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First creodont carnivore from the Rupelian Clays (Oligocene) of the Clay Pit Unterfeld at Rauenberg (Rhein-Neckar-Kreis, Baden-Württemberg): *Apterodon rauenbergensis* n.sp.

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Zusammenfassung

Mit dem Fund eines rechten Unterkieferfragmentes mit Teilen der Bezahnung wurde zum ersten Mal ein Landsäugetier in den marinen Ablagerungen der Fischschiefer-Subformation (Rupelium, Graue Schichtenfolge) der aufgelassenen Tongrube Unterfeld bei Rauenberg (Rhein-Neckar-Kreis, Baden-Württemberg) nachgewiesen: *Apterodon rauenbergensis* n. sp. (Creodonta, Hyaenodontidae). Das Fundstück unterscheidet sich morphologisch von den beiden bisher aus Europa bekannten Formen von *A. intermedius* LANGE-BADRÉ & BÖHME, 2005 and *A. gaudryi* FISCHER, 1880 darin, dass p4, m_1 und m_2 etwa gleich lang und breit sind. Das Vorkommen der Gattung *Apterodon* lässt eine säugetierstratigraphische Eingrenzung der Fundschichten in die MP-Zonen 22 bis 23 zu. Der Fund belegt die unmittelbare Ufernähe des Ablagerungsraumes im Bereich der Fundstelle, möglichweise im Bereich einer Flussmündung.

Abstract

The discovery of a right mandibular ramus including a fragmentary dentition for the first time proves evidence for the presence of terrestrial Mammalia in the marine deposits of the Fish Shale subformation (Rupelian, Graue Schichtenfolge) of the opencast Clay Pit Unterfeld at Rauenberg (Rhein-Neckar-Kreis, Baden Württemberg, Southern Germany): *Apterodon rauenbergensis* n.sp. (Creodonta, Hyaenodontidae). The specimen morphologically differs from the other two species of *Apterodon* known from Europe *A. intermedius* LANGE-BADRÉ & BÖHME, 2005 and *A. gaudryi* FISCHER, 1880 in having p4, m_1 and m_2 of nearly the same length and width. The occurrence of *Apterodon* allows for an identification of the layers as coming from MP 22 or MP 23. The specimen proves the immediate vicinity of the shoreline of the sediments at the finding place, probably close to a river mouth.

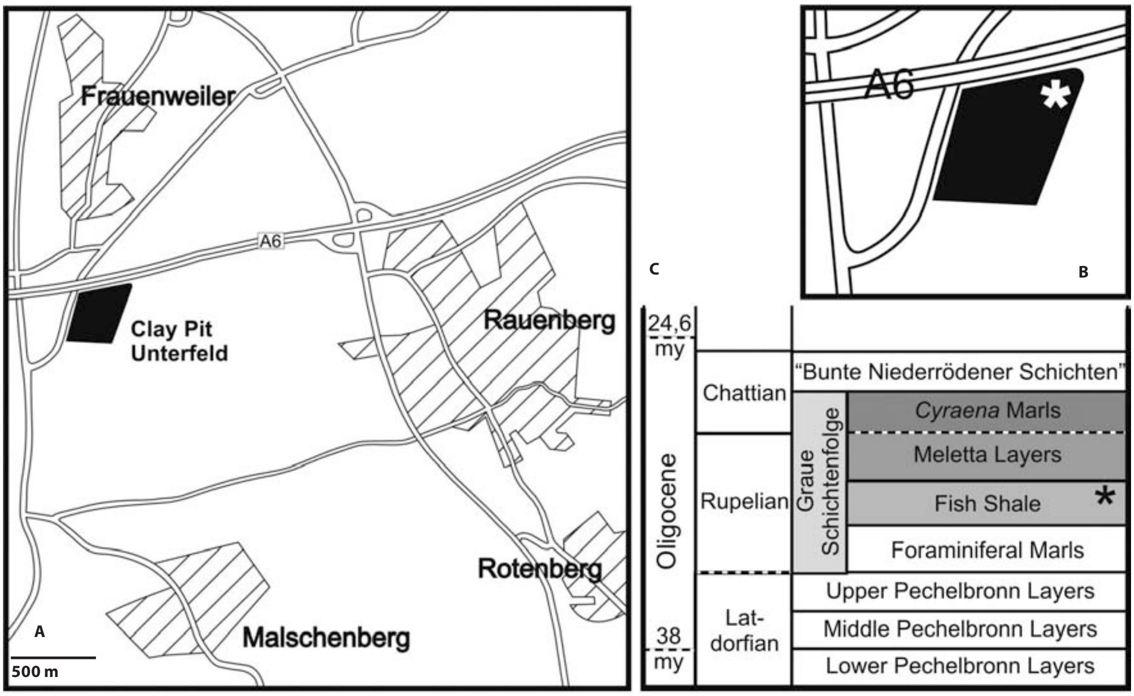


Figure 1: Geography and stratigraphy of the clay pit Unterfeld; A: Location of the clay pit, B: finding place within the clay pit, C: schematised stratigraphical column of the German Oligocene, the asterisk marks the finding position of SMNK PAL 6524.

Introduction

Since Roman times the Rupelian clays (Early Oligocene) in the northern Baden area (Baden-Württemberg) were exploited for the production of bricks and concrete. It was in the early seventies when the sediment became recognised for their fossil content. Until today more then 70 taxa of teleost fishes and chondrichthyans have been described with *Aeoliscus* and *Sardinites* being the most abundant genera (Micklich 1998, Micklich & Parin 1996, Micklich & Hildebrandt 2005). In some layers, the sediment is full of plant debris, cuticula preservation and foraminifera. Seaweed, gastropods, bivalves, crustations and fossil logs are comparably rare (Grimm et al. 2002), as are sea turtles (Alexander & Frey, this volume), which are only known from a handful of specimens. Plants are not the only remnants from the life of the coastal back lands. A few species of birds have been described, whereby typical coastal or seabirds are rarer than typical inland birds (Mayr et al. 2002, Mayr 2004b). The fossil record of the North Baden Rupelian yielded trogons as well as Europe's oldest songbirds and woodpeckers (Mayr 2005). The bird fossil with the highest impact factor form the clay pit Unterfeld near Rauenberg is a fossil humming bird, *Eurotrochilus inexpectatus*, which proved an early origin of the group in the Old World (Mayr 2004a, 2007). The insect assemblage is dominated by Coleoptera and Hemiptera. Other taxa, like Hymenoptera, Amphiesmenoptera (Lepidoptera + Trichoptera), Diptera and Mantodea are only known from single specimens (Monninger & Frey, this volume). Remnants of mammals are generally rare as well. From what is guarded in public collections there are a few fragments and one single sub-complete skeleton of Sirenia (cf. *Halitherium*) and two Microchiroptera, which both are under description. Today, the last open clay pit with palaeontological excavation activites is the Clay Pit Unterfeld, territory of Rauenberg (Fig. 1A).

During the emergency excavation in the year 2007 the fragment of a right mandibular ramus was discovered in the debris along a dirt path in the north eastern corner of the clay pit Unterfeld (Fig. 1 A) leading to the excavation area by the private collector Klaus-Dieter Weiß (Fischbach, Hesse State). He pre-prepared the specimen and handed it over to SMNK. After a final cleaning, the specimen was incorporated into the palaeontology collection of the SMNK under the number SMNK PAL 6524. It represents the first creodont record from the area and thus the first evidence for a terrestrial tetrapod in the Northern Badish Rupelium.

It should be mentioned here that more that 80 % of all finds registered in public collections come from private collectors. Without them the fossil treasures of the Northern Badish Rupelian clay pits could never have been secured to such an amount for the scientific community. As representatives for all the those enthusiasts that worked in the clay pits over years we like to dedicate this article to Klaus-Dieter Weiß as well as to Annette and Harald Oechsler (Paläo-Geo e.V.) for their unselfish contributions to science.

Material and methods

The specimen SMNK PAL 6524 was mechanically prepared and photographed with an Olympus E 620 (wide angle zoom 14–42 mm) in macro mode. The image was composed with CorelDraw 12 and X3. The schematic drawings were created with Corel Trace.

Geology and palaeoenvironment

The mandibular fragment was discovered in the debris of the strongly weathered north-eastern shoulder of the clay pit Unterfeld. From the finding position, which was recorded by the finder, the specimen very likely derives from a layer not beyond layer 11 according to the geological section of Grimm et al. (2002, Fig. 1 B). In any case the specimen comes from the Fish Shale sub-formation. In contrast to the western area of the clay pit, the previous overburden of the Rupelian including the entire *Meletta* sub-formation and the top ten meters of the Fish Shales was eroded away during the pre-glacial era (Doebl 1976, Trunko & Munk 1998). The geological section of Grimm et al. (2002) shows the exclusive presence of the bottom part of the Fish Shales below the Pleistocene covering layers. The Fish Shale sub-formation mostly consists of dark-grey, predominantly well layered, water rich marly mudstone. Within this mudstone, thin, light grey bands of silty carbonates occur in irregular distances.

The deposition depth of the sediments is still discussed controversially. Some authors suggest a water depth of 100 to 200 metres based on benthontic foraminifera (Trunko & Munk 1998, Grimm et al. 2002), while Weiler (1966) and Micklich & Hildebrandt (2005) suggest a shallow water regime based on the occurrence of many shallow water fish taxa and the abundancy of juveniles. The main fault of the escarpment runs approximately 250 metres east of the finding place. The clay pit itself likely belongs to a shallow water area distal to this fault with a width of about one kilometre. The coastline itself was formed by another fault running parallel to the east of the main fault. This coastline fault that already existed in the Palaeogene today passes the eastern margin of the city of Wiesloch and continues along the western margin of Rauenberg southbound into the Langenbrücken dip (Thürach 1904, Doebl 1976, Foellmer & Hoppe 1993).

According to Pross et al. (1998) the middle part of the northern European Oligocene was dominated by a humid, subtropical climate. This refers to a Cfa clima with annual average temperatures between 16° and 18° and an average rainfall of 1000 mm to 1300 mm (Köppen 1931). As is concluded by finds of logs, plant debris and leaf litter, the back land was covered with a dense forest of laurels, palms and rarely conifers, likely interrupted by rivers, an ideal habitat for small to middle-sized predators like *Apterodon*.

Systematik palaeontology

Class: Mammalia Linné, 1758
Infraclass: Eutheria Huxley, 1889
Superorder: Laurasiatheria Murphy, 2001
Order: ›Creodonta‹ Cope, 1875

Remark: Todate, the order ›Creodonta‹ is regarded as diphyletic by all modern authors and thus believed to be not valid (e.g. Lewis & Morlo 2010). As a consequence, the two included families, Hyaenodontidae and Oxyaenidae, have to be raised to order level, but this has not yet been formally published.

Family: Hyaenodontidae Leidy, 1869
Subfamilie: Apterodontinae Szalay, 1967
Genus: *Apterodon* Fischer, 1880
Species: *Apterodon rauenbergensis* n. sp.

Derivatio nominis: *rauenbergensis* (lat.) = of Rauenberg; in honour of the City of Rauenberg, the city government of which was much engaged to secure the scientific excavations in the Clay Pit Unterfeld for the future. The Clay Pit Unterfeld lies on the territory of the City of Rauenberg.

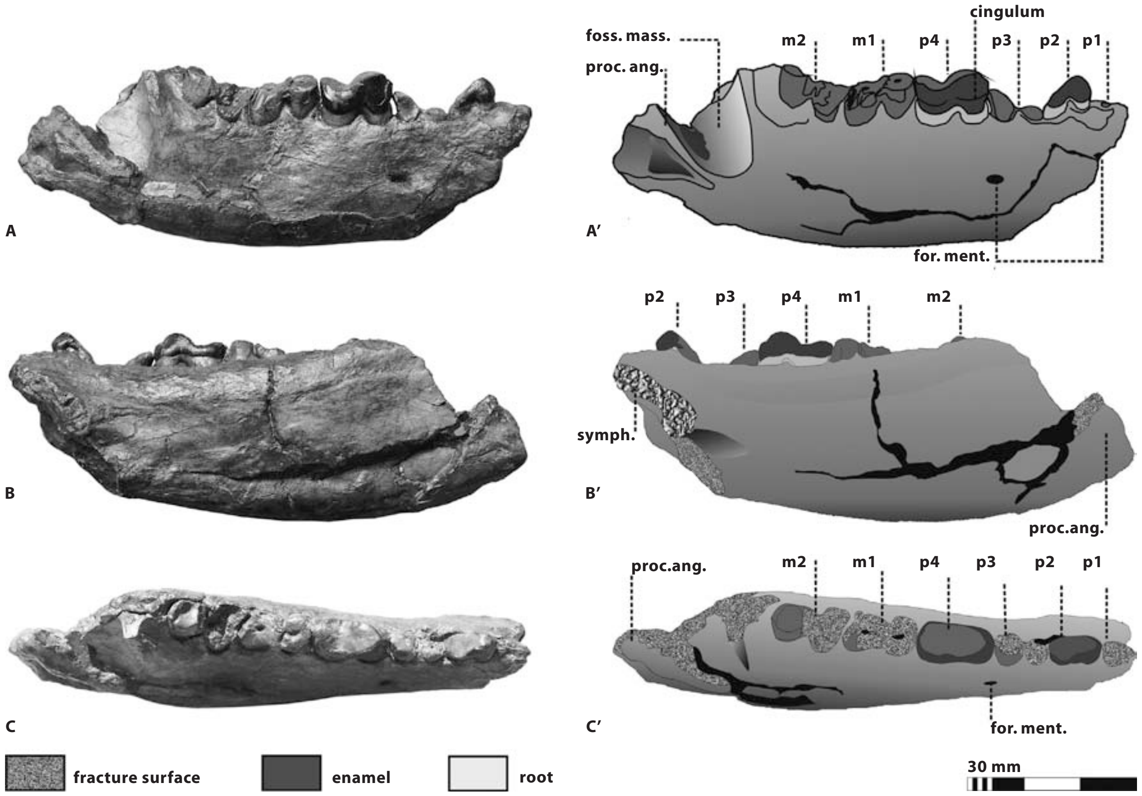
Holotypus and only specimen: smnk pal 6524, palaeontology collections of the Staatliches Museum für Naturkunde Karlsruhe.

Locus typicus: Fish Shale sub-formation, Rupelian, Early Oligocene, Clay Pit Unterfeld at Rauenberg, North Baden, South Germany. The official locality name as published by Grimm et al. 2002 and numerous other authors is »Frauenweiler«.

Diagnosis: The specimen is identified as *Apterodon* (Fischer 1830) because of its short mandibula, which was about four times as long as its maximum height (Fig. 2 A, A', B, B'). Further diagnostic features according to Andreae (1887), Matthew (1909), Dashzeveg (1964), Lange-Badré & Böhme (2005) are: caudal end of mandibular symphysis level with the caudal margin of p_3 (Fig. 2 B, B'); p_3 with cingulid; p_4 molariform (Fig. 2 A, A', C, C'); protoconid almost twice as massive as paraconid as reconstructed from p_3 and m_1 (Fig. 2 A, A', C, C'), however, the height of the crowns is not preserved, talonid one third of molar length (visible in p_3 and m_1; Fig. 2 A, A', C, C').

smnk pal 6524 differs from all other *Apterodon* species, including the European taxa *A. intermedius* (Lange-Badré & Böhme, 2005)and *A. gaudry* (Fischer, 1880) in p_4, m_1 and m_2 having about the same length and width, even if the value may differ a few tenths of millimetres (Fig. 2 C, C'). Closest in relative length of m_1/m_2 is *A. altidens* (Schlosser, 1930), but in this species p_4 is clearly longer than m_1 (as in the other African species *A. macrognathus* (Andrews, 1905) and *A. saghensis*). In *A. intermedius* (Simons & Gingerich, 1976) the m_2 is clearly longer than m_1, and the same is true for *A. gaudryi* (see Tab. 1, Fig. 3). Due to these differences in relative tooth size we attribute the new specimen smnk pal 6524 to a new species: *A. rauenbergensis.* As p_4 is larger relative to m_2 in *A. gaudryi* in comparison to *A. intermedius* the specimen appears to be closer to the former species (Tab. 1, Fig. 3).

Figure 2. ***Apterodon rauenbergensis* n.sp. SMNK PAL 6524:**
A, A′: lateral view,
B, B′: Medial view,
C, C′: occlusal view.
foss. mass. = fossa masseterica,
for. ment. = foramen mentale,
proc. ang. = processus angularis,
symph. = symphysis, m = molar,
p = premolar.



Description

The fragment of a right mandibular ramus has a total length of 88 mm (Fig. 2). The processus coronoideus including the caput mandibulae and the processus angularis are broken off along an oblique line, running from the cranial base of the processus coronoideus at an angle of about 45° caudoventrally through the fossa masseterica to the ventral margin of the dentary and terminates at the base of the processus angularis (Fig. 2 A, A'). The ventral half of fossa masseterica is preserved with a triangular piece of bone missing at the caudodorsal fracture line (Fig. 2 A, A'). The lateral wall of the base of the processus angularis is missing. Rostrally, the madibular ramus has broken at the caudal terminus of the mandibular symphysis with a fracture line running caudoventrally at an angle of about 50° to the dental margin of the mandibular ramus (Fig. 2). Of the mandibular symphysis the caudal-most part is visible, terminating ventral to the caudal margin of p3 (Fig. 2 B, B'). The highest dorsoventral expansion of the specimen with 31 mm lies level with the fracture caudal to m_2. On the labial face the caudal foramen mentale opens ventral to the caudal root of p3 at about the mid height of the mandibular ramus (Fig. 2 A, A'). The caudal margin of a second foramen mentale is visible 20 mm further rostrally and is cut half by the rostral fracture. It lies ventral to the middle of p_2 and level with the dorsal third of the mandibular ramus.

Incisivi and canini are missing due to the loss of the symphyseal part of the mandibular ramus. All other teeth are preserved with their crowns strongly abraded (Fig. 2 A, A', C, C'). Of p_2 only an indistinctive fragment of the root is preserved. p_3 has two roots. The crown is the best preserved of the dental series of the specimen and bears a protoconid which is about twice the size of the paraconid in occlusal view, whereas the paraconid is mostly eroded. The tooth is 8 mm long, 5 mm high and at the crown base has a width of 4.5 mm. P_3 lacks the entire crown but both roots are in situ showing circular cross-sections. The tooth had a length of about 10 mm as is estimated from the space between p_2 and p_4. P_4 also preserves two roots with circular cross-sections. The crown is extremely eroded but apparently has been tricuspid. The protoconid likely was the biggest of the three cusps. Labially, the trace of a cingulid is visible. The tooth has a length of 12.3 mm and a maximum width at the mid crown height is 6.6 mm. The double rooted m_1 lacks the entire crown. Both roots are circular in cross-section. The tooth fragment is 12.0 mm long at the break along the roots. M_2 is preserved similar to m_1 with most of the crown missing. The length measured along the breakage face of the roots, which are circular in cross section, is about 12.4 mm. At the base of the crown both teeth were certainly a little longer. M_3 is completely missing and not even a trace of the rostral border of its alveolus is visible. This suggests that the specimen comes from a juvenile individual with all permanent premolars and molars erupted except m_3. However, the eruption sequence of apterodontines remains unknown, even though it is aparent that m_3 and the canine are the latest erupting teeth in hyaendontines (Mellett 1977).

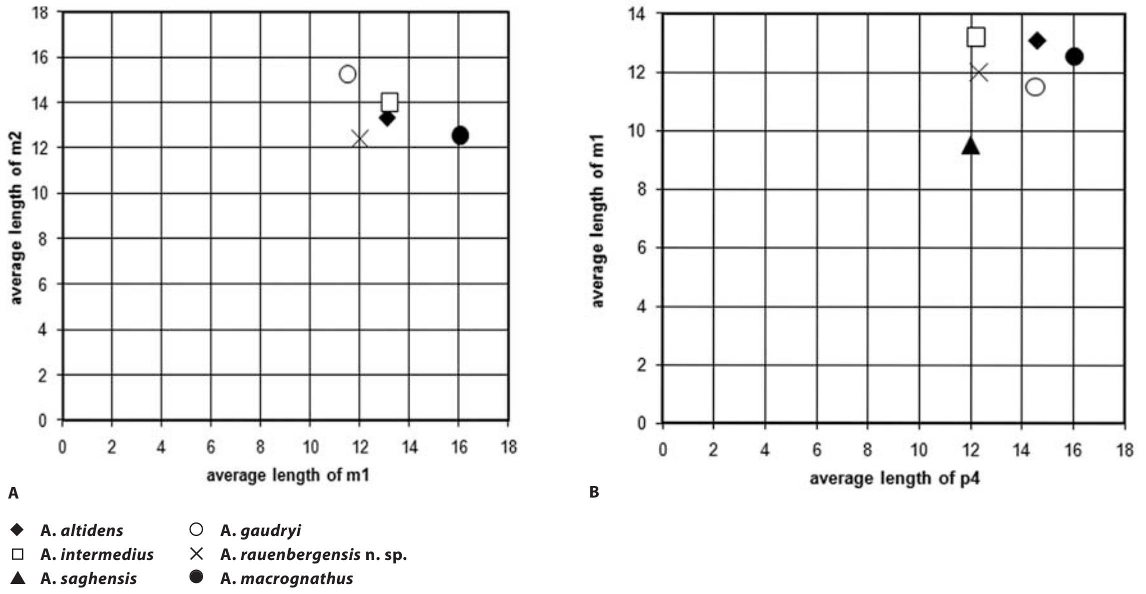


Figure 3: Plots of selected tooth ratios in *Apterodon*.
A) ratio m1/m2,
B) ratio p4/m1.

Taphonomy and diagenesis

The specimen was embedded within a concretion-like mudstone nodule. Only the ventral ridge of the mandibular ramus was visible, when it was collected. Therefore it represents a primary fragment. The abrasion of the teeth and the margins of the fractures suggest, that the specimen has been transported to the place of deposition, either by a near-by river, where the animal died a few kilometres upstream and travelled downstream already isolated. Another possibility would be that the animal died at the shore and was dismembered by the action of the surge. In both cases scavengers may have initially dismembered the carcass. Because the massive bone would not have drifted at the water surface, it must have been transported to the final embedding place by currents. A final short distance transport from the shore by a seabird (e.g. *Diomedoides brodkorbi* Mayr, Peters & Rietschel 2002) would also be an option to explain the arrival of the specimen at the embedding place.

During late diagenesis some compaction breaks were either caused by sediment compaction or possibly tectonical compression or both. This compaction caused a deep shear fracture that runs parallel to the ventral margin of the mandibular ramus. The specimen finally was impregnated with iron sulfide and very likely is with pyrite.

Discussion

According to Lange-Badré & Böhme (2005) the genus *Apterodon* consists of five valid species, two of which come from Europe: *A. gaudryi* Fischer, 1880 (syn. *A. flonheimensis* Andreae, 1887; Lange-Badré & Böhme 2005), *A. intermedius* Lange-Badré & Böhme, 2005, and three are reported from Egypt: *A. macrognathus* Andrews, 1905, *A. altidens* Schlosser, 1910, *A. saghensis* Simons & Gingerich, 1976.
Because of the fragmentary fossil record the taxonomy of the genus remained controversial for a long time (for a review see Langer-Badré & Böhme 2005). Until today the fragmentary preservation states of *Apterodon* remnants in Europe make a diagnosis to species level problematic, because many characters cannot be directly compared with each other on species level. Until further finds, the diagnostic differences are extremely critical with regard to statistical evaluations but still are justified on the level of distinct morphotypes (see e.g. Lange-Badré & Böhme 2005). The specimen presented here differs from the hitherto described European and African species in the ratios of functionally crucial teeth: p_4 and the two molars (see Tab. 1, Fig. 3). Give the functional impetus of the masticatory apparatus of apterodontines we feel it justified to erect a new morphotype that formally adds a third *Apterodon* species to the European inventory of this genus. However, further discoveries may yield more data that may show the plasticity of the masticatory apparatus of *Apterodon*. Such data are only available for *A. macrognathus* which shows a variation of p_4/m_1-length ratio between 1.27 and 1.40 (n = 4 specimens; Fig. 3 B) and of m_1/m_2-length ratio between 0.72 and 0.79 (n = 4 specimens, Fig. 3 A). The European branch of the genus *Apterodon* is restricted to MP 22 and 23, which means that for the first time the Rupelian Clays in the Rauenberg-Wiesloch area are referable to a comparably narrow mammalian biozone.

Figure 4: ***Apterodon rauenbergensis n.sp.*****, temptative reconstruction as a short-faced, semi-aquatic predator.**

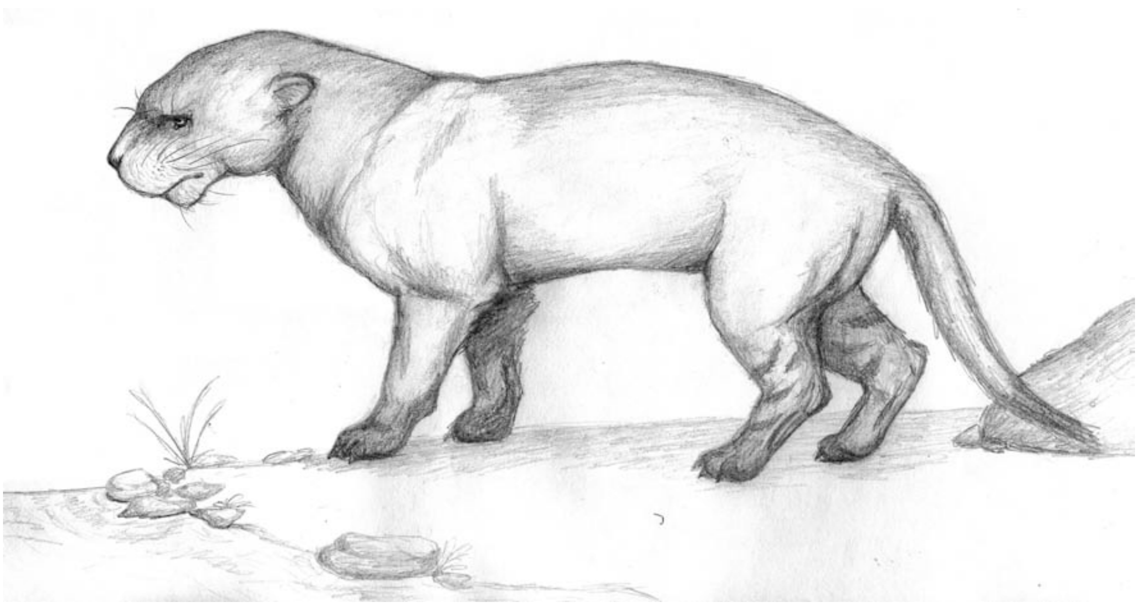


Table 1: Comparative mesurements of five species of Apterodon according to LANGE-BADRÉ & BÖHME (2005).

Specimen	Length	(in mm)			ratios			
	p3	p4	m1	m2	p3/p4	p4/m1	p3/m1	m1/m2
A. macrognathus								
C. 8982	14,7	16,1	12,7	16,1	0,91	1,27	1,16	0,79
C.8815			12,9	17				0,76
M8437b	11,3	13,2			0,86			
1905 XIII 9		17,9	13,1	18,1	0,00	1,37		0,72
12643		15,3	10,7	14,4	0,00	1,43		0,74
11950		15,1		15,7	0,00			0,00
UCMP 62218	15,8	18,7	13,4		0,84	1,40	1,18	
average	**13,9**	**16,1**	**12,6**	**16,3**	**0,87**	**1,28**	**1,11**	**0,77**
A. altidens								
12644	13,1			13,3				0,00
YPM 18160		15,1	12,7		0,00	1,19	0,00	
new 43465	14,3	14,1	13,5	13,4	1,01	1,04	1,06	1,01
average	**13,7**	**14,6**	**13,1**	**13,35**	**0,94**	**1,11**	**1,05**	**0,98**
A. gaudryi								
Quercy		13	11	14		1,18		0,79
Flonsheim		16	12	16,5		1,33		0,73
average		**14,5**	**11,5**	**15,25**		**1,26**		**0,75**
A. intermedius								
2008/43		**12,2**	**13,2**	**14**		**0,92**		**0,94**
A. saghensis								
CGM 40006	**10,7**	**12**	**9,5**		**0,89**	**1,26**	**1,13**	
A. rauenbergensis								
SMNK-PAL 6524		**12,3**	**12**	**12,4**		**1,02**		**0,97**

So far, the European fossils of *Apterodon* are coming from three sites: the fissure fillings of the Phosphorites du Quercy (Dept. Lot, France; a juvenile individual of *A. gaudryi*, Fischer, 1880), and the coastal-marine sands of Flonheim (Mainz Basin; *A. gaudryi*, syn.: *A. flonheimensis*, Andrae, 1987) and Espenhain (Weisselster Basin; *A. intermedius*, Böhme, 2001). The new find from Unterfeld again originate from coastal-marine sediments, which opens the question about the possibility of a semi-aquatic (otter-like, see also the temptative reconstruction in Fig. 4) lifestyle of *Apterodon.* However, no characters typical for a semi-aquatic lifestyle are known from postcranial remains of *Apterodon* (MM, unpubl. data). The peculiar occlusal pattern with the reduction of the paraconid and the loss of the metaconid on the lower molars and the absence of carnassial cutting blade suggest a feeding mechanism unlike those of other creodonts and carnivorans (Lange-Badre & Böhme 2005), but close to that of mesonychids. Mesonychia, however, have been interpreted as bone/meat feeder (Morlo, Gunnell & Nagel 2010). The habitat of the short-faced *Apterodon* may thus may have been the immediate vicinity of large rivers or even coastal-marine settings.

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Herr Klaus-Dieter Weiß (Fischbach/Ts.), mit dem bereits seit vielen Jahren eine äußerst fruchtbare Zusammenarbeit besteht, machte den Fund im September 2007 und übereignete ihn danach dem SMNK. Das Fundstück wurde von Herrn René Kastner (SMNK) präpariert. Bei der Schichtzuweisung des Fundstückes im Profil gab Herr Harald Oechsler (Waghäusel) wertvolle Hinweise. Allen Genannten sei bestens gedankt.

Literature

Andreae, A. 1887. Ein neues Raubtier aus dem mitteloligocänen Meeresand des Mainzer Beckens. - Bericht über die Senckenbergische Naturforschende Gesellschaft, 125–133; Frankfurt a. M.

Doebl F. 1976. Tertiär im mittleren Rheingraben (Baden-Pfalz). Exkursionsführer. - **46**. Jahrestagung der Paläontologischen Gesellschaft, Exkursion D, 25 pp, Karlsruhe. D1–D25; Karlsruhe.

Dashzeweg, D. On two Oligocene Hyaenodontidae from Erghilyin-Dzo (Mongolian People's Republic). - Acta Palaeontologica Polonica 9(2): 263–267; Warshaw.

Fischer, P. 1880. Note sur un nouveau genre de mammifère fossile (*Apterodon gaudryi*) des Phosphorites du Quercy. - Bulletin de la Société géologique de France **8**, 280–290; Paris.

Foellmer, A. & Hoppe, A. 1993. Die Randverwerfung des Oberrheingrabens bei Malsch im Kraichgau. - Jahresberichte und Mitteilungen des Oberheinischen Geologischen Vereins, Neue Folge. **75**, 287–290; Stuttgart.

Grimm, K.I., Grimm, M.C., Köthe, A. & Schindler, T. 2002. Der »Rupelton« (Rupelium, Oligozän) der Tongrube Bott-Eder bei Rauenberg (Oberrheingraben, Deutschland). - Courier Forschungsinstitut Senckenberg, **237**, 229–253; Frankfurt a. M.

Köppen, W. (1931): Grundriß der Klimakunde. : 388 pp; De Gruyter, Berlin.

Lange-Badré, B. & Böhme, M. 2005. *Apterodon intermedius*, sp. nov., a new European Creodont Mammal from MP 22 of Espenhain (Germany). - Annales de Paléontologie **91**, 311–328; Paris.

Leopold, M., Munk, W. & Trunkó, L. (1990): Erster Nachweis von Landsäugetierresten im marinen Mittel-Oligozän des Mittleren Oberrheingrabens bei Eschbach, Pfalz, BRD. - Carolinea, **46**: 13–20; Karlsruhe.

Lewis, M. E. & Morlo, M. 2010. Chapter 26 – ›Creodonta‹. In: Werdelin L. & Sanders W. J. (eds.): Cenozoic Mammals of Africa: 543–560; University of California Press, Berkeley.

Matthew, W.D. 1909. The Carnivora and Insectivora of the Bridger Basin, middel Eocene. - Memoirs of the American Museum of Natural History **4**: 291–567; New York.

Mayr, G. 1999. A new *Trogon* from the middle Oligocene of Céreste, France. - The Auk **116** (2), 427-434; Jacksonville, Florida, USA.

Mayr, G. 2000. A new mousebird (Coliiformes: Coliidae) from the Oligocene of Germany. - Journal of Ornithology **141**, 85–92; Berlin, Heidelberg.

Mayr, G., Peters, S.D. & Rietschel, S. (2002): Petrel-like birds with a pekular foot morphology from the Oligocene of Germany and Belgium (Aves: Procellariformes). - Journal of Vertebrate Paleontology **22**(3): 667–676; Deerfield, Ilinois, USA.

Mayr, G. (2004a): Old World fossil record of modern-type hummingbirds; Science **304**: 861–864; Washington D.C., USA.

Mayr, G. 2004a. A partial skeleton of a new fossil loon (Aves, Gaviiformes) from the early Oligocene of Germany with preserved stomach content. - Journal of Ornithology **145**: 182–186; Berlin, Heidelberg.

Mayr, G. & Manegold A. (2004): The oldest European fossil songbird from the early Oligocene of Germany. - Naturwissenschaften 91: 173–177; Berlin, Heidelberg.

Mayr, G. 2005. Fossil hummingbirds in the Old World. - Biologist, **52**: 12–16; London.

Mayr, G. 2007. New specimens of the early Oligocene Old World hummingbird *Eurotrochilus inexpectatus*. - Journal of Ornithology **148**, 105–111; Berlin, Heidelberg.

Mellett, J. S. (1977). Paleobiology of North American *Hyaenodon* (Mammalia, Creodonta). - Contributions to Vertebrate Evolution 1:1–134; New York.

Micklich, N. & Parin, N.N. 1996. The fishfauna of Frauenweiler (Lower Oligocene, Rupelian; Germany): Preliminary results of a revision. - Publicationes Especiales Instituto Espanol de Oceanographia **21**, 129–148; Madrid.

Micklich, N. (1998): New information on the fish fauna of the Frauenweiler fossil site. - Italian Journal of Zoology, **65**: 169–184; Modena.

Micklich, N. & Hildebrandt, L. (2005): The Frauenweiler clay pit (Grube Unterfeld). - Kaupia, **14**: 113–118; Darmstadt.

Morlo M., Gunnell, G. & Nagel, D. (2010). Chapter 10 – Ecomorphological analysis of carnivore guilds in the Eocene through Miocene of Laurasia. In: Goswami A. & Friscia, A. (eds.): New Contributions to the Natural History of Carnivora: 269–310; Cambridge University Press.

Pross, J., Bruch A. A., Kvacek, Z. (1998): Paläoklima-Rekonstruktionen für den Mittleren Rupelton (Unter-Oligozän) des Mainzer Beckens auf der Basis mikro- und makrobotanischer Befunde. - Mainzer geowissenschaftliche Mitteilungen, **27**: 79–92; Mainz.

Thürach, H. 1904. Erläuterungen zu Blatt Wiesloch (Nr. 41). - Geologische Spezialkarte des Großherzogtums Baden, **41**: 48 S.; Heidelberg.

Tobien, H. (1987): The Position of the »Grande Coupure« in the Paleogene of the Upper Rhine Graben and the Mainz Basin.- Münchner geowiss. Abh., A, **10**: 197–202; München.

Trunkó, L. & Munk, W. 1998. Geologische Beobachtungen in drei tertiären Aufschlußkomplexen im Randbereich des Mittleren Rheingrabens.- Carolinea, **56**: 9–28; Karlsruhe.

Weiler, W. (1966): Die Bedeutung der Fischfunde im Rupelton der Tongrube Frauenweiler bei Wiesloch südlich von Heidelberg. - Zeitschrift der Rheinischen naturforschenden Gesellschaft Mainz, **4**: 1–37; Mainz.