Netherlands Journal of Geosciences / Geologie en Mijnbouw 81 (2): 177-183 (2002)

Biostratigraphy and paleoecology of continental Tertiary vertebrate faunas in the Lower Rhine Embayment (NW-Germany)

Th. Mörs

Naturhistoriska Riksmuseet/Swedish Museum of Natural History, Department of Palaeozoology, P.O. Box 50007, SE-104 05 Stockholm, Sweden;
e-mail: thomas.moers@nrm.se

Manuscript received: October 2000; accepted: January 2002

Abstract

This paper discusses the faunal content, the mammal biostratigraphy, and the environmental ecology of three important continental Tertiary vertebrate faunas from the Lower Rhine Embayment. The sites investigated are Rott (MP 30, Late Oligocene), Hambach 6C (MN 5, Middle Miocene), Frechen and Hambach 11 (both MN 16, Late Pliocene). Comparative analysis of the entire faunas shows the assemblages to exhibit many conformities in their general composition, presumably resulting from their preference for wet lowlands. It appears that very similar environmental conditions for vertebrates reoccurred during at least 20 Ma although the sites are located in a tectonically active region with high subsidence rates. Differences in the faunal composition are partly due to local differences in the depositional environment of the sites: lake deposits at the margin of the embayment (Rott), coal swamp and estuarine conditions in the centre of the embayment (Hambach 6C), and flood plain environments with small rivulets (Frechen and Hambach 11). The composition of the faunal assemblages (diversity and taxonomy) also documents faunal turnovers with extinctions and immigrations (Oligocene/Miocene and post-Middle Miocene), as a result of changing climate conditions.

Additional vertebrate faunal data were retrieved from two new assemblages collected from younger strata at the Hambach mine (Hambach 11C and 14). They are important for the understanding of the Plio-Pleistocene transition in the southern part of the Lower Rhine Embayment and for correlating depositional sequences in the Dutch/German borderland.

Keywords: mammal biostratigraphy, Middle Miocene, Late Oligocene, Late Pliocene, vertebrate environments

Introduction

The southern part of the Tertiary graben structure of the Lower Rhine Embayment in NW-Germany is characterised by the intercalation of marine and continental sediments. They contain the thick, economically important deposits of Miocene lignitic brown coal which is exploited in vast open cast mines by the Rheinbraun AG mining company. Although well exposed due to intensive mining, and studied by geologists and palaeontologists for two centuries, these deposits yielded only few biostratigraphical and palaeoecological data. The reason for the rare occurrence of faunistic remains is the high content of humic acids in the deposits. The acids decalcified the sediments and often resolved both mollusc shells as well as vertebrate bones and teeth. In contrast to the oil shale deposits of Rott, from which vertebrate remains were studied for 170 years (Bronn, 1828; for further references see von Koenigswald et al., 1992; Mörs, 1997), the first vertebrate fossils from the large open cast lignite mines were published by Strauch (1990) ten years ago.

New discoveries of vertebrate, especially mammalian remains from boreholes near Rott as well as from different stratigraphic levels in the Frechen and Hambach coal mines (Fig. 1) were described in the last years (e.g. Mörs, 1995; van Kolfschoten et al.,

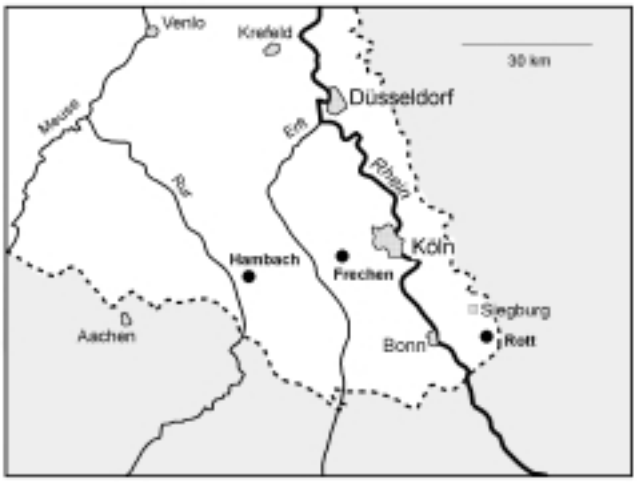

Fig. 1. Geological sketch map of the southern part of the Lower Rhine Embayment with the location of the palaeontological sites Rott, Hambach, and Frechen.

1998; Mörs et al., 2000). The unusually rich and to some degree spectacular material especially provides new and reliable biostratigraphic data for the sedimentary fill of the Lower Rhine Embayment. The vertebrate fossils from the Hambach and Frechen mines also provide insight into palaeoecological conditions of terrestrial environments in NW Europe during the Neogene, and supply new data for palaeobiogeographical analysis.

Vertebrate faunas and biostratigraphic setting

The Late Oligocene fauna of Rott (Table 1)

The fossil site Rott near Bonn at the southern margin of the Lower Rhine Embayment (Fig. 1) is famous for its rich flora, as well as its insect and vertebrate fauna (von Koenigswald, 1996). The lacustrine oil shales produced exceptionally well preserved, articulated skeletons with imprints of scales, skin, feathers, and fur ('Messel-like' preservation). The vertebrate fauna consists of freshwater fish, many amphibian species, reptiles, and mammals. The biostratigraphic setting into the Mammalian Paleogene biozones MP 28-30 was based on the occurrence of the small anthracotheriid *Microbunodon* (von Koenigswald et al., 1992).

A recently discovered fauna from overlaying lake shore and flood plain deposits consists of 20 small mammal species including the didelphid *Amphiperatherium*, talpids, dimylids, soricids, chiropterans, the flying squirrel *Blackia* aff. *miocaenica*, the castorid *Steneofiber*, glirids, eomyids, and cricetids (Mörs, 1995, 1996). This newly recorded mammal assemblage enhances biostratigraphic precision and places the deposits in MP 30, most probably in the upper part of this zone. This indicates a depositional age of latest Oligocene (Chattian) for the sediments at the southern margin of the basin.

The Middle Miocene fauna of Hambach 6C (Table 2)

In the Lower Rhine Embayment west of Köln, large open cast mines expose thick series of Miocene and Pliocene strata. The Miocene Ville Series with the Main Coal Seam never produced any vertebrate remains due to slightly acidic ground waters. The discovery of a well preserved and rich vertebrate fauna in a channel fill within the Frimmersdorf seam at the Hambach mine (Fig. 1) is therefore of immense interest. Among various marine and freshwater fish, amphibians and reptiles, more than 70 mammal species were identified to date (Mörs et al., 2000). They document the occurrence of the didelphid *Amphiperatherium*, of insectivores like erinaceids, the metacodontid *Plesiosorex*, talpids, soricids, and dimylids, of chiropterans, of rodents like sciurids, petauristids, glirids, eomyids, cricetids, and castorids, and of lagomorphs (Ziegler & Mörs, 2000; von Koenigswald & Mörs, 2001). Large mammals are represented by the primate *Pliopithecus*, by carnivores like the hyaenid ?*Protictitherium*, mustelids, amphicyonids, and the ursid *Ursavus*, by artiodactyls like the suid *Hyotherium*, the palaeochoerid *Taucanamo*, tragulids, cervids, and bovids, by cetaceans, by perissodactyls like the equid *Anchitherium*, rhinos, and by proboscideans (Rössner & Mörs, 2001). Small mammals are predominant within this fauna with at least 50 species. Of particular interest is that usually rare taxa like *Lanthanotherium*, *Plesiosorex*, *Miopetaurista*, *Myoglis*, *Fahlbuschia*, and *Karydomys* are very abundant. Larger mammals are dominated by beavers and tragulids of the genus *Dorcatherium*. In addition, at Hambach 6C there is evidence for extremely rare mammals like *Orygotherium*, *Anchitheriomys* and *Pliopithecus*.

Based on the rich association of mammalian taxa that includes about 30 rodent species, this late Orleanian fauna can be correlated with the upper part of the Mammalian Neogene biozone MN 5 (Mörs et al., 2000). The depositional age of the middle part of the Main Coal Seam (horizon 6C of the local lithostratigraphy) can therefore be assigned to the early middle Miocene. This means Langhian or Reinbekian according to the stratigraphy of the NW German Tertiary, and a numerical age range between 15.2-16.0 Ma. The vertebrates of Hambach 6C are also of great palaeobiogeographic importance as they represent the northwesternmost extension of terrestrial Miocene faunas in Europe.

The Late Pliocene composite fauna of Frechen and Hambach 11 (Table 3)

The Pliocene Reuver Clay, exposed at the Frechen and Hambach mines (Fig. 1), produced two excellently preserved small vertebrate faunas with freshwater fish, amphibians, reptiles, and mammals. The composite mammalian fauna of the Reuver Clay includes talpids, soricids, a mustelid, petauristids, sciurids, castorids, glirids, arvicolines, murids, a lagomorph, a cervid, and a rhino (Strauch, 1994; Reumer, 1995; van Kolfschoten et al., 1998; Mörs et al., 1998). The evolutionary stage of the arvicoline teeth allows a stratigraphic setting of this Early Villanyian fauna in the Mammalian Neogene biozone MN 16a (Hambach) and MN 16b (Frechen). This means an estimated numerical age of 2.5 Ma for the deposition of the Reuver Clay (horizon 11 of the local lithostratigraphy). To date, the Hambach 11 fauna represents the richest Late Pliocene assemblage of small vertebrates in Germany.

Paleoecology of the vertebrate faunas

Paleoecology of the fish faunas

Regarding the fish faunas, in Rott and Hambach 11 only fresh water forms occur. Rott is characterised by two abundant cyprinid species that prefer currentless lake conditions as does the rare pike (Martin, 1996). The presence of a few specimens of *Hypomesus* also indicate rivulet environments. At Hambach 11 the fish association is much more diverse: three carp species, pike, catfish, bass, and zander document well oxygenated waters and currents in what appears to be a river channel setting in close association with lakes or oxbows (Schwarz & Mörs, 2000; Hierholzer & Mörs, in prep.). In contrast to these faunas, the Hambach 6C fauna is characterised by abundant marine fish like sharks and marine teleosts as well as by fresh water cyprinids (Mörs et al., 2000; Hierholzer & Mörs, in prep.). This association indicates estuarine conditions and slow currents in a larger channel.

Palaeoecology of the amphibian and reptilian faunas

Within the Urodela, the aquatic giant salamander *Andrias* occurs at all three localities, documenting zones of slow currents as well as favourable climatic conditions until the Late Pliocene. The terrestrial crocodile newt *Chelotriton*, a typical element in Oligocene and Miocene faunas, is absent at the Pliocene site Hambach 11, indicating a climatic change during the Late Miocene and Pliocene. Adult individuals of terrestrial discoglossid anurans as well as of toads are rare at all three localities. Only at Rott the aquatic tadpoles are common. Due to the different stratigraphic setting of the localities, the discoglossids are represented by different taxa. Aquatic palaeobatrachid anurans are very common in Rott (Wuttke, 1996), indicating optimal living conditions in a currentless freshwater lake. They are absent at Hambach 6C and rare at Hambach 11. Their absence at Hambach 6C may be due to pronounced estuarine conditions.

Turtles are common at all three localities, but differ in their composition as well as in frequency (Böhme & von Koenigswald, 1996; Mörs, 1998; Mörs et al., 2000; Klein & Mörs, in prep.). The snapping turtle *Chelydropsis*, a characteristic faunal element in Tertiary lakes of Central Europe, is the most common turtle at Rott, but quite rare at the Hambach 6C site. In contrast, the river-inhabiting soft-shelled turtle *Trionyx* is rare at Rott, but is the most common turtle at Hambach 6C. This genus is lacking at Hambach 11 due to climatic change. The latest stratigraphic record of Chelydrids from the lower Rhine Embayment was reported by Strauch (1990) from the Upper Miocene Inden Series, but *Chelydropsis* is still present at Hambach 11. 'Swamp turtles' of the family Emydidae were also documented from all three localities, but are represented by different genera and species. In Hambach 6C there are at least two taxa present. A terrestrial, giant tortoise is only known from Hambach 6C, indicating the Middle Miocene climatic optimum during the deposition of the Ville Series. The single carapax fragment (in comparison with hundreds of fragments from other turtles) documents that the wet surroundings of the Hambach channel were not the ideal habitat for this animal since giant tortoise remains are frequent in contemporaneous but rather dryer habitats of Southern Germany.

The alligator *Diplocynodon* is present at Rott and very common at Hambach 6C, whereas chameleons are only known from the latter, indicating the Middle Miocene climatic optimum. Both taxa became extinct in Central Europe long before the deposition of the Reuver Clay. Snakes and limbless glass lizards occur at all three localities, but with different taxa in different stratigraphic layers.

Paleoecology of the small mammal faunas

Opossums of the genus *Amphiperatherium* are present at Rott and Hambach 6C with different species. Because of the cooling during the Middle Miocene they became extinct in Europe and cannot be expected at Hambach 11.

The insectivores of all three localities are dominat-

ed by aquatic/semiaquatic forms, or at least by taxa with preferences for wet conditions. Hambach 6C shows the greatest variety and individual numbers with the echinosoricid *Lanthanotherium*, the metacodontid *Plesiosorex*, moles and water moles, shrews and dimylids (Ziegler & Mörs, 2000). Rott has produced also moles and water moles, shrews, and dimylids, but typical palaeogene taxa (Mörs, 1995, 1996). The Reuver Clay shows the lowest taxonomic diversity; from the groups represented in Hambach 6C, only talpids (mostly water moles) and soricids survived the Mio-/Pliocene cooling (Reumer, 1995; Mörs et al., 1998).

Rodent teeth are mainly accumulated by owl pellets, and therefore they represent different habitats. Only beavers, as the largest rodents of the northern hemisphere, clearly indicate rivers or lakes. They are present at all tree localities, and especially at Hambach 6C castorids are very common. Generally, this locality shows the greatest diversity in rodents with about 30 species (Mörs et al., 2000), which agrees with the Miocene climatic optimum during the deposition of the Ville series. Especially dormice and hamsters are very diverse and are represented by ten respectively eight species. The hamsters, already occurring with several taxa at Rott, are replaced in the Reuver Clay by voles and mice (van Kolfschoten et al., 1998; Mörs et al., 1998). Only eomyids are relatively rare at Hambach 6C, indicating that there were no or only few real dry habitats in the surroundings of the river channel. In contrast, eomyids are very common in Rott (Mörs, 1995, 1996), suggesting that orographically higher, dry areas were close to the lake. There is no record of eomyids in the Reuver Clay, they became very rare during the Late Miocene/ Pliocene cooling phase. On the other hand, the climatic conditions of the Reuverium still allowed a great variety of flying squirrels to live in the surrounding forest areas (Mörs et al., 1998). Ground squirrels are well documented from Hambach 6C only.

Lagomorphs are recorded from all three localities, but are rare due to generally wet conditions. At Rott and Hambach 6C ochotonids are present, whereas at Hambach 11 a leporid occurs instead.

Paleoecology of the large mammal faunas

Only Hambach 6C has produced a primate. The rare *Pliopithecus* is restricted to a short time interval that correlates with the Middle Miocene climatic optimum.

Within the order Carnivora, mustelids are present at all three localities, and especially at Hambach 6C a great variety of these small- to medium-sized carnivores occurs, including the aquatic otter-like *Potamotherium* (Mörs et al., 2000). Large-sized carnivores of the extinct family Amphicyonidae were only recorded from Rott and Hambach 6C.

The swampy palaeoenvironments of Rott and Hambach 6C are characterised by small, primitive artiodactyls. *Microbunodon*, a small 'coal pig', is the most common large mammal at Rott (von Koenigswald & Mörs, 1996). It is replaced at Hambach 6C by two species of the water chevrotain *Dorcatherium*, which are so abundant that this locality is one of the richest in Europe. Hambach 6C has also produced a single tooth of the extremely rare 'swamp deer' *Orygotherium*, only known from two other lignite deposits in Europe (Rössner & Mörs, 2001). *Dorcatherium* and *Orygotherium* might be adapted to a semi-aquatic life. In addition, pigs were recorded from Hambach 6C with the palaeochoerid *Taucanamo* and the suid *Hyotherium*.

Hambach 6C is the only of the three faunas that includes a few whale and dolphin remains, providing further evidence for marine conditions in an estuarine environment. Within the Perissodactyla, rhinos are present at all three localities, but with different taxa due to the stratigraphic position. Especially the rhinos from Hambach 6C are short-legged and seem to be adapted to a hippo-like, semiaquatic mode of living.

Discussion and further research

The recent discoveries of fossil mammals provide the first reliable biostratigraphic data for the continental Tertiary of the southern part of the Lower Rhine Embayment. The three checkpoints cover a timespan from the Late Oligocene of Rott (late MP 30, about 23 Ma) via the Middle Miocene of Hambach 6C (late MN 5, about 15.5 Ma) to the Late Pliocene of Frechen/Hambach 11 (MN 16 a+b, about 2.5 Ma). Although these are only three checkpoints within the entire sedimentary sequence, the reliable data allow a calibration and is part of a multidisciplinary approach. This approach includes palynostratigraphy, paleoclimatology, and sequence stratigraphy to develop a stratigraphic framework of the continental series of the Lower Rhine Embayment (Schäfer et al., 1997).

The rich vertebrate assemblages also provide new data for reconstructing the paleoecology of continental faunas and their paleoenvironments in NW Germany during the Tertiary. The three faunas investigated show many conformities in their general composition (e.g. many aquatic or semiaquatic forms; identical or related taxa in lower vertebrates; Tables 1-3), due to similar environmental conditions in wet low-

land habitats. This indicates rather similar (depositional) environments reoccurring during at least 20 Ma in the Lower Rhine Embayment – a region that is characterised by long-term tectonic activity and high subsidence rates. The paleoecological differences observed result from local differences in the depositional environments of the fossil sites. Rott represents a lake and flood plain environment adjacent to orographically higher (and drier) habitats positioned at the southern margin of the basin (Fig. 1). Hambach 6C is characterised by its location in the centre of the embayment within vast coal swamps and lacking higher, dry areas (except arboricol habitats), and by the large channel within an estuarine environment. For Frechen and Hambach 11, conditions are similar, but with smaller channels and without any marine influence. On the other hand, species and diversity differences of the faunas result from the different stratigraphic positions of the localities. The faunal differences (Tables 1-3) reflect the change of climate conditions. The great diversity of Hambach 6C as well as certain taxa indicate the climatic optimum (e.g. rodents, chameleon, and *Pliopithecus*). The lower diversity at Frechen/Hambach 11 as well as some taxa reflect the post-middle Miocene climatic change (e.g. reptiles and glirids, *Sylvaemus*). The faunal changes at the three localities document extinctions and immigrations of taxa or entire groups (e.g. different cricetid genera in Rott and Hambach 6C; no *Diplocynodon* and *Amphiperatherium* at Frechen/Hambach 11; arvicolines and murines instead of cricetines at Frechen/Hambach 11).

Additional research was conducted at the Plio-/Pleistocene boundary in the Lower Rhine Embayment. Discovered within a channel fill, the new, rich vertebrate fauna Hambach 11C (formerly horizon 13 in the local lithostratigraphy; see Heumann, in prep.) resembles both associations from Frechen and Hambach 11. This indicates a Reuverian age for this horizon, a sequence that was placed previously in the Tegelen series. This association is particularly important because of its rich flying squirrel and beaver remains, especially many teeth of *Pliopetaurista pliocaenica* and *Trogontherium minus*, which complete the findings of Hambach 11. The second new discovery is Hambach 14, a rich assemblage of small vertebrates from a clay horizon within gravel and sands of the main terrace of the Rhine river (horizon 14 in the local lithostratigraphy). The fauna consists of *Esox*, cyprinids, anurans, desmanines (*Galemys*, *Desmana*), *Talpa minor*, Soricines, *Eliomys*, Arvicolines, and murines (*Sylvaemus*, *Micromys*). The joint occurrence of the arvicolines *Mimomys* and *Allophaiomys* at Hambach 14 suggests an early Biharian fauna with an Early Pleistocene depositional age. The Early Villanyian Hambach 11C fauna and the Early Biharian Hambach 14 assemblage indicate that the Tegelen series is absent at least in the Hambach mine. The Tegelen series may be lacking in the entire southern part of the Lower Rhine Embayment. Therefore, Hambach 11C and 14 are crucial for our understanding of the Plio-Pleistocene transition in the southern part of the Lower Rhine Embayment and for correlating sequences in the Dutch/German borderland.

Over the last decade, new discoveries of fossil vertebrates have provided a new perspective and important biostratigraphical and paleoecological data to infer the paleoenvironmental constrains prevailing in the Lower Rhine Embayment. Ongoing investigations in the excellent exposures of the Rheinbraun AG lignite mines will supply more information about biostratigraphy, biogeography and ecology of Tertiary continental paleofaunas of NW Europe.

Acknowledgements

For continuous help during fieldwork at the Hambach mine, and for the generous donation of many vertebrate fossils from this site to the collections of the Institute of Palaeontology, University of Bonn (IPB), I thank the Rheinbraun AG, and especially the employees Bertram Wutzler and Fritz von der Hocht. The help of many colleagues and students including comments, discussions, possibility to compare material and laboratory assistance to improve this long-term project is gratefully acknowledged. I thank the editors of this volume, Andreas Schäfer and Agemar Siehl, as well as Daniela C. Kalthoff and Martin R. Langer (both IPB) for comments on the manuscript. The reviews by Jens L. Franzen (SNG, Frankfurt a.M.) and Thijs van Kolfschoten (Univ. Leiden) are greatly appreciated. This research was supported mainly by the Deutsche Forschungsgemeinschaft (DFG) under the auspices of the Sonderforschungsbereich 350. Fieldwork at the Rott locality was partly financed by the Landschaftsverband Rheinland and by the Stadtmuseum Siegburg.

List 1: The Late Oligocene fauna of Rott.

OSTEICHTHYES
SALMONIFORMES, Salmonidae: *Enoplophthalmus* sp.; Esocidae: *Esox* (*Kenoza*) *papyraceus*
CYPRINIFORMES, Cyprinidae: *Palaeorutilus papyraceus*, *Tarsichthys macrurus*
AMPHIBIA
CAUDATA, Cryptobranchidae: *Andrias scheuchzeri*; Salamandridae: *Chelotriton paradoxus*, *Brachycormus noachicus*

ANURA, Palaeobatrachidae: *Palaeobatrachus diluvianus*, *P. gigas*, *Lithobatrachus europaeus*; Discoglossidae: *Discoglossus troscheli*; Pelobatidae: *Pelobates decheni*, *Eopelobates anthracinus*; Ranidae: *Rana noeggerathi*, *R. meriani*

REPTILIA

CHELONIA, Chelydridae: *Chelydropsis decheni*; Trionychidae: *Trionyx* sp.; Emydidae: *Palaeochelys mlynarskii*

CROCODYLIA, Alligatoridae: *Diplocynodon ratelii*

SQUAMATA, Lacertidae: *Lacerta* sp., '*Lacerta*' *pulla*; Cordylidae vel Gerrhosauridae: '*Lacerta*' *rottensis*; Anguidae: *Ophisaurus* sp., *Pseudopus heymanni*; Boidae: *Rottophis atavus*

AVES

Aves indet. (two species)

MAMMALIA

MARSUPIALIA, Didelphidae: *Amphiperatherium exile*

LIPOTYPHLA, Talpidae: *Desmanella* sp., *Paratalpa* sp., Talpidae indet.; Dimylidae: Dimylidae indet.; Soricidae: *Ulmensia ehrensteinensis* vel *Soricella discrepans*, *Dinosorex* sp. vel *Heterosorex* sp.

CHIROPTERA, Vespertilionidae: Vespertilionidae indet.; Chiroptera indet.

CARNIVORA, ?Mustelidae: ?Mustelidae indet. (two species); Amphicyonidae: *Amphicyon* sp.

RODENTIA, Petauristidae: *Blackia* aff. *miocaenica*; Gliridae: *Bransatoglis* cf. *fugax*, *Glirudinus glirulus*, *Peridyromys* cf. *murinus*; Eomyidae: *Rhodanomys* aff. *hugueneyae*, *Rhodanomys* sp., *Eomyodon weidmanni*, *Pseudotheridomys* cf. *schaubi*; Cricetidae: *Eucricetodon* cf. *collatus*, *Pseudocricetodon* cf. *thaleri*, *Adelomyarion vireti*; Castoridae: *Steneofiber* cf. *eseri*

LAGOMORPHA, Ochotonidae: *Amphilagus* sp. vel *Piezodus* sp.

ARTIODACTYLA, Anthracotheriidae: *Microbunodon breviceps*; Moschidae: *Pomelomeryx* sp. vel *Amphitragulus* sp.

PERISSODACTYLA, Rhinocerotidae: *Brachydiceratherium lemanense*

List 2: The Middle Miocene fauna of Hambach 6C

CHONDRICHTHYES

LAMNIFORMES, Odontaspididae: *Odontaspis vorax*, *Carcharias* cf. *reticulata*

CARCHARHINIFORMES, Scyliorhinidae:'*Scyliorhinus' distans*; Carcharhinidae: *Physogaleus* sp.

MYLIOBATIFORMES, Dasyatidae: *Dasyatis* sp.; Dasyatidae vel Myliobatidae indet.

OSTEICHTHYES

CYPRINIFORMES, Cyprinidae: *Palaeotinca* sp., *Barbus* sp., *Palaeoleuciscus* sp.

PERCIFORMES, Sparidae: Sparidae indet.; Sciaenidae: *Atractoscion* sp.

AMPHIBIA

CAUDATA, Cryptobranchidae: *Andrias scheuchzeri*; Proteidae: Proteidae indet.; Salamandridae: *Chelotriton paradoxus*, cf. *Salamandra* sp., Salamandridae indet. (several species)

ANURA, Discoglossidae: *Latonia seyfriedi*; Pelobatidae: *Pelobates* sp. vel *Eopelobates* sp.

REPTILIA

CHELONIA, Chelydridae: *Chelydropsis* cf. *murchisoni;* Trionychidae: *Trionyx* sp.; Emydidae: *Ocadia* cf. *sophiae*, *Clemmydopsis* sp.; Testudinidae: *Testudo* sp. vel *Geochelone* sp.

CROCODYLIA, Alligatoridae: *Diplocynodon* sp.

SQUAMATA, Chamaeleontidae: Chamaeleontidae indet.; Lacertidae: *Lacerta* sp.; Anguidae: *Ophisaurus* sp.; Serpentes indet. (several species)

AVES

Aves indet. (several species)

MAMMALIA

MARSUPIALIA, Didelphidae: *Amphiperatherium frequens*

LIPOTYPHLA, Erinaceidae: *Lanthanotherium* aff. *sansaniense*, '*Mioechinus' sansaniensis*; Metacodontidae: *Plesiosorex germanicus*; Talpidae: *Mygalea* cf. *antiqua*, Desmaninae indet., *Proscapanus sansaniensis*, Talpini indet., Talpidae indet.; Soricidae: *Dinosorex* aff. *zapfei*, *Heterosorex* sp., *'Allosorex' gracilidens*, Soricidae indet. (several species); Dimylidae: *Plesiodimylus chantrei*, *Chainodus* aff. *intercedens*

CHIROPTERA, Rhinolophidae: *Rhinolophus* cf. *delphinensis*; Vespertilionidae: *Eptesicus* cf. *campanensis*

PRIMATES, Pliopithecidae: *Pliopithecus antiquus*, Pliopithecidae indet.

CARNIVORA, Hyaenidae: *?Protictitherium* sp.; Mustelida: *Amphictis* sp., *Potamotherium miocenicum*, *Trocharion albanense*, Mustelidae indet. (four species); Amphicyonidae: *Pseudocyon steinheimensis*, Amphicyonidae indet.; Ursidae: *Ursavus elmensis*

RODENTIA, Sciuridae: *Heteroxerus* sp., *Palaeosciurus sutteri*, *Spermophilinus* aff. *bredai*, *?Ratufa* sp.; Petauristidae: *Hylopetes* sp., *Miopetaurista lappi*, *Blackia miocaenica*; Gliridae: *Eomuscardinus sansaniensis*, *Eomuscardinus* sp., *Myoglis meini*, *Glirudinus undosus*, *Glirudinus* sp., *Microdyromys* cf. *legidensis*, *Paraglirulus werenfelsi*, *P.* cf. *agelakisi*, *Miodyromys aegercii*, *Bransatoglis* cf. *astaracensis*; Eomyidae: *Eomyops* cf. *catalaunicus*, *Keramidomys carpathicus*, Eomyidae indet.; Cricetidae: *Megacricetodon collongensis*, *Fahlbuschia koenigswaldi*, *Democricetodon mutilus*, *Anomalomys minor*, *Neocometes* cf. *similis*, *Eumyarion* cf. *weinfurteri*, *Eu.* cf. *bifidus*, *Karydomys zapfei*; Castoridae: *Steneofiber depereti*, *Anchitheriomys suevicus*

LAGOMORPHA, Ochotonidae indet.

ARTIODACTYLA, Suidae: *Hyotherium soemmeringi*; Palaeochoeridae: *Taucanamo sansaniense*; Tragulidae: *Dorcatherium guntianum*, *D. naui*; Cervoidea: *Orygotherium escheri*; Cervidae: *Dicrocerus elegans*, *Lagomeryx ruetimeyeri* vel *L. parvulus*; Bovoidea: *Amphimoschus pontileviensis*

CETACEA, Acrodelphidae: cf. *Acrodelphis* sp.; Cetacea indet.

PERISSODACTYLA, Equidae: *Anchitherium aurelianense*; Rhinocerotidae: *Brachypotherium brachypus*, cf. *Prosantorhinus* sp.

PROBOSCIDEA, Elephantoidea indet.

List 3: The composite Late Pliocene fauna from the Reuver Clay of Frechen and Hambach 11

OSTEICHTHYES

SALMONIFORMES, Esocidae: *Esox* cf. *lucius*

CYPRINIFORMES, Cyprinidae: *Tinca* cf. *tinca*, *Scardinius* cf. *erythrophthalmus*, *Rutilus* cf. *rutilus*

SILURIFORMES, Siluridae: *Silurus* sp.

PERCIFORMES, Percidae: *Lucioperca* cf. *lucioperca*, *Perca* cf. *fluviatilis*

AMPHIBIA

CAUDATA, Cryptobranchidae: *Andrias* sp.; Proteidae: *Mioproteus* sp.; Salamandridae indet.

ANURA, Palaeobatrachidae indet.; Discoglossidae: *Latonia* sp.; Pelobatidae: *?Pelobates* sp.; Ranidae indet.

REPTILIA

CHELONIA, Chelydridae: *Chelydropsis* sp.; Emydidae: *Emys* sp.

SQUAMATA, Lacertidae: *Lacerta* sp.; Anguidae: *Pseudopus pannonicus*; Colubridae: *Natrix* sp.

AVES

Aves indet.

MAMMALIA

LIPOTYPHLA, Talpidae: *Galemys* cf. *kormosi*, *Galemys* sp., *Desmana* cf. *thermalis*, *D.* cf. *nehringi*, *Talpa* (cf.) *minor*, *T. europaea*, Talpinae indet.; Soricidae: *Deinsdorfia hibbardi*, *Deinsdorfia* sp.,

Blarinoides mariae, Beremendia fissidens, Sorex cf. *minutus*
CARNIVORA, Mustelidae indet.
RODENTIA, Petauristidae: *Pliopetaurista pliocaenica*, *Blackia* aff. *miocaenica*, *Blackia* sp., *Hylopetes hungaricus*; Sciuridae: *Sciurus* sp.; Castoridae: *Castor fiber*, *Trogontherium minus*; Gliridae: *Glis minor*, *Muscardinus* aff. *helleri*, *Glirulus* (cf.) *pusillus*; Cricetidae: *Ungaromys altenburgensis*, *Mimomys hassiacus*, *M*. cf. *polonicus*; Anomalomyidae: *Prospalax* sp.; Muridae: *Sylvaemus* cf. *dominans*, *S*. cf. *atavus*
LAGOMORPHA, Leporidae indet.
ARTIODACTYLA, Cervidae: '*Cervus*' cf. *pyrenaicus*, Cervidae indet.
PERISSODACTYLA, Rhinocerotidae indet.

References

Böhme, W. & von Koenigswald, W. 1996. Schwanzlurche und Reptilien aus Rott. *In:* von Koenigswald, W. (ed.): Fossillagerstätte Rott bei Hennef im Siebengebirge. Das Leben an einem subtropischen See vor 25 Millionen Jahren. Rheinlandia (Siegburg): 75-81.

Bronn, H.G., 1828. Über die fossilen Reste der Papierkohle vom Geistinger Busch im Siebengebirge. Zeitschrift für Mineralogie, Neue Fassung, Taschenbuch für Mineralogie 22: 374-384.

Heumann, G., in prep. Stratigraphie und Paläoökologie des Jungpliozän und Altpleistozän im Tagebau Hambach (Niederrheinische Bucht).- GeoArchaeoRhein.

Hierholzer, E. & Mörs, Th., in prep. Cypriniden-Schlundzähne (Teleostei) aus dem Tertiär von Hambach (Niederrheinische Bucht, Deutschland). Palaeontographica A.

Klein, N. & Mörs, Th., in prep. Die Schildkröten (Reptilia: Testudines) aus dem Mittel-Miozän von Hambach (Niederrheinische Bucht, NW-Deutschland). Palaeontographica A.

von Koenigswald, W. (ed.), 1996. Fossillagerstätte Rott bei Hennef im Siebengebirge. Das Leben an einem subtropischen See vor 25 Millionen Jahren. Rheinlandia (Siegburg): 109 pp.

von Koenigswald, W., Martin, Th., Mörs**,** Th**.** & Pfretzschner, H.U., 1992. Die oberoligozäne Wirbeltierfauna von Rott bei Hennef am Siebengebirge. Synonymien und Literatur 1828-1991. Decheniana 145: 312-340.

von Koenigswald, W. & Mörs, Th., 1996. Die Säugetierfunde von Rott. *In:* von Koenigswald, W. (ed.): Fossillagerstätte Rott bei Hennef im Siebengebirge. Das Leben an einem subtropischen See vor 25 Millionen Jahren. Rheinlandia (Siegburg): 83-97.

von Koenigswald, W. & Mörs**,** Th**.**, 2001. The enamel microstructure of *Anchitheriomys* (Rodentia, Mammalia) in comparison with that of other beavers and of porcupines. Paläontologische Zeitschrift 74: 601-612.

van Kolfschoten, Th., van der Meulen, A. & Boenigk, W., 1998. The Late Pliocene rodents (Mammalia) from Frechen (Lower Rhine Basin, Germany). Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO 60: 161-172.

Martin, Th., 1996. Die Rotter Fischfauna. *In:* von Koenigswald, W. (ed.): Fossillagerstätte Rott bei Hennef im Siebengebirge. Das Leben an einem subtropischen See vor 25 Millionen Jahren. Rheinlandia (Siegburg): 61-67.

Mörs**,** Th**.**, 1995. Die Sedimentationsgeschichte der Fossillagerstätte Rott und ihre Alterseinstufung anhand neuer Säugetierfunde (Oberoligozän, Rheinland). Courier Forschungsinstitut Senckenberg 187: 1-129.

Mörs**,** Th**.**, 1996. Die Säugetiere der oberoligozänen Fossillagerstätte Rott bei Bonn (Rheinland). Decheniana 149: 205-232.

Mörs, Th., 1997. Zur Erforschungsgeschichte der Fossillagerstätte Rott bei Bonn. Zeitschrift für geologische Wissenschaften 25: 481-488.

Mörs**,** Th**.**, 1998. Über das Vorkommen von *Trionyx* s.l. (Testudines: Trionychidae) im Oberoligozän von Rott (Rheinland). Bonner zoologische Beiträge 48: 31-34.

Mörs**,** Th**.**, von Koenigswald, W. & von der Hocht, F., 1998. Rodents (Mammalia) from the Late Pliocene Reuver Clay of Hambach (Lower Rhine Embayment, Germany). Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO 60: 135-160.

Mörs**,** Th**.**, von der Hocht, F. & Wutzler, B., 2000. Die erste Wirbeltierfauna aus der miozänen Braunkohle der Niederrheinischen Bucht (Ville-Schichten, Tagebau Hambach). Paläontologische Zeitschrift 74: 145-170.

Reumer, J.W.F., 1995. Insectivora (Mammalia: Soricidae, Talpidae) from the Late Pliocene of Frechen, Germany. Deinsea 2: 9-15.

Rössner, G.E. & Mörs**,** Th**.**, 2001. A new record of the enigmatic Eurasian Miocene ruminant artiodactyl *Orygotherium*. Journal of Vertebrate Paleontology 21: 591-595.

Schäfer, A., Utescher, T. & von der Hocht, F., 1997. Klastische Sedimentsysteme im Tertiär der Niederrheinischen Bucht.- Terra Nostra 1997: 68-113.

Schwarz, J. & Mörs, Th., 2000. Charophyten aus dem oberpliozänen Reuverton des Braunkohlen-Tagebaus Hambach (Niederrheinische Bucht, Deutschland). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 215: 297-319.

Strauch, F., 1990. Schildkrötenfunde aus den Inden-Schichten (Oberes Miozän) des rheinischen Braunkohlenreviers. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1990: 308-320.

Strauch, F., 1994. Ein pliozäner Cerviden-Rest aus dem Tagebau Frechen, Rheinland. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1994: 129-142.

Wuttke M., 1996. Die Frösche von Rott und Orsberg. *In:* von Koenigswald, W. (ed.): Fossillagerstätte Rott bei Hennef im Siebengebirge. Das Leben an einem subtropischen See vor 25 Millionen Jahren. Rheinlandia (Siegburg): 69-74.

Ziegler, R. & Mörs**,** Th**.**, 2000. Marsupialia, Lipotyphla und Chiroptera (Mammalia) aus dem Miozän des Braunkohlentagebaus Hambach (Niederrheinische Bucht, NW-Deutschland). Palaeontographica A 257: 1-26.