, numerous avian fossils have been described from Eocene deposits, but no other fossil site offers a volume of specimens comparable to Messel, and only few others have yielded similarly complete remains. While most mammalian groups from Messel had been previously known from other fossil sites, many of the bird species were documented for the first time in Messel, and several are still only known from this site. Moreover, since the study of bird fossils began rather late, the knowledge gained in regard to the Messel avifauna over the last 20 years surpasses that of most other vertebrate groups from the site.

Many of the birds from Messel can be assigned to phylogenetic lineages still in existence today. However, some of them belong to groups that are probably unfamiliar to most readers. These will be introduced later in their respective places; in order to better understand the following text, we simply give a brief overview here of a few new insights regarding the relationships among extant birds (Neornithes) (Fig. 11.2). Recent birds can be divided into two groups that differ in regard to the structure of their bony palate. The Palaeognathae ("old jaws") comprise the ostrich-like birds (ratites) and their relatives, while the Neognathae ("new jaws") include all remaining species. Neognathous birds are further subdivided into two groups, the Galloanseres, comprising the gallinaceous birds and waterfowl, and Neoaves, which include the majority of all living birds today. The relationships among the Neoaves are insufficiently understood, but analyses of genetic data support three major groups that are termed Strisores, Aequornithes, and Telluraves (Fig. 11.2; Ericson et al. 2006; Hackett et al. 2008; Prum et al. 2015). The taxon Strisores contains nightjars and allies as well as swifts and hummingbirds. Aequornithes comprises the aquatic and semi-aquatic groups within the Neoaves, while Telluraves, in addition to owls, diurnal raptors, and parrots, includes the majority of all small, tree-dwelling bird species.

Almost certainly the split of the Neornithes into Palaeognathae and Neognathae already took place in the Mesozoic. However, the fossil record of neornithine birds from the Cretaceous is rather sparse, although remains of presumed representatives of the

Fig. 11.1: The Messel swift *Scaniacypselus szarskii*. Scale: 1 cm.



Chapter 12.3
With and Without Spines: the Hedgehog Kindred from Messel

Thomas Lehmann

Long considered to represent the most primitive order of placental mammals, the "Insectivora" was thought to incorporate almost all insectivorous placental mammals, but lacked clear unifying features. A growing number of studies has shown that "Insectivora" does not constitute a monophyletic group (e.g., Novacek 1986). Today, hedgehogs, moles, shrews and solenodons are the exclusive living members of the monophyletic order Lipotyphla (also referred to as Eulipotyphla), whereas certain superficially similar taxa such as tenrecs and golden-moles are now included in the clade Afrotheria (e.g. Stanhope et al. 1998), while others even belong to the placental stem. Lipotyphla seems now securely established within the clade Laurasiatheria, where it is probably in a basal position.

The Lipotyphla lineage could go back as far as the Cretaceous, but the oldest ascertained representatives are found in the Paleocene of Mongolia (Lopatin 2006). With almost 400 living species, the Lipotyphla is one of the most species-rich orders of placentals, mostly thanks to the high diversity of shrews. But in the past, the hedgehog-like Erinaceomorpha were more numerous and quite diverse, with representatives in Europe, Asia and North America. Erinaceomorpha is today entirely absent from the American continent.

Lipotyphla was long considered to be divided in two major clades: the Erinaceomorpha (hedgehogs, gymnures, and their fossil relatives) and the Soricomorpha (shrews, moles, solenodons, and their fossil relatives) (Symonds 2005). In the phylogenetic tree presented here (Fig. 12.3.2), the Soricomorpha are disbanded, following the most recent genetic studies (Roca et al. 2004; Brace et al. 2016), and the Talpidae are clearly separated from the Erinaceomorpha.

The oldest fossil lipotyphlans belong to the Erinaceomorpha (Gould 1995). The Amphilemuridae for instance, which were successively considered primates, and then "insectivores," is a common family in Paleogene sites (Maître et al. 2008). However, a recent study (Hooker & Russell 2012) suggests that Amphilemuridae were stem macroscelideans (i.e., elephant shrews and fossil allies), and thus members of the clade Afrotheria instead. This hypothesis has not always been confirmed in subsequent studies (e.g., Hooker 2014; Manz & Bloch 2015).

In Messel, only two lipotyphlan genera are known, both referred to Amphilemuridae: *Macrocranion* (Fig. 12.3.1) and *Pholidocercus* (Fig. 12.3.6). Although they are represented by complete skeletons in Messel, most fossil amphilemurids are known from teeth and jaw fragments. Thus, *Macrocranion* and *Pholidocercus* have been assigned to the family based on dental features. For instance, all amphilemurids retain a primitive placental dentition, with three incisors, one canine, four premolars and three

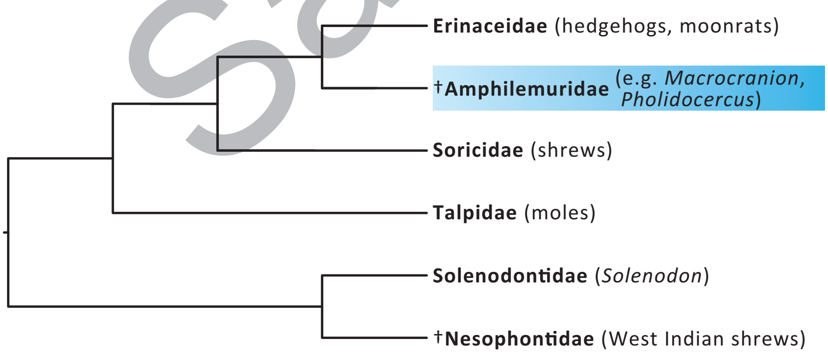


Fig. 12.3.2: Simplified phylogenetic tree of the Lipotyphla. Taxa known from Messel are highlighted in blue.

Fig. 12.3.1: *Macrocranion tupaiodon,* with delicate hair preservation, including numerous vibrissae on the snout (inset). Photos were taken before transfer. Scale: 1 cm.

When the first fossil discovery – of a crocodile – was made public in the year 1876 from the oil shale near the Hessian municipality of Messel in the middle of Germany, nobody could predict the future importance of this fossil site. In 1995, the fossil site was recognized as a World Heritage Site and placed on the UNESCO list.

In the early 1970s, the development of a special transfer method made it possible for the first time to permanently store the fossils from Messel. This finally enabled long-term scientific research on the discoveries. Over the past 25 years, new finds and modern analytical methods have led to rapid progress in research on Messel.

28 internationally renowned scientists describe the Eocene ecosystem found at Messel. More than 390 illustrations show the fauna and flora of an ancient world. The reader is offered insights into the current knowledge about the fossil site's geology and paleontology. Few other fossil sites in the world yield fossils of the quality known from Messel – which are exceptional in their completeness and their level of preservation.

This book about the UNESCO World Heritage Site 'Messel Pit Fossil Site' opens a new window that allows us to take a closer look at the development of the ecological communities in the Eocene. The comprehensive presentation of this book on Messel will make it a standard reference work for scientists, while the lush illustrations of flora and fauna will captivate everyone from fossil enthusiast to interested layperson.

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