

The ‘unknown beast’ is back: Reconstructing *Agnotherium* for exhibition

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Kurzfassung

Das „unbekannte Tier“ ist zurück: Die Rekonstruktion von *Agnotherium*

Das Naturhistorische Museum Mainz eröffnete 2019 eine neue Dauerausstellung zu den fossilen Funden aus der spätmiozänen Fundstelle von Eppelsheim. Der Bärenhund (Amphicyonidae) *Agnotherium* ist Teil dieser Ausstellung, obwohl aus Eppelsheim von der Art nur ein einzelner Zahn und der Unterkiefer eines Jungtiers bekannt sind. Die Rekonstruktion von *Agnotherium* basiert daher zusätzlich auf anderen bekannten Stücken der Art und der Unterfamilie Thaumastocyoninae, insbesondere auf einem bislang unbeschriebenen Skelettrest aus dem spanischen Batallones-3. Damit steht in Mainz die einzige Rekonstruktion dieses Raubtieres weltweit.

Neben der auf Fossilien basierenden Rekonstruktion der Anatomie beruht das gewählte Lebensbild vornehmlich auf heute lebenden Raubtieren. Wir entschieden uns für eine friedlich-neugierige Pose, die das Tier zudem jugendlich wirken lässt. Dieser Eindruck wird unterstützt durch übergroße Augen. Für die Rekonstruktion nicht erhaltener Körperteile (Fell, Nasenknorpel, Ohrmuscheln, Klauen) standen heutige Verwandte von *Agnotherium* Pate, vornehmlich Schwarzbär (*Ursus americanus*) und Kurzohrhund (*Atelocynus microtis*) als solitär lebende, hundeartige Waldformen. Da *Agnotherium* als Lauerjäger aber in seiner Lebensweise mit heutigen Großkatzen vergleichbar ist, wurden zusätzlich Leopard (*Panthera pardus*), Tiger (*Panthera tigris*) und jugendliche Löwen (*Panthera leo*) herangezogen. Obwohl die wissenschaftliche Rekonstruktion eine dunkelbraune bis schwarze Fellfarbe als wahrscheinlich ergab, da diese bei der Mehrheit waldbewohnender, solitärer Lauerjäger vorkommt, wurde ein helleres, meliertes (synthetisches) Wolfsfell gewählt, um die Rekonstruktion vom schwarzen Untergrund abzuheben, der ein wesentliches Designelement der neuen Ausstellung ist.

Als Ergebnis findet der Besucher das sehr realistische Lebensbild eines jugendlichen *Agnotherium* vor, das in direktem Kontakt mit seiner Umgebung zu stehen scheint. Das Originalfossil des Unterkiefers ist direkt benachbart ausgestellt und ermöglicht dem Besucher so, zwischen Fossil und Rekonstruktion einen unmittelbaren Bezug herzustellen.

Abstract

In 2019 the Mainz Natural History Museum opened a new exhibition of mammals unearthed at the Late Miocene locality of Eppelsheim. The amphicyonid carnivoran *Agnotherium* is part of this new exhibition, even though only a single tooth and a partial juvenile mandible are known from the locality. The reconstruction of *Agnotherium* is thus additionally based on related fossils, especially on a skeleton from the Spanish locality Batallones-3.

The process of reconstruction is two-fold: first reconstruction of the anatomy, based on bone measurements and bone connections, and second the reconstruction of a life-like appearance. We decided to reconstruct *Agnotherium* in a peaceful and curious manner to emphasize its juvenile appearance. Reconstructions of unpreserved characters, e. g., fur color, shape of nose or of the outer ear, are based on recent relatives of the caniform *Agnotherium*, mainly bears and dogs. As the environment of the Late Miocene Eppelsheim was mainly wooded, we concentrate on species which today live in woods, especially the black bear (*Ursus americanus*) and short-eared dog (*Atelocynus microtis*). However, the lifestyle of *Agnotherium* was clearly different from that of recent bears and dogs and was much closer to that of large cats, such as lions or tigers, or leopards, which is why we also used young lions (*Panthera leo*), tigers (*Panthera tigris*), and panthers (*Panthera pardus*) as recent comparatives.

Key words

Museum Exhibition, reconstruction, Amphicyonidae, *Agnotherium*, Eppelsheim, Late Miocene

1. Introduction

Amphicyonidae or “bear dogs” are an extinct caniform family regarded to be most closely related to ursids (bears) due to similarities of the middle ear region in the most primitive amphicyonid taxa (HUNT 1998a). However, the origin of Amphicyonidae lies in the middle to late Eocene (TOMIYA & TSENG 2016), and thus before the first Oligocene records of the putative oldest ursid *Parictis* (HUNT 1998b). The amphicyonid *Agnotherium antiquum* was first described by KAUP (1833) based on a single tooth unearthed in Eppelsheim (early Upper Miocene, Germany). *Agnotherium* belongs to the amphicyonid subfamily Thaumastocyoninae that is characterized by hypercarnivorous predators. More than 180 years later, a second specimen, a juvenile mandible, was found at the same locality. Based on this specimen, MORLO et al. (2020) could clarify the enigmatic status of the species and regarded it as the most carnivorous amphicyonid to have ever lived. Based on an analysis of the tooth eruption pattern, MORLO et al. (2020) interpreted the mandible to belong to an about two-year-old juvenile to subadult.

The reconstruction of *Agnotherium* is a challenge, as only about 65 fossil specimens of thaumastocyonines exist, most of them isolated teeth (MORLO et al. 2020). Though more closely related to recent bears and dogs than to cats, the lifestyle of *Agnotherium* (and of the other Thaumastocyoninae) was similar to that of recent tigers or leopards. It was an ambush rather than a pursuit hunter but slightly larger and heavier built than even the largest cats today. *Agnotherium* is only known from the early Upper Miocene (MN 9, 11.4–9.7 Ma) of Europe. In addition to Eppelsheim, close relatives occur at the Swiss locality Charmoille, from where also a partial ulna is known, and the Spanish locality Pedregueras 2A, which bore isolated teeth (MORLO et al. 2020).

Eppelsheim represents one of the historically oldest localities in Europe from which finds of Miocene mammals have been published. Locals have worked in the fluvial deposits of the Proto-Rhine system in Rheinhessen since

at least the 18th century (WAGNER 1947). The sediments are known as “Dinotheriensande”, because *Deinotherium*, an ancient proboscidean, was first described from Eppelsheim (KAUP 1829). It should be noted that the fossils from Eppelsheim represent a subtropical forest fauna (TOBIEN 1955, SOMMER et al. 2009), as this massively influences the reconstructed appearance of the juvenile *Agnotherium*.

As part of the reconstruction of the Mainz Natural History Museum, the Eppelsheim exhibition was also rebuilt. The new diorama contains a collection of mammals: a cow of *Deinotherium*, a chalicothere, a pliopithecoid primate, and also *Agnotherium* as the most carnivorous animal of the fauna besides the sabre-tooth cat *Machairodus*. We opted to include a sculpture of the much rarer *Agnotherium*, because the scientific knowledge of this taxon is strongly based on the specimens from Eppelsheim and because a model of *Machairodus* is already part of an exhibition of fossils from the Spanish locality Batallones (<https://youtu.be/VmO6Gi7F96o>). Now, Mainz is the only place world-wide, where a sculpture of *Agnotherium* is available to visitors. In this contribution we document the process of building the sculpture of *Agnotherium* and discuss the scientific background of the reconstruction.

2. Material

The reconstruction took place in the Quagga laboratory of the co-author in Barcelona. The following material was used: Plasteline (NSP Chavant, USA), Silicone (Dow-Corning Ltd, USA), Glass eyes (Karl Lange Glasaugen, Germany), Fake Fur (The Trow Company, United Kingdom).

As in fossils normally no soft parts are preserved, we used several modern animals to reconstruct these soft parts of the body, especially nose and outer ears, fur, and eyes. As Eppelsheim animals lived in a forested environment, we mainly chose extant forest-dwelling taxa: the black bear (*Ursus americanus*), the short-eared dog (*Atelocynus microtis*), the tiger (*Panthera tigris*), and the black va-

riety of leopards (*Panthera pardus*). Finally, we used pictures of two-year-old lions (*Panthera leo*) to match the overall appearance of an old juvenile or young semi-adult carnivore.

3. Reconstruction of the anatomy

The *Agnotherium* hypodigm is comprised of an isolated lower molar (the holotype, pictured in KAUP 1833: pl. 1, fig. 4, KAUP 1861: pl. 2, fig. 3, KUSS 1962: fig. 1, KURZ & GRUBER 2004: fig. 10, MORALES et al. 2017: fig. 4), and the juvenile mandible (Fig. 1) from Eppelsheim. Referred material includes an adult mandible and a partial ulna from the Swiss locality Charmoille, and isolated dental remains from the Spanish locality Pedregueras 2A. Doubtful assignments come from the Tunisian locality Bled Douarah with a maxillar fragment, a partial radius and a metatarsal V (KURTÉN 1978). As this amount of material is not sufficient to build a sculpture, we additionally use skeletal measurements from a partial thaumastocyonine skeleton from the locality Batallones-3 that was briefly described by MORALES et al. (2017). Skeletal measurements of this specimen were provided by Jorge MORALES (Museo Nacional de Ciencias Naturales, Madrid), notably mandi-

ble length and height, skull length and width, and height, and lengths and widths of the humerus, radius, ulna, and tibia.

To scale these measurements, we used the distance from the posterior margin of the canine alveolus to the posterior end of the lower second molar, resulting in an approximately 20 % smaller individual from Eppelsheim.

This roughly fits growth rates in brown bears, where two-year-old juveniles are about 20 % smaller than adults (BARTAREAU et al. 2011).

The reconstruction of the skull (Fig. 2) has a morphology closer to the amphicyonid *Magericyon* than to *Amphicyon*. This is not surprising as *Magericyon* is also regarded to be hypercarnivorous (i. e., a diet comprised nearly exclusively of meat) (PEIGNÉ et al. 2008) while the diet of *Amphicyon* generally is thought to be carnivorous (diet comprised between 50-70 % of meat), as the slicing components of the dentition (especially the paraconid-protocoid blade of m1) are relatively larger in *Agnotherium* and *Magericyon* than in *Amphicyon* (MORLO et al. 2020).

After adjusting all measurements, we compared the results to skeletal measurements of *Amphicyon major* (see AGUSTI & ANTÓN 2002: fig. 4.21) and found some remarkable differences, especially concerning the humerus, which is 36 % longer in *Agnotherium*, the



Fig. 1: Left juvenile mandible of *Agnotherium antiquum* KAUP, 1833 from the early Late Miocene of Eppelsheim.

Abb. 1: Linke Mandibel eines juvenilen *Agnotherium antiquum* KAUP, 1833 aus dem frühen Spätmiozän von Eppelsheim.

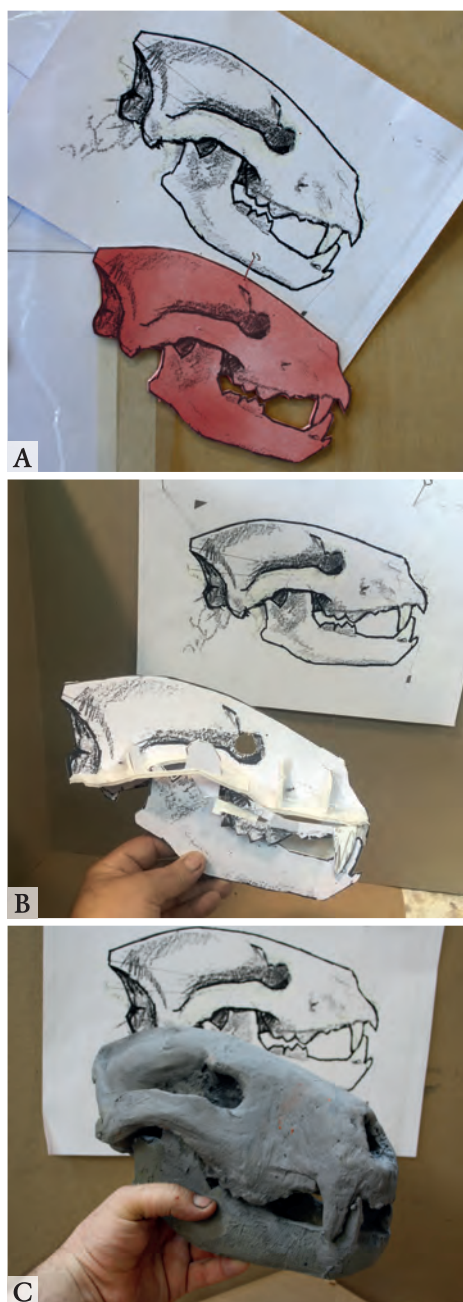


Fig. 2: Reconstruction of the skull of *Agnotherium*. A: Sketches. B: 3D-paper model. C: 3D-plasteline model.
 Abb. 2: Rekonstruktion des Schädels von *Agnotherium*. A: Zeichnerische Rekonstruktion. B: räumliches Papiermodell. C: Plastelinmodell.

radius (5 % longer), and skull (3 % longer). Adult *Agnotherium* obviously had proportionally longer forelimbs than *Amphicyon*. It can also be concluded that *Agnotherium* was heavier and stronger built than *Amphicyon*, even if the first lower molars are of similar size. Combined with the strong ulna from Charmoill, our data corroborate MORLO et al. (2020) who envisioned *Agnotherium* as ‘an at least lion-sized, solitary, strictly carnivorous animal that ambushed its prey with great force’. The relatively longer forelimb also confirms that *Agnotherium* was probably faster than *Amphicyon* as has already been inferred from the morphology of the metatarsal (KURTÉN 1978, MORLO et al. 2020).

4. Reconstruction of the appearance

The morphological results were used to create a small plasteline model in 1/10 scale (Fig. 3) to discuss possible positions. Should the animal walk, stand or sit, look ahead, have the mouth open or closed?

Tigers, the largest extant hunters, sleep or rest about 16 hours per day (BIOLATTI et al. 2016). An encounter with *Agnotherium* would thus probably find it sleeping or resting. We therefore decided to give the animal a peaceful and curious appearance with the mouth closed, rather than show it in a rare attacking mode. Instead, the animal has the head lifted and the eyes open, creating the appearance that it just awakened by the arrival of a visitor and observing the disturbance.

After having decided the posture, the basic sculpture was built (Fig. 4), followed by forming of the details (Fig. 5) and transport and finish in Mainz. These steps include forming the soft parts as nose and outer ear, applying the fur, and inserting the eyes. As these parts are not fossilized, we surveyed the literature on recent carnivorans to make a likely reconstruction for *Agnotherium*.

Fur: For the fur we used synthetic wolf skins. One of the most critical issues during 3D-sculpturing of mammals is the reconstruction of fur color, density, and length, as these factors very much influence the reception of the

reconstruction. Three factors mainly influence these fur parameters in recent carnivorans: environment, phylogeny, and ontogeny.

Concerning environmental effects, CARO (2005) has demonstrated that mammals (including carnivorans) living in forests are mainly dark colored. Moreover, large hunting carnivorans have an ‘aggressive camouflage’, resulting in cryptic visibility (ORTOLANI 1999). In contrast, color patterns used for communication must be visible, resulting in white spots on the fur of forest dwelling carnivorans (ORTOLANI 1999). Moreover, leopards with black fur (“black panthers”) nearly exclusively occur in the forests of Southeast Asia, but not in the savannas of Africa (KITCHENER et al. 2010). Concerning phylogeny, the majority of bears are uniformly black to dark brown (ORTOLANI 1999) and the forest living canids *Atelocynus* (BERTA 1986) and *Speothos* (BEISIEGEL & ZUERCHER 2005) are dark-colored, as well. Juveniles of *Speothos* have an even darker fur color than adults (BEISIEGEL & ZUERCHER 2005), verifying an ontogenetic effect on fur color. In contrast to feliforms, in which fur spots are the primitive condition (KITCHENER et al. 2010), only few recent bears and canids have multi-colored fur (ORTOLANI 1999: fig. 2). Moreover, as *Agnotherium* prob-

ably was a solitary ambush hunter (MORLO et al. 2020), it needed ‘aggressive camouflage’ *sensu* ORTOLANI (1999), but probably needed less (white) color patterns for intraspecific communication. We therefore reconstructed the fur color of *Agnotherium* to probably be more or less uniform and lacking spots for intraspecific communication.

Concerning fur length and density, bears are not a good comparison for *Agnotherium*, as most of them live in much cooler habitats than the Late Miocene of Eppelsheim and therefore need longer and denser fur. However, fur is also generally longer and denser in juveniles, e. g., in lions (KITCHENER et al. 2010), perhaps due to heat regulation: juveniles have greater surface area to body volume ratios. Due to this, fur density also increases with decreasing size in nearly all felids (KITCHENER et al. 2010, an exception is the mane of the lion), and presumably also in caniforms. As *Agnotherium* is of tiger size, we use the data of HEPTNER & SLUDSKII (1992) for fur length and density of the largest felid, *Panthera tigris*. Because of these studies, an unstructured, uniform dark brown to black fur color with the approximate length of that of a young tiger would be the most probable fur covering for our juvenile to subadult *Agnotherium*. This



Fig. 3: Plasteline model of the *Agnotherium* sculpture in planned lifestyle appearance.

Abb. 3: Plastelinmodell der *Agnotherium*-Rekonstruktion in geplanter Haltung mit erhobenem Kopf und geschlossenem Maul in 1/10 der natürlichen Größe. Die aufgesteckten 2D-Rekonstruktionen von Schädel und Gliedmaßen erlauben die korrekte Modellierung der Proportionen.



Fig. 4: Basic sculpture of *Agnotherium* at natural size with paper sketches of the skeletal elements placed to ensure correct proportions.

Abb. 4: Basisskulptur von *Agnotherium* in natürlicher Größe. Wie beim Modell in 1/10 natürlicher Größe, sichern die 2D-Elemente die korrekten Proportionen ab.

would enable the visitor to imagine *Agnotherium* as a forest-living, solitary hunter with a lifestyle comparable to a black panther. However, we needed to adjust this result to the exhibition concept, which planned to place the sculpture on a black wooden block as a major design element of the new Eppelsheim exhibition. Making the fur of *Agnotherium* as dark as the literature survey suggested would create low contrasts between the sculpture and its surface. We thus instead decided to choose an erratically spotted, synthetic wolf fur with colors from black to lighter brown (Fig. 5) which was colored slightly darker. The relatively long fur reminds the visitor that the presented specimen is not fully-grown, but still juvenile. To achieve this, the fur was fluffed before the exhibition opened.

A feature connected to fur is the presence and length of whiskers. As all carnivorans have whiskers, *Agnotherium* very probably had them as well. However, in relation to pantherine cats, bears and dogs have relatively short whiskers. As *Agnotherium* as a forest-dwelling ambush hunter probably had a pantherine-like life-style, we inserted long whiskers similar to pantherines instead short ones like in bears or dogs.

A special question concerning fur is the possible presence of a tail fluff at the tip as possessed by lions. However, as tail puffs do not occur in recent caniforms we avoided that for *Agnotherium*. Moreover, fur length of tail hair is considered to be short, resembling most canids, as amphicyonids have much longer

tails than recent bears, and among other caniforms bushy tails are only known from musteloids and wolves.

Claws: No information has been given on the morphology of amphicyonid claws, only the bony final phalanges are known. However, at least some amphicyonids built dens (HUNT et al. 1983) arguing for strong claws. We thus used bear claws (Fig. 7).

Senses: Another critical issue is the reconstruction of the soft tissues, especially the nose and outer ear. As much as with fur coloration, facial morphology highly influences the appearance perception by museum visitors. Obviously, the morphology of nose and outer ears relies on olfactorical and hearing capabilities of the animal, but is also influenced by phylogeny and environment. The same is true for eye coloration, while eyeball size can be inferred from skull size and morphology.

Nose: RADINSKY (1980) stated that one of the latest North American amphicyonids, *Pliocyon*, apparently had an extremely large brain even compared to modern carnivorans. *Pliocyon* had large *bulbus olfactorii*, the region of the brain responsible for olfactorical signals. GREEN et al. (2012) demonstrated that turbinate size is large in vertebrate-consuming vertebrates and increases allometrically positively with increasing size, but does not correlate with climate. VAN VALKENBURGH et al. (2014) proved that olfaction is more important for caniforms than for feliforms. We thus inferred that olfaction might have been



Fig. 5: Applying the fur on the basic sculpture.

Abb. 5: Applikation des synthetischen Wolffells auf die Basisskulptur.

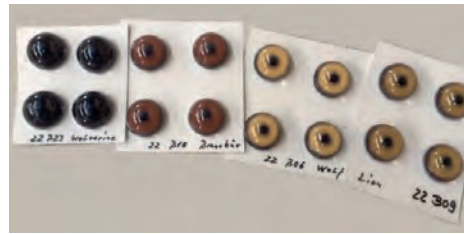


Fig. 6: Variety of glass eyes. We chose the far left one, 22 B23 Wolverine, with a diameter of 25 mm.

Abb. 6: Auswahl an Glasaugen. Wir entschieden uns für das Modell ganz links, 22 B23 Wolverine, mit einem Durchmesser von 25 mm, da die meisten Waldformen sehr dunkle Augen haben und relativ große Augen den jugendlichen Eindruck der Rekonstruktion verstärken.

the most important sense for *Agnotherium* and consequently modeled a long cartilaginous nose similar to that in bears or wolves (Fig. 7).

Outer Ear: Among carnivorans, the form of the outer ear is influenced by phylogeny and environment. Besides enabling sound location, the outer ear is also used for communication, especially in canids. Size and structure of the middle ear, morphology of the inner ear, and brain structure define hearing capability. While brain structure and inner ear morphology have not yet been studied for amphicyonids, their middle ear is well known. Among late Oligocene and Miocene species, it has a morphology that represents the plesiomorphic arctoid type and is similar to living ursids (HUNT 1998a). As ‘the frequency range of the greatest sensitivity[,] is determined by the mechanics of the middle ear’ (FLEISCHER 1978) it seems reasonable to compare the hearing capability of amphicyonids to that of ursids. In recent polar bears hearing sensitivity was found to be best between 11200 and 22500 Hz (NACHTIGALL et al. 2007). All bears have relatively small, rounded ears that separate them from the mostly triangular outer ears of other carnivorans (except the red panda, *Ailurus fulgens*). To show the difference of *Agnotherium* to bears or ailurids, we chose a triangular shape for the outer ear. The forest living, recent canids *Atelocynus* and *Speothos* have relatively small outer ears. As *Agnotherium* presumably was a solitary ambush hunter (MORLO et al. 2020), we reconstructed its outer ears (Fig. 7) with the same form and relative size as in the solitary *Atelocynus* (see BERTA 1986) rather than in *Speothos* which lives in small packs (BEISIEGEL & ZUERCHER 2005) and thus uses its outer ears much more for social communications.

Eyes: We know no comparative studies on eye coloration of Carnivora. However, one study demonstrated that intraspecific variability in eye coloration nearly exclusively exists in humans and domestic animals, but not in wild animals (NEGRO et al. 2017). As all bears and forest dwelling canids have dark brown eyes, we regarded this color as the most probable for *Agnotherium*. We chose

glass eyes modeled after the eyes of the wolferine (*Gulo gulo*) as these were the darkest available (Fig. 6). Based on skull size, an eye diameter of 22 mm would have been appropriate, but to enhance the juvenile appearance of the sculpture, we inserted glass eyes with a diameter of 25 mm.

5. Finalizing

Due to the detailed analyses and comparisons with recent carnivorans, the final sculpture (Fig. 7) appears very realistic. The canid-like head equipped with long whiskers, the long forelimbs with bear claws and the long tail, however, reinforce the impression of an animal the visitor has never seen among recent carnivorans. On the other hand, the lightly built body and the large eyes make it easily recognizable as a juvenile or subadult and due to its posture, it seems to directly look curiously at the visitor. As expected for a young individual, the aspect of *Agnotherium* as a very strong, ferocious hunter, is not accentuated, but still present, especially due



Fig. 7: Sculpture of *Agnotherium antiquum* KAUP, 1833 placed in the Eppelsheim diorama of the Mainz Natural History Museum. Notice the juvenile appearance, strong nose, long whiskers, short, triangular outer ears, and large claws.

Abb. 7: Rekonstruktion von *Agnotherium antiquum* KAUP, 1833 im Eppelsheim-Diorama des Naturhistorischen Museums Mainz. Deutlich sind jugendliches Erscheinungsbild, die kräftige Nase, die langen Schnurrhaare, die kurzen, dreieckigen Ohren, die langen Vorderbeine und die kräftigen Krallen zu erkennen.

to the strong claws. First experiences with visitors corroborate the realistic appearance as a juvenile to subadult dog-like creature: the sculpture had to be placed further back in the diorama to prevent it being touched by visitors, especially children. The juvenile mandible is on display in a showcase directly in front of the sculpture (Fig. 8). This enables the visitor to compare the original fossil with the reconstruction of this animal. *Agnotherium antiquum*, the “old, unknown beast” is back to life.

6. Acknowledgements

Jorge MORALES (Museo Nacional de Ciencias Naturales Madrid) provided measurements of an undescribed thaumastocyonine skeleton from Batallones 3 (MORALES et al. 2017). Cathrin PFAFF (University of Vienna) provided literature that enabled us to infer listening capabilities and outer ear morphology of *Agnotherium*. Renate RABENSTEIN, Doris NAGEL, and Tony FRISCIA improved the article by their constructive comments.



Fig. 8: Sculpture of *Agnotherium antiquum* KAUP, 1833 placed in the Eppelsheim diorama of the Mainz Natural History Museum with the original fossil placed in front of it and the legs of *Deinotherium* in the background.

Abb. 8: Rekonstruktion von *Agnotherium antiquum* KAUP, 1833 im Eppelsheim Diorama des Naturhistorischen Museums Mainz mit dem Originalfossil im Vordergrund und den Beinen von *Deinotherium* im Hintergrund.

7. Literature

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