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Article

Large mammals from the late Middle Miocene of Markt Rettenbach (Bavaria, Germany)

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With 5 figures and 1 table

Abstract: Herein the fossil assemblage of the Middle Miocene (12.06 Ma) locality of Markt Rettenbach (Southern Germany) is studied. The fossil-bearing sediments of the clay pit have been known for almost a century, but until now only little is known about its fauna. A small sample of fossils collected in the 1940s is housed in the collections of the Kempten-Museum in the Zumsteinhaus (Germany). Since then, the clay pit has been re-naturalised and is not available for any further excavations and collecting of fossils. Thereby, this material, along with a single mandible of a *Listriodon splendens* described in the past, are the only information about the Middle Miocene fauna of this locality. Herein, five large mammals were identified: a proboscidean, a hornless rhino, a large-sized suid, a small ruminant (possibly a tragulid), and a medium-sized pecoran (possibly a small bovid). Thus, this work represents the first detailed study of the known mammalian fauna of Markt Rettenbach overall. Its fauna is comparable to other Middle Miocene sites such as Gratkorn (Austria) and matches the late Middle Miocene age previously suggested for the locality.

Key words: Neogene, Vertebrata, Mammalia, Proboscidea, Perissodactyla, Artiodactyla, taxonomy, Central Europe.

1. Introduction

The North Alpine Foreland Basin (NAFB) in Central Europe comprises Upper Eocene to Miocene molasse sediments which have been studied extensively (e.g., Lemcke et al. 1953; Kuhlemann & Kempf 2002; Doppler et al. 2005; Hofmayer et al. 2019). The 'Obere Serie' is the uppermost lithostratigraphic unit of the southwestern Bavarian part of the Upper Freshwater Molasse (Doppler 1989; Doppler et al. 2005), representing the youngest preserved molasse sediments in that region. Magnetostratigraphy and regional correlation constrain the age of the 'Obere Serie' to the late Middle to earliest Late Miocene (Serravallian to early Tortonian), between 13.8 and 11.1 Ma (Kirscher et al. 2016). This is the time right after the Middle Miocene Climatic Optimum, a significant climatic event that affected the fauna of Europe (Böhme 2003). However, the record of vertebrate fossil localities in the 'Obere Serie' of the NAFB is rather scanty (Böhme & Ilg 2003); nonetheless, the closely situated site of Hammerschmiede exhibits a highly diverse community, including all major vertebrate groups, as well as hominids (Kirscher et al. 2016; Böhme et al. 2019; Hartung et al. 2020; Mayr et al. 2020a; Mayr et al. 2020b; Kargopoulos et al. 2021a, Kargopoulos et al. 2021b; Kargopoulos et al. 2021c).

In general, fossiliferous localities of the 'Obere Serie' containing mammals are recorded around and in Munich (Stromer von Reichenbach 1928; Fuss et al. 2015), along the river Inn in south-eastern Bavaria (Dehm 1955), and in Swabia of southwestern

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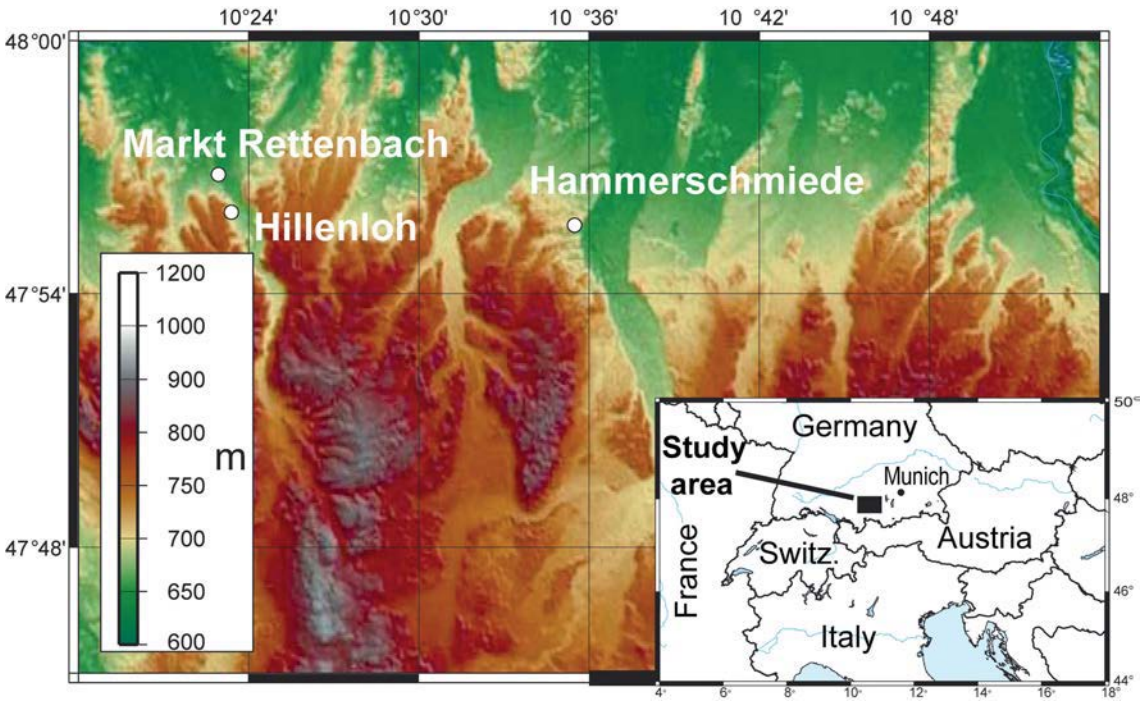

Fig. 1. Topographic map of southwestern Bavaria (Germany), indicating the position of the Middle and Late Miocene localities Markt Rettenbach, Hillenloh, and Hammerschmiede in the area. The map was made with GMT6 (Wessel et al. 2013).

Bavaria. The latter region contains the localities Hammerschmiede, Hillenloh and Mark Rettenbach (Fig. 1; Kirscher et al. 2016). This study deals with fossils from the Markt Rettenbach locality, situated 15.8 km west of the vertebrate-bearing Hammerschmiede clay pit (Fig. 1). They were collected in the 1940s from the former brickyard Lämmle, south of the chapel Maria Schnee of Markt Rettenbach, between 658 and 670 m a.s.l. (Fig. 2; Schäfer & Berlinger 1954). Since the clay pit is no longer accessible, the following description of its sediments is based on the one provided by Schäfer & Berlinger (1954: 19). The base of the succession is formed by consolidated bluish-grey to greenish-grey sandy clays. They are overlain by unconsolidated yellow to yellowish-grey marly sands. The sediment adhering to some fossil bones is a consolidated, bright greenish sandy marl, suggesting that the fossils derive from the lower part of the succession. Most bones are partially covered by a haematitic coating or crust, giving them a reddish spotted appearance.

The occurrence of Miocene fossil mammals in the clay pit of Markt Rettenbach (Fig. 2) was reported for the first time almost a century ago by Ernst Freiherr Stromer von Reichenbach based on material that he had received from Dr. Eberl (Stromer von Reichenbach 1930). Stromer von Reichenbach (1930) mentioned the presence of a distorted mandible and some isolated teeth that he assigned to *Dorcatherium crassum*, an impressive, almost complete mandible of *Listriodon splendens*, and a fragment of a humerus that he assigned to an indeterminate carnivoran. Both the *Dorcatherium* and the carnivoran specimens cannot be relocated in the collections of the Bavarian State Collections of Natural Sciences – Bavarian State Collection of Palaeontology and Geology, in Munich (SNSB – BSPG) (Gertrud Rössner, pers. comm.). Beside the vertebrate fossils, Stromer von Reichenbach (1930) also mentioned the existence of land snail shells that even preserved colour bands.

Shortly after, Dehm (1934) provided an extensive description of *Listriodon splendens* from Markt Rettenbach with detailed morphological and metrical comparisons to *Listriodon* material from other localities and even provided a phylogenetic tree for several species of this genus. Beside the mandible that was illustrated and described by Stromer von Reichenbach (1930), Dehm (1934) described several other *Listriodon splendens* remains from Markt Rettenbach.

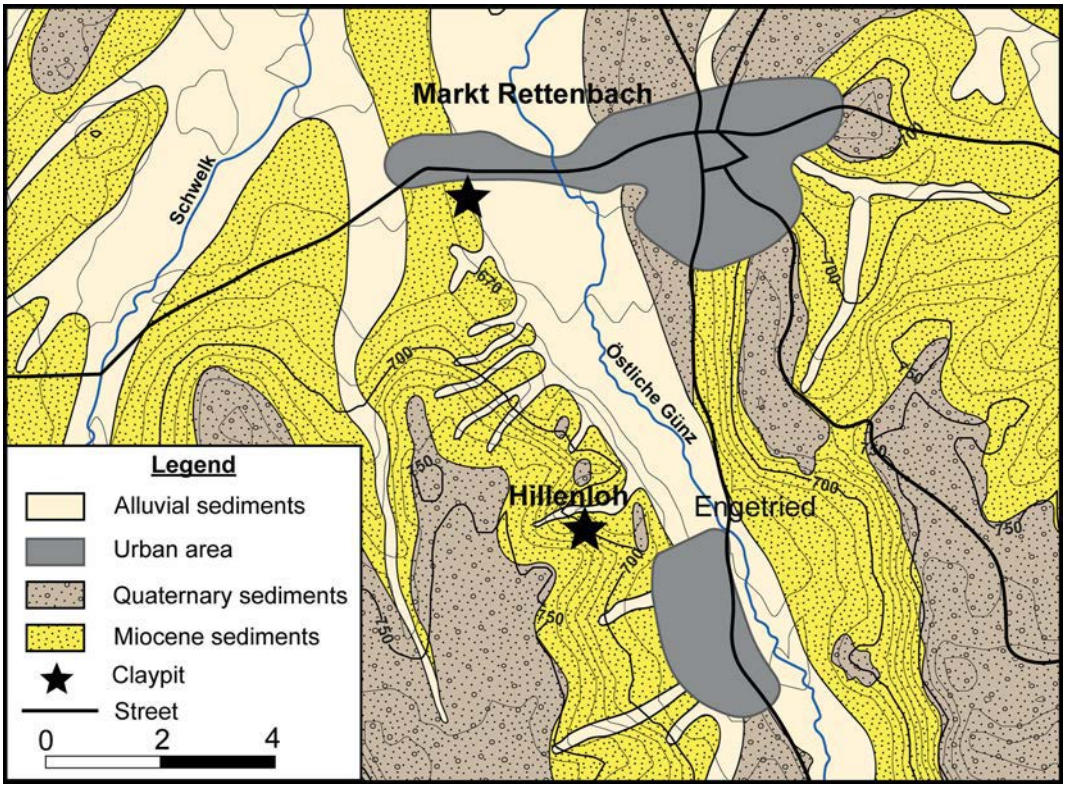

Fig. 2. Geological map of the study area (see Fig. 1) after Schäfer & Berlinger (1954: 22). The topography was generated with GMT6 (Wessel et al. 2013). The black stars indicate the fossil localities Markt Rettenbach and Hillenloh.

This material includes numerous isolated teeth and some postcranial elements, deposited in the SNSB – BSPG.

Recently, Kirscher et al. (2016) provided a taxon list of the mammalian fauna of Markt Rettenbach comprising five large mammal species as well as one micromammal. This list was based on literature data and preliminary observations from undescribed material. Most importantly, Kirscher et al. (2016) provided a dating for the fossil-bearing sediments of Markt Rettenbach. They correlated the sediments of the Markt Rettenbach clay pit to a 150 m long drill core, obtained in Irsee, which was magnetostratigraphically dated in detail, and established an age of 12.06 Ma for the locality (Kirscher et al. 2016), which is similar to the 12.2–12.0 Ma old vertebrate locality of Gratkorn in the Styria Basin of Austria (Gross et al. 2014).

Herein we report undescribed mammalian remains from the Markt Rettenbach clay pit and attribute them to five different large mammal taxa. Thus, adding to the knowledge about the fossil record of the 'Obere Serie' from the Upper Freshwater Molasse Formation in South Germany.

2. Material and methods

The original material is housed in the collections of the Kempten-Museum in the Zumsteinhaus in Bavaria (Germany). The material was collected by J. Rampf in the 1940s. Casts of the fossils have been deposited in the Geologisch-Paläontologisches Institut of the University of Tübingen (GPIT). Comparative fossils from the Middle Miocene localities of Gratkorn, Steinheim am Albuch, Sansan and the Late Miocene locality of Hammerschmiede were studied at the GPIT and the Staatliches Museum für Naturkunde Stuttgart, Germany (SMNS). The measurements of the specimens were taken with a digital caliper with an error of 0.01 mm and were then rounded to the closest 0.1 mm.

Fig. 3. Proboscidea indet. from the Middle Miocene locality of Markt Rettenbach. Caudal vertebra (M-OS 2146) in anterior (**A**), dorsal (**B**), and lateral (**C**) views. Scale bar equals 10 cm.

3. Systematic palaeontology

Class Mammalia Linnaeus, 1758
Order Proboscidea Illiger, 1811

Proboscidea indet.
Fig. 3

Material: Caudal vertebra (M-OS 2146).

Description and comparison: Specimen M-OS 2146 represents the body of a large caudal vertebra (Lph = 90.0 mm). The transversal processes are broken, with only the medialmost 1–2 cm being preserved, but they are anteroposteriorly very wide (55 mm) and strongly developed. The neural arch is broken off, but its opening is preserved with the neural archs bases and has a transversal width (30 mm) much narrower than the vertebral body, as is typical for caudal vertebrae. However, based on the presence of a well-defined neural canal, it can probably be placed in the anterior portion of the animals' tail. The articular facets are dorsoventrally compressed, another common feature in caudal vertebrae. In anterior view, a small, rounded, and shallow depression is visible in the middle of the articular facet of the vertebral body. On the posterior articular facet, a clearly deeper, elliptical depression is visible. The width of the anterior articular facet (BEcr = 67 mm) is somewhat larger than the posterior one (BEcd = 58 mm).

Based on its size alone, M-OS 2146 could not belong to any other animal that lived during this time in Europe, except a proboscidean. The dimensions of the Markt Rettenbach vertebra (Lph × BEcr × BEcd = 90 × 67 × 58 mm) are comparable to the anterior caudal vertebrae of *Gomphotherium* aff. *steinheimense* from the Late Miocene of Gweng near Mühldorf in Bavaria (Caudal vertebra 3: Lph × BEcr × BEcd = 62 × 63 × 58; Göhlich 1998: tab. 32), while the Markt Rettenbach vertebra is somewhat longer. However, the morphology of the caudal vertebrae is quite uniform amongst proboscideans and not much comparative material is available. Therefore, no further identification is possible, beside the attribution of the specimen to a proboscidean.

Order Perissodactyla Owen, 1848
Family Rhinocerotidae Gray, 1821
Subfamily Aceratheriinae Dollo, 1885
Genus *Hoploaceratherium*
Ginsburg & Heissig, 1989

cf. *Hoploaceratherium* sp.
Fig. 4

Material: partially preserved ramus of a left hemimandible, with the m3 (M-OS 2147-1), left m2? (M-OS 2147-2) and ectolophid of a left lower molar, potentially the m1 (M-OS 2147-3).

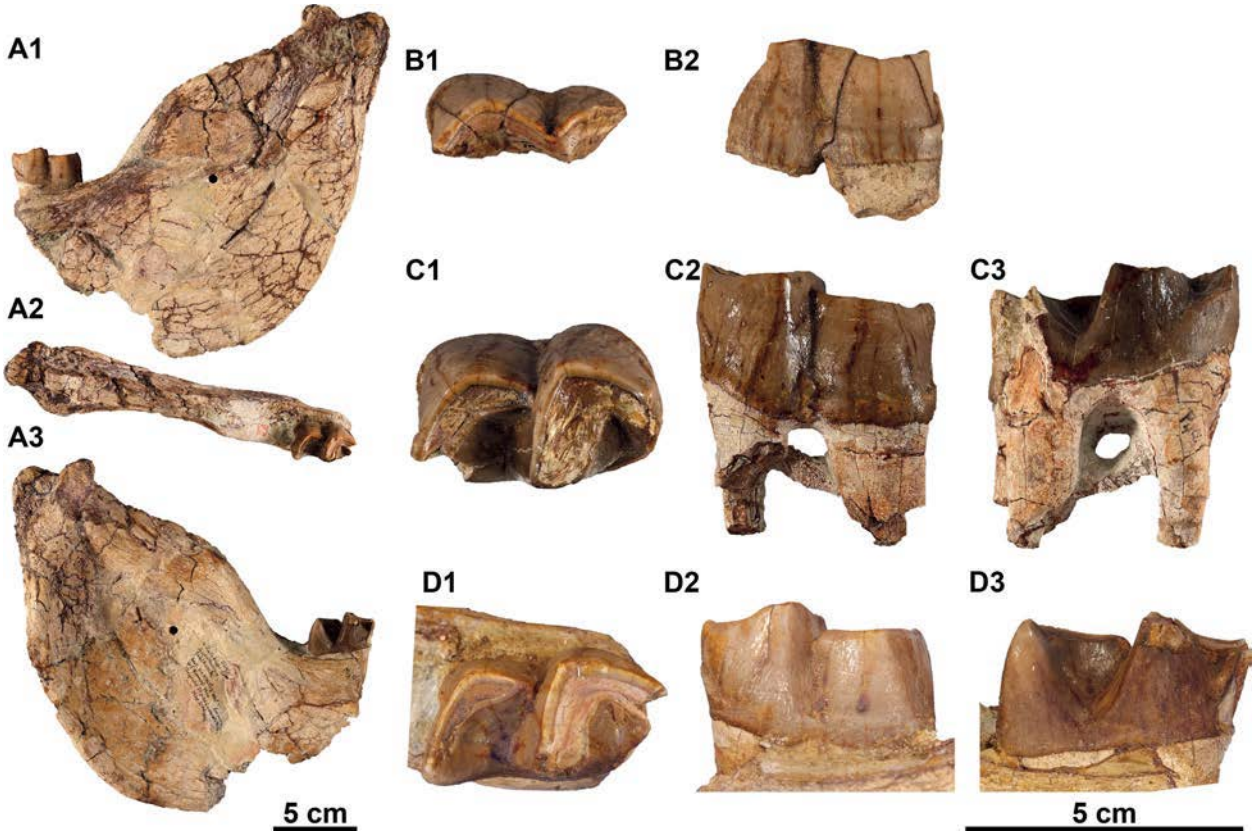

Fig. 4. cf. *Hoploaceratherium* sp. from the Middle Miocene locality of Markt Rettenbach. **A** – Posterior portion of a left mandible (M-OS 2147-1) in lateral (1), dorsal (2) and medial (3) views; **B** – left m1? (M-OS 2147-3) in occlusal (1) and buccal (2) views; **C** – left m2? (M-OS 2147-2) in occlusal (1), buccal (2) and lingual (3) views; and **D** – left m3 (M-OS 2147-1, same as in Fig. 4A, in occlusal (1), buccal (2) and lingual (3) views. Scale bars equal 5 cm.

Remarks: The material exhibits a similar state of preservation and the different wear stages of the three teeth indicate that they might represent the m1 (M-OS 2147-3), m2 (M-OS 2147-2), and m3 (M-OS 2147-1) of the same individual.

Description and comparison: Specimen M-OS 2147-1 represents the most posterior portion of the corpus and the ramus of the left hemimandible with the m3 *in situ*. The specimen is broken anterior to the m3 and the ventral portion of the corpus, below the m3, is also missing. The mandibular angle is relatively rounded, and the ramus is subvertical. The coronoid process is not preserved, and the articular condyle is almost entirely missing, with only a small remnant preserved. Posteriorly and below the articular condyle a strong post-articular tubercle is visible.

In total, three teeth have been recovered from Markt Rettenbach, M-OS 2147-3 represents a buccal fragment of a lower molar, probably the m1, M-OS 2147-2 is probably an m2, missing the posterior end of the entoconid, and M-OS 2147-1 is the m3, associated with the mandible fragment, missing the anterior tip of the paralophid. Specimen M-OS 2147-3 is heavily worn and a connection between the metalophid and the hypolophid is well established. A well-developed posterior cingulum exists and continues slightly on the buccal side, before merging into the ectolophid and leaving only a marginally protruding enamel bar on the postero-buccal part of the talonid. A small, smooth enamel tubercle exists at the base of the ectolophid groove

Specimen M-OS 2147-2 is moderately worn, with the metalophid and hypolophid remaining separated. The paralophid is short, lingually merging into the anterolingual cingulum. The anterior cingulum is not fully visible due to the anterior abrasion from the neighbouring tooth. This cingulum continues both on

the lingual and the buccal side to some extent. The anterior valley is shallower than the posterior valley. A small enamel tubercle exists at the base of the ectolophid groove. The posterior cingulum also continues somewhat on the buccal side, before vanishing. The posterior portion of the entoconid is not preserved and the morphology of the postero-lingual cingulum cannot be assessed.

Specimen M-OS 2147-1 is moderately worn, less so than M-OS 2147-2 with the metalophid being well separated from the metalophid. The paralophid is broken, but it must have been quite short and probably, as is the case in M-OS 2147-2, merged into an antero-lingual cingulum, because a small remnant of this cingulum is visible posterior to the entrance of the anterior valley. The anterior cingulum also continues on the buccal side to some extent and at the base of the ectolophid groove a small enamel tubercle is visible. The anterior valley is shallower than the posterior one and two very small tubercles are present ventral to the entrance of the posterior valley. In place of a posterior cingulum, a small enamel "cuspid" exists.

The rhino material from Markt Rettenbach is quite fragmentary and the preserved portion of the mandible cannot be used for species identification. Yet, the teeth are too small to be associated with the large rhinocerotid genus *Brachypotherium* (Heissig 1971; Handa 2018; Becker & Tissier 2020), which is well known from the Middle Miocene of Central Europe. However, some features, such as a short paralophid that continues into an anteroposterior cingulum, an anterior cingulum that slightly extends toward the lingual and buccal side of the tooth, and a posterior cingulum (only in m1 and m2, not in m3) along with a small tubercle in the posterior valley in the studied lower molars, are features associating the rhino material from Markt Rettenbach with the Aceratheriini (Heissig 2012; Aiglstorfer et al. 2014c). On the other hand, these features are absent in *Lartetotherium*, which is the most common horned rhino in Europe during this time period (Heissig 2012; Aiglstorfer et al. 2014c).

Within the Middle Miocene Aceratheriini many issues regarding the taxonomy and phylogenetic relationship of the genera *Aceratherium*, *Alicornops*, and *Hoploaceratherium* have been discussed in the past (e.g., Giaourtsakis 2003; Heissig 2004; Aiglstorfer et al. 2014c; Giaourtsakis 2022). Metrically, specimen M-OS 2147-2 (m?2: L = 43.8 mm, Want = 26.4 mm), which is the only mostly complete tooth, fits very well into the lower value range of *Hoploaceratherium tetradactylum* from Sansan (L = 38.5–45.0, Want = 25.0–33.0, n = 17; Heissig 2012). They also seem to be somewhat smaller than *Aceratherium incisivum* (L = 40.0–46.0 mm, W = 27.0–30.0 mm, n = 5) and *Hoploaceratherium belvederense* (L = 44.5 mm, W = 28.5–30.0, n = 3) from Rudabánya (Heissig 2004). Also, based on the measurements of the upper teeth provided by Heissig (2012, tabs. 4, 8), *Aceratherium* (*Alicornops*) *simorrense* from Sansan is smaller than *Hoploaceratherium tetradactylum*. Nonetheless, the taxonomic attribution of such scanty material is very difficult; thus, the rhino material from Markt Rettenbach is tentatively referred to as cf. *Hoploaceratherium* sp.

Order Artiodactyla Owen, 1848
Superfamily Suoidea Gray, 1821
Family Suidae Gray, 1821
Genus *Listriodon* Meyer, 1846

Listriodon splendens Meyer, 1846
Fig. 5A–D

Material: right upper canine crown fragment and left upper canine root fragment (both M-OS 2143), right astragalus, right distal humerus, distal end of lateral metapodium (all M-OS 2157).

Description and comparison: The preserved portion of the right upper male canine crown is ~107.0 mm high (though the apical end is reconstructed with gypsum), 42.0 mm wide labiolingually (DT), and 36.0 mm wide anteroposteriorly (DAP) at the preserved basal end. The tooth is very high-crowned, though its exact height cannot be assessed. The tooth is sub-conical and almost triangular in cross section. The upper canine bends to the side and slightly posteriorly. A small fragment of the enamel layer is only preserved on the dorsoposterior side. The anteroventral side of the tooth is strongly worn, due to attrition with the lower canine and exhibits a slender, elongated enamel wear facet on the anterior portion of the tooth. The Markt Rettenbach material also includes a root fragment of a left upper canine. The preserved portion of the root is large; its apical end is labiolingually compressed and its basal portion is subtriangular in cross section. It is similar in size and shape to the right upper canine from Markt Rettenbach.

Van der Made (1996) reviewed the Listriodontinae and reported a value range of 22.0–47.0 mm for the width of the upper male canines of *Listriodon splendens* (van der Made 1996: fig. 53). The right upper canine from Markt Rettenbach (M-OS 2143) perfectly

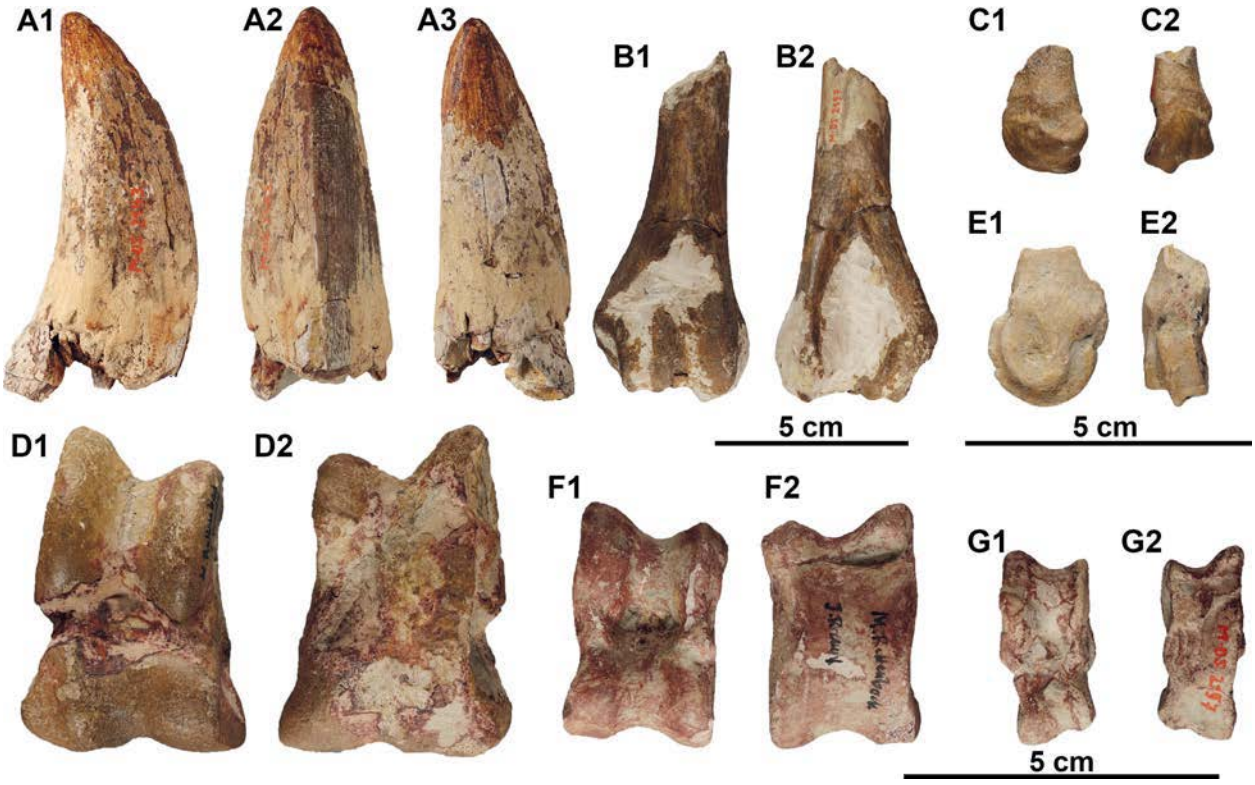

Fig. 5. Artiodactyla from the Middle Miocene locality of Markt Rettenbach. **A** – *Listriodon splendens*, right upper male canine (M-OS 2143) in medial (1), anterior (2) and posterior (3) views, note that the apical end of the canine is reconstructed with plaster; **B** – *Listriodon splendens*, right distal humerus (M-OS 2157) in anterior (1) and posterior (2) views; **C** – *Listriodon splendens*, distal end of lateral metapodium (M-OS 2157) in lateral (1) and anterior (2) views; **D** – *Listriodon splendens*, right astragalus (M-OS 2157) in anterior (1) and posterior (2) views; **E** – Pecora indet., distal metapodium (M-OS 2157) in lateral (1) and anterior (2) views; **F** – Pecora indet., right astragalus in anterior (1) and posterior (2) views; and **G** – Ruminantia indet., right astragalus (M-OS 2157) in anterior (1) and posterior (2) views. Scale bars equal 5 cm.

fits within this size range. This value fits also well with three male canines from Massenhausen (late Middle Miocene, Germany) (DT = 37.0–40.0 mm), as reported by VAN DER MADE (1996).

The right astragalus (M-OS 2157) measures 51.0 mm in proximodistal length, mediolaterally it is 26.4 mm wide at the proximal trochlea and 31.4 mm at the distal trochlea. The diameter of the medial ridge of the proximal trochlea (measurement 'R' of VAN DER MADE 1996) is 30.6 mm. The trochlea groove is steep, and the ridges of the proximal trochlea are sharp and asymmetrical with the lateral one being larger than the medial one. The proximal trochlea is slightly medially inclined and the distal trochlea broadens, especially at its navicular part, towards the distal end, resulting in a significantly wider distal trochlea in comparison to the proximal one. The cuboid facet is prominent and 11.0 mm wide. Although somewhat abraded, the sustentacular facet is flat to slightly concave mediolaterally and a medial crest (sensu DEHM 1934; LEINDERS 1976) is lacking.

This specimen shows general suoid affinities by the medially inclined proximal trochlea and the prominent cuboid facet. It differs from the generalised suid bauplan (see HUSSAIN et al. 1983) by the flat to slightly concave sustentacular facet lacking a medial crest. Both features, however, are characteristic for *Listriodon splendens* (DEHM 1934; LEINDERS 1976). The large dimensions correspond to the largest known specimens of *Listriodon splendens* (Table 1). However, M-OS 2157 is somewhat unusual in comparison to described astragali (DEHM 1934; VAN DER MADE 1996; VAN DER MADE 1998) by the significantly broadened distal trochlea, the wide cuboid facet and the robust

Table 1. Astragalus measurements [in mm] of *Listriodon splendens* according to VAN DER MADE (1996) and DEHM (1934).

	DAP	DTp	DTd	DTd/DTp	R	d
M-OS 2157	51	26.4	31.4	1.19	30.6	11.0
Markt Rettenbach	51	24.5	27	1.10	–	–
Aumeister	49.5	21.5	26.5	1.23	–	–
Simorre						
MNHNPS Si 170	43.0	20.9	25.8	1.23	22.1	9.6
Arroyo del Val IV						
AR IV 35	49.6	25.0	28.1	1.12	27.9	8.7
AR IV 65	46.2	24.3	25.3	1.04	25.5	9.1
AR IV 66	46.3	23.8	27.6	1.16	25.5	8.1
MPZ DPZ/AV 54	46.3	24.1	27.2	1.13	25.8	8.5
La Grive						
MGL LGr 757	43.1	21.7	23.9	1.10	23.2	–
MGL LGr 759	>43.3	23.5	26.1	1.11	>24.3	9.6
MGL LGr 1532	47.9	23.3	24.8	1.06	25.1	8.5
MGL LGr 1548	40.9	22.4	23.7	1.06	22.3	6.9
MGL LGr 1549	47.5	24.6	26.4	1.08	26.5	8.0
MGL LGr 1550	43.2	19.5	23.4	1.20	22.3	9.0
MGL LGr 1551	>42.4	19.6	21.7	1.11	24.1	–
MGL LGr 1552	38.9	17.5	20.8	1.19	20.8	9.1
La Chaux-de-Fonds						
MHNCF	49.0	24.7	28.7	1.16	26.4	9.4
MHNCF	–	23.6	26.7	1.13	25.3	9.5
Cerro del Otero						
NMCN 191	>51.5	25.8	28.6	1.11	26.4	9.6
Castel del Barbera						
PIS 1569	45.7	21.8	23.3	1.07	26.1	9.4
IPS -	51.0	25.6	29.3	1.14	28.6	8.7

diameter 'R'. Whereas the relative width of the distal trochlea (DTd/DTp) falls in the upper range of published specimens (Table 1), the diameter of the Markt Rettenbach astragalus is significantly larger and the cuboid facet is wider than in any known *Listriodon splendens*. As the specimen is placed at the upper size range of *Listriodon splendens*, an assignment to the contemporary suid *Parachleuastochoerus steinheimensis*, is most unlikely, as this taxon is generally smaller than *Listriodon splendens* (FORTELIUS et al. 1996).

The distal end of the humerus is 38.0 mm deep anteroposteriorly and the articular facet of the trochlea is 30.9 mm wide mediolaterally. In posterior view, the medial epicondyle is larger than the lateral epicondyle and the medial one is forming a sharp ridge. The fossa olecrani is large compared to the rest of the humerus. In anterior view, the lateral epicondyle is well developed and encompasses the trochlea laterally. The ridges of the trochlea are flat and faint.

The humerus is "pig-like" if compared to other artiodactyls by being robust and rather stout, possessing a prominent medial epicondyle encompassing the trochlea in anterior view, a large fossa olecrani, and a less-developed trochlea. The specimen shows morphological similarities with *Hyotherium* from Sandelzhausen (early Middle Miocene, Germany) (VAN DER MADE 2010: fig. 26A), although the fossa olecrani is deeper, but shorter than in M-OS 2157. Based on its size and association with the dental material that was assigned to *Listriodon splendens*, the specimen can be assigned to this species.

The articular facet of the distal part of the lateral metapodium is 12.4 mm wide mediolaterally and 13.9 mm high anteroposteriorly. The articulation facet proceeds from the anterior to the posterior side and contains a flat dorsal ridge at its centre.

The morphology of the lateral metapodium is also "pig-like" if compared to the extant *Sus scrofa*, although the central ridge is less developed in the extant pig. The articular facet also shares the general mor-

phology with the lateral metapodium of *Hyotherium* from Sandelzhausen (van der Made 2010: fig. 28B). Compared to other artiodactyls, it is rather stout and less reduced compared with ruminants for example. Therefore, the specimen is also assigned to *Listriodon splendens*.

Suborder Ruminantia Scopoli, 1777

Ruminantia indet.
Fig. 5G

Material: Right astragalus (M-OS 2157).

Description and comparison: The right astragalus M-OS 2157 is ~30.7 mm long proximodistally and mediolaterally it is ~13.9 mm wide at the proximal trochlea and ~12.6 mm at the distal trochlea. The preservation is poor, and the bone exhibits cracks that slightly deformed its shape. The ventral portion of the distal trochlea is broken. The proximal trochlea is slightly inclined medially with the lateral ridge being larger than the medial one. The trochlea groove and the central fossa are shallow. The distal trochlea is poorly preserved, but quite narrow compared to the proximal trochlea, with no distinct cuboid facet.

The Markt Rettenbach astragalus exhibits no distinct cuboid facet, a characteristic feature for suids, therefore an attribution to a suiform can be excluded and an assignment to a ruminant seems most suitable. However, the proximal trochlea slightly inclined, a feature that is absent in pecora, like bovids and cervids. Also, the trochlear ridges are very asymmetrical, with the lateral one being larger, which is a typical character of tragulids. The astragalus from Markt Rettenbach is relatively small and most similar in morphology to astragali of *Dorcatherium crassum* (Morales et al. 2012: figs. 63–64) from Sansan (France) but has a somewhat stronger level of inclination of the proximal trochlea. Moreover, the size of the astragalus from Markt Rettenbach fits within the size range of *Dorcatherium* astragali from Sansan (Middle Miocene, France) (GPIT: length = 28.0–30.6 mm; width = 15.5–16.4 mm; n = 3). Though, it differs from *Dorcatherium naui* from the Hammerschmiede (pers. obs. at GPIT) and Gratkorn (Aiglstorfer et al. 2014d) in being slenderer and more elongated proximodistally and having a more medially inclined proximal trochlea. However, based solely on this deformed astragalus a specific identification is not possible and the specimen is attributed to Ruminantia indet.

Pecora Linnaeus, 1758

Pecora indet.
Fig. 5E–F

Material: Right astragalus and distal metapodial epiphysis (M-OS 2157).

Description and comparison: The right astragalus is 36.1 mm long proximodistally, mediolaterally it is 22.0 mm wide at the proximal trochlea and 22.8 mm at the distal trochlea, and dorsoplantarly 20.0 mm thick. The proximal trochlea is separated by a faint and shallow groove and the lateral trochlea ridge is larger than the medial one. The distal trochlea is symmetrical.

The general morphology of the astragalus corresponds to cervid and bovid astragali (Heintz 1970) and differs from tragulids in lacking the inclination of the proximal trochlea. According to Heintz (1970) bovids slightly differ from cervids in a more symmetrical distal trochlea, where both condyles are subequal in size and the intercondylar groove takes a medial position. This is the case in the specimen from Markt Rettenbach.

The Markt Rettenbach astragalus is somewhat larger than cervid astragali from the Middle Miocene of Steinheim (Germany) and Sansan (France). More specifically, the specimen described herein is slightly larger compared to the *Euprox* vel *Heteroprox* cervid astragali from Steinheim am Albuch (length: 27.7–34.0 mm, anteroposterior width: 16.8–21.4 mm, n = 168). Also, the specimen is smaller in size than *Miotragocerus monacensis* from Hammerschmiede (length: 39.3–44.7, anteroposterior width: 21.3–24.8, n = 8). Sansan is also known for the occurrence of the early bovid *Eotragus clavatus*, the dimensions of which fall between the Steinheim cervids and the larger bovid *Miotragocerus*; however, the exact size range of *E. clavatus* is not known. Suraprasit et al. (2013) described an astragalus of the new species *Eotragus lampangensis* from Thailand and figured astragali from this species and *Eotragus clavatus* from Sansan (Suraprasit et al. 2013: fig. 4), which are morphologically very similar to the astragalus from Markt Rettenbach, including a lateral trochlea ridge that is larger than the medial one in the proximal trochlea, and a symmetrical distal trochlea. Also, the present specimen falls into the size range (i.e. between Steinheim cervids and *Miotragocerus*) of *Eotragus clavatus*. However, a small bovid species, *Tethytragus* sp., is known from the late Middle Miocene of Gratkorn (Aiglstor-

fer et al. 2014d), but no astragalus has been reported. Another bovid of comparable size, *Protragocerus*, is also known from the Middle Miocene (Thenius 1956; Fuss et al. 2015). According to these uncertainties, it is preferable to assign this specimen to Pecora indet.

The distal metapodial epiphysis is 11.8 mm wide mediolaterally and 18.1 mm thick anteroposteriorly. The lateral part of the articular facet is flatter than the medial part, separated by a well-developed and continuous keel as typical for cervids and bovids (compare Hillenbrand et al. 2009: pl. 3).

4. Discussion

The locality Markt Rettenbach has been dated by magnetostratigraphic correlation to 12.06 Ma (Kirscher et al. 2016), thus placing it into the Serravallian, near the end of the Middle Miocene (11.63 Ma). This time period is characterised by climatic and faunal changes (Böhme 2003; Böhme et al. 2008). Markt Rettenbach is one of the few dated mammal localities of this period in Central Europe. As it stands now, it includes a fossil assemblage that fits well into this period, including a proboscidean, a hornless rhino, a large-sized suid, a small ruminant (possibly a tragulid), and a medium-sized pecoran (possibly a bovid).

This taxon list differs from the one provided by Kirscher et al. (2016) by the absence of the genera *Deinotherium* and *Parachleuastochoerus*. A *Deinotherium* tusk deposited in the Zumsteinhaus collection (M-OS 2189) was the basis for the identification of this taxon in the Markt Rettenbach fauna. This specimen has a similar haematitic crust as seen on the Markt Rettenbach material, which is relatively uncommon in molasse fossils, but is also present on the similarly-aged locality of Hammerschmiede. It was erroneously labelled as originating from the Markt Rettenbach clay pit, but instead it originates from the closely located Hillenloh clay pit as confirmed by its collector (Manfred Schmid, pers. comm., collector of the specimen). The occurrence of *Parachleuastochoerus* was based on the postcranial remains of *Listriodon* described here and has to be omitted, as this material is too large to belong to *Parachleuastochoerus*.

During the Middle Miocene, several proboscidean taxa were present in Central Europe (Göhlich 1998; Göhlich 2010; Aiglstorfer et al. 2014b; Konidaris et al. 2017; Alba et al. 2020). Based on the caudal vertebra from Markt Rettenbach it is not possible to identify the genus or even the family it belongs to; thus, it is preferred to refer to it as Proboscidea indet.

The rhino from Markt Rettenbach can be assigned to the Aceratheriini. This group was very common in Central Europe during the Middle Miocene (Tütken et al. 2006; Heissig 2012; Aiglstorfer et al. 2014c) and also continued into the Late Miocene (Hünermann 1989; Heissig 1999; Heissig 2004; Giaourtsakis 2018; Böhme et al. 2019), with *Aceratherium* and *Hoploaceratherium* being the most frequent genera. The material from Markt Rettenbach is most similar to the hornless rhino genus *Hoploaceratherium*, which was known from the Bavarian part of the Molasse Basin before (Heissig 1984; Heissig 1999). This genus is represented by two species, *Hoploaceratherium tetradactylum* and *Hoploaceratherium belvederense* (Wang 1928; Wang 1929; Heissig 1999; Heissig 2004). Heissig (1999, 2004) suggested that the former is the Middle Miocene representative of the genus, whereas the latter is the Late Miocene one. Considering the Middle Miocene age of Markt Rettenbach, an assignment to *Hoploaceratherium tetradactylum* seems plausible. However, the exact taxonomic association of these two species is not yet resolved. Therefore, the material from Markt Rettenbach is assigned to cf. *Hoploaceratherium* sp.

One large suid has been identified in the new material from Markt Rettenbach. *Listriodon splendens* has already been described in the past from this locality, based on an almost complete mandible, some isolated teeth and postcranial material (Stromer von Reichenbach 1930; Dehm 1934). This large suid is fairly common during the Middle Miocene of Central Europe, with its occurrence in a plethora of localities in Europe (van der Made 1996; Eronen & Rössner 2007; Kirscher et al. 2016; Prieto & Mayr 2017), such as the typical ones of Sansan, Gratkorn, and Steinheim am Albuch (Pickford 2012; van der Made et al. 2014). Van der Made et al. (2014) and Aiglstorfer et al. (2014a) compared the dental morphology and isotopic signature of *Parachleuastochoerus* and *Listriodon* from Gratkorn and concluded that the two suids occupied different environments, with *Listriodon* representing a browser with some mixed feeding.

Stromer von Reichenbach (1930) reported also the presence of *Dorcatherium crassum* in Markt Rettenbach, based on a distorted mandible and some upper teeth. However, he did not describe or illustrate any of the specimens and the material cannot be relocated in the collections of the SNSB – BSPG (Gertrud Rössner, pers. comm.), where the simultaneously de-

scribed mandible of *Listriodon* is housed. In the limited material that was studied here, a badly preserved ruminant astragalus (M-OS 2157) could potentially be associated with a tragulid. Tragulids are in general very common faunal elements in Central Europe during the Middle and early Late Miocene (Rössner & Heissig 2013; Aiglstorfer et al. 2014d; Koufos 2020). The deformed astragalus from Markt Rettenbach is most similar to *Dorcatherium*, but the absence of more characteristic material and the bad preservation state of the specimen do not allow for a specific identification. Therefore, it is herein preferred to assign the specimen to Ruminantia indet.

Cervids and bovids are common faunal elements in the late Early, Middle and early Late Miocene of Europe (e.g., Thenius 1948; Gentry et al. 1999; Rössner & Heissig 1999; Aiglstorfer et al. 2014d). Two specimens among the Markt Rettenbach material, an astragalus and a distal metapodial epiphysis, can be attributed to Pecora. They might represent a bovid smaller than *Miotragocerus*, such as *Eotragus* or *Tethytragus* restricted to the Middle Miocene (Thenius 1956; van der Made 2012; Aiglstorfer et al. 2014d; Fuss et al. 2015; Hartung et al. 2020), but the limited knowledge on the small bovids of this time prevent any further comparisons.

5. Conclusions

This study represents the first dedicated description of all known fossils from the Middle Miocene deposits of the Markt Rettenbach clay pit. Thereby, adding to our knowledge about the mammalian fossil record of the 'Obere Serie'. The clay pit has been known to yield mammalian remains for over a century, but only few specimens have ever been studied before. Herein, five distinct large mammal taxa are identified: Proboscidea indet. cf. *Hoploaceratherium* sp., *Listriodon splendens*, Ruminantia indet. (possibly a tragulid), and Pecora indet. (possibly a small bovid). This fossil assemblage reflects the known faunas of a number of similarly aged localities like the Middle Miocene localities of Gratkorn (Austria), Sansan (France), Steinheim am Albuch (Germany), but also the early Late Miocene locality of Hammerschmiede (Germany) that is situated very close to the clay pit of Markt Rettenbach.

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References

Aiglstorfer, M., Bocherens, H. & Böhme, M. (2014a): Large mammal ecology in the late Middle Miocene Gratkorn locality (Austria). – Palaeobiodiversity and Palaeoenvironments, **94** (1): 189–213. doi: 10.1007/s12549-013-0145-5.

Aiglstorfer, M., Göhlich, U.B., Böhme, M. & Gross, M. (2014b): A partial skeleton of *Deinotherium* (Proboscidea, Mammalia) from the late Middle Miocene Gratkorn locality (Austria). – Palaeobiodiversity and Palaeoenvironments, **94** (1): 49–70. doi: 10.1007/s12549-013-0140-x.

Aiglstorfer, M., Heissig, K. & Böhme, M. (2014c): Perissodactyla from the late Middle Miocene Gratkorn locality (Austria). – Palaeobiodiversity and Palaeoenvironments, **94** (1): 71–82. doi: 10.1007/s12549-013-0138-4.

Aiglstorfer, M., Rössner, G.E. & Böhme, M. (2014d): *Dorcatherium naui* and pecoran ruminants from the late Middle Miocene Gratkorn locality (Austria). – Palaeobiodiversity and Palaeoenvironments, **94** (1): 83–123. doi: 10.1007/s12549-013-0141-9.

Alba, D.M., Gasamans, N., Pons-Monjo, G., Luján, À.H., Robles, J.M., Obradó, P. & Casanovas-Vilar, I. (2020): Oldest *Deinotherium proavum* from Europe. –

Journal of Vertebrate Paleontology, **40** (2): e1775624. doi: 10.1080/02724634.2020.1775624.

Almécija, S., Hammond, A.S., Thompson, N.E., Pugh, K.D., Moyà-Solà, S. & Alba, D.M. (2021): Fossil apes and human evolution. – Science, **372** (6542): eabb4363. doi: 10.1126/science.abb4363.

Becker, D. & Tissier, J. (2020): Rhinocerotidae from the early middle Miocene locality Gračanica (Bugojno Basin, Bosnia-Herzegovina). – Palaeobiodiversity and Palaeoenvironments, **100** (2): 395–412. doi: 10.1007/s12549-018-0352-1.

Böhme, M. (2003): The Miocene Climatic Optimum: evidence from ectothermic vertebrates of Central Europe. – Palaeogeography, Palaeoclimatology, Palaeoecology, **195** (3–4): 389–401. doi: 10.1016/S0031-0182(03)00367-5.

Böhme, M. & Ilg, A. (2003): fosFARbase. – www.wahre-staerke.com/: [access date: 15.12.2021].

Böhme, M., Ilg, A. & Winklhofer, M. (2008): Late Miocene "washhouse" climate in Europe. – Earth and Planetary Science Letters, **275** (3–4): 393–401. doi: 10.1016/j.epsl.2008.09.011.

Böhme, M., Spassov, N., Fuss, J., Tröscher, A., Deane, A.S., Prieto, J., Kirscher, U., Lechner, T. & Begun, D.R. (2019): A new Miocene ape and locomotion in the ancestor of great apes and humans. – Nature doi: 10.1038/s41586-019-1731-0.

Dehm, R. (1934): *Listriodon* im südbayrischen Flinz (Obermiocän). – Centralblatt für Mineralogie, Geologie und Paläontologie, Abteilung B, **12**: 513–528.

Dehm, R. (1955): Die Säugetier-Faunen in der Oberen Süßwassermolasse und ihre Bedeutung für die Gliederung. – In: Erläuterung zur geologischen Übersichtskarte der Süddeutschen Molasse, 1:300,000: 81–88; München (Bayerisches Geologisches Landesamt).

Dollo, L. (1885): Rhinocéros vivants et fossiles. – Revue de Questions Scientifiques, **17**: 293–299.

Doppler, G. (1989): Zur Stratigraphie der nördlichen Vorlandmolasse in Bayerisch-Schwaben. – Geologica Bavarica, **94**: 83–133.

Doppler, G., Heissig, K. & Reichenbacher, B. (2005): Die Gliederung des Tertiärs im süddeutschen Molassebecken. – Newsletters on Stratigraphy, **41** (1–3): 359–375. doi: 10.1127/0078-0421/2005/0041-0359.

Eronen, J. & Rössner, G.E. 2007. Wetland Paradise Lost: Miocene Community Dynamics in Large Herbivore Mammals from the German Molasse Basin. – Ecology and Evolutionary Research, **9**: 471–494.

Fortelius, M., van der Made, J. & Raymond, B.L. (1996): A new listriodont suid, *Bunolistriodon meidamon* sp. nov., from the middle Miocene of Anatolia. – Journal of Vertebrate Paleontology, **16** (1): 149–164. doi: 10.1080/02724634.1996.10011293

Fuss, J., Prieto, J. & Böhme, M. (2015): Revision of the boselaphin bovid *Miotragocerus monacensis* Stromer, 1928 (Mammalia, Bovidae) at the Middle to Late Miocene transition in Central Europe. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **276** (3): 229–265. doi: 10.1127/njgpa/2015/0481.

Giaourtsakis, I.X. (2003): Late Neogene Rhinocerotidae of Greece: distribution, diversity and stratigraphical range. – Deinsea, **10**: 235–253.

Giaourtsakis, I.X. (2018): A preliminary reassessment of the rhinocerotid diversity (Rhinocerotidae, Mammalia) at the Late Miocene locality of Höwenegg (Hegau, Germany). – In: 1st Palaeontological Virtual Congress online. Book of Abstracts.

Giaourtsakis, I.X. (2022): The fossil record of rhinocerotids (Mammalia: Perissodactyla: Rhinocerotidae) in Greece. – In: Fossil Vertebrates of Greece, **2**: 409–500; Cham (Springer). doi: 10.1007/978-3-030-68442-6_14.

Ginsburg, L. & Heissig, K. (1989): *Hoploaceratherium*, a new generic name for "*Aceratherium*" *tetradactylum* . – In: Prothero, D.R. & Schoch, R.M. (eds.): The Evolution of Perissodactyls: 418–421; New York & London (Clarendon Press & Oxford University Press).

Gentry, A.W., Rössner, G.E. & Heizmann, E.P.J. (1999): Suborder Ruminantia. – In: Rössner, G.E. & Heissig, K. (eds.): The Miocene Land Mammals of Europe: 225–258; Munich (Verlag Dr. Friedrich Pfeil).

Göhlich, U.B. (1998): Elephantoidea (Proboscidea, Mammalia) aus dem Mittel- und Obermiozän der Oberen Süsswassermolasse Süddeutschlands: Odontologie und Osteologie. – Münchner Geowissenschaftliche Abhandlungen, (A), **36**: 1–245.

Göhlich, U.B. (2010): The Proboscidea (Mammalia) from the Miocene of Sandelzhausen (southern Germany). – Paläontologische Zeitschrift, **84** (1): 163–204. doi: 10.1007/s12542-010-0053-1.

Gray, J.E. (1821): On the natural arrangement of vertebrose animals. – London Medical Repository, **15**: 297–310.

Gross, M., Böhme, M., Havlik, P. & Aiglstorfer, M. (2014): The late Middle Miocene (Sarmatian s.str.) fossil site Gratkorn – the first decade of research, geology, stratigraphy and vertebrate fauna. – Palaeobiodiversity and Palaeoenvironments, **94** (1): 5–20. doi: 10.1007/s12549-013-0149-1.

Handa, N. (2018): *Brachypotherium* (Perissodactyla, Rhinocerotidae) from the late Miocene of Samburu Hills, Kenya. – Geobios, **51**: 391–399. doi: 10.1016/j.geobios.2018.08.003

Hartung, J., Lechner, T. & Böhme, M. (2020): New cranial material of *Miotragocerus monacensis* (Mammalia: Bovidae) from the late Miocene hominid locality Hammerschmiede (Germany). – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **298** (3): 269–284. doi: 10.1127/njgpa/2020/0948

Heintz, E. (1970): Les Cervidés villafranchiens de France et d'Espagne. – 1–206; Paris (Muséum national d'Histoire naturelle).

Heissig, K. (1971): *Brachypotherium* aus dem Miozän von Südwestafrika. – Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie, **11**: 125–128.

Heissig, K. (1984): Nashornverwandte (Rhinocerotidae) aus der Oberen Süsswassermolasse und ihre Bedeutung für deren Lokalstratigraphie. – Heimatliche Schriftenreihe des Landkreises Günzburg, **2**: 62–74.

Heissig, K. (1999): Family Rhinocerotidae. – In Rössner, G. & Heissig, K. (eds.): The Miocene Land Mammals of Europe: 175–188; Munich (Verlag Dr. Friedrich Pfeil).

Heissig, K. (2004): The fossil Rhinoceroses of Rudabánya. – Palaeontographia Italica, **90**: 217–258.

Heissig, K. (2012): Les Rhinocerotidae (Perissodactyla) de Sansan. – In: Peigné, S. & Sen, S. (eds.): Mammifères de Sansan: 317–485; Paris (Muséum national d'Histoire naturelle).

Hillenbrand, V., Göhlich, U.B. & Rössner, G.E. (2009): The early Vallesian vertebrates of Atzelsdorf (Late Miocene, Austria) 7. Ruminantia. – Annalen des Naturhistorischen Museums in Wien, **111**: 519–556.

Hofmayer, F., Kirscher, U., Sant, K., Krijgsman, W., Fritzer, T., Jung, D., Weissbrodt, V. & Reichenbacher, B. (2019): Three-dimensional geological modeling supports a revised Burdigalian chronostratigraphy in the North Alpine Foreland Basin. – International Journal of Earth Sciences, **108** (8): 2627–2651. doi: 10.1007/s00531-019-01780-0.

Hünermann, K.A. (1989): Die Nashornreste (*Aceratherium incisivum*) aus dem Jungtertiär vom Höwenegg im Hegau. – Andrias, **6**: 5–116.

Hussain, S.T., Sondaar, P.Y., Shah, S.M.I., Thewissen, J.G.M., Cousin, E.F.H.M. & Spoor, C.F. , 1983. Fossil Mammal Bones of Pakistan – A Field Atlas. Part 1: The artiodactyl astragalus. – Memoirs of the Geological Survey of Pakistan, **14**: 1–30.

Illiger, C. (1811): Prodromus systematis mammalium et avium additis terminis zoographicis utriusque classis. – 1–301; Berlin (Salfeld). doi: 10.5962/bhl.title.106965

Kargopoulos, N., Kampouridis, P., Lechner, T. & Böhme, M. (2021a): A review of *Semigenetta* (Viverridae, Carnivora) from the Miocene of Eurasia based on material from the hominid locality of Hammerschmiede (Germany). – Geobios: **69**: 25–36. doi: 10.1016/j.geobios.2021.07.001.

Kargopoulos, N., Kampouridis, P., Lechner, T. & Böhme, M. (2021b): Hyaenidae (Carnivora) from the Late Miocene hominid locality of Hammerschmiede (Bavaria, Germany). – Historical Biology: 1–10. doi: 10.1080/08912963.2021.2010193.

Kargopoulos, N., Valenciano, A., Kampouridis, P., Lechner, T. & Böhme, M. (2021c): New early late Miocene species of *Vishnuonyx* (Carnivora, Lutrinae) from the hominid locality of Hammerschmiede, Bavaria, Germany. – Journal of Vertebrate Paleontology,: **41**:e1948858. doi: 10.1080/02724634.2021.1948858.

Kaup, J. (1833): Briefliche Mittheilungen an Professor Bronn. – , Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde, **1833**: 419–420.

Kirscher, U., Prieto, J., Bachtadse, V., Aziz, H.A., Doppler, G., Hagmaier, M. & Böhme, M. (2016): A biochronologic tie-point for the base of the Tortonian stage in European terrestrial settings: Magnetostratigraphy of the topmost Upper Freshwater Molasse sediments of the North Alpine Foreland Basin in Bavaria (Germany). – Newsletters on Stratigraphy, **49** (3): 445–467. doi: 10.1127/nos/2016/0288.

Konidaris, G.E., Roussiakis, S.J., Athanassiou, A. & Theodorou, G.E. (2017): The huge-sized deinothere *Deinotherium proavum* (Proboscidea, Mammalia) from the Late Miocene localities Pikermi and Halmyropotamos (Greece). – Quaternary International, **430**: 5–21. doi: 10.1016/j.quaint.2016.05.008.

Koufos, G.D. (2020): New tragulid remains from the early/middle Miocene and a revision of their occurrence in Greece. – Historical Biology, **33**: 2371–2386. doi: 10.1080/08912963.2020.1795650.

Kuhlemann, J. & Kempf, O. (2002): Post-Eocene evolution of the north Alpine foreland basin and its response to Alpine tectonics. – Sedimentary Geology, **152**: 45–78. doi: 10.1016/S0037-0738(01)00285-8

Leinders, J.J.M. (1976). Some aspects of the ankle joint of artiodactyls with special reference to *Listriodon* (Suina). – Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, series B, **79** (1): 45–54.

Lemcke, K., Engelhardt, W. & Füchtbauer, H. (1953): Geologische und sedimentpetrographische Untersuchungen im Westteil der ungefalteten Molasse des süddeutschen Alpenvorlandes. – Geologisches Jahrbuch, (B), **11**: 1–182.

Linnaeus, C. (1758): Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis (Editio decima, reformata). – 1–824; Holmiae (Laurentius Salvius).

Mayr, G., Lechner, T. & Böhme, M. (2020a): The large-sized darter *Anhinga pannonica* (Aves, Anhingidae) from the late Miocene hominid Hammerschmiede locality in Southern Germany. – PLoS ONE, **15** (5): e0232179. doi: 10.1371/journal.pone.0232179.

Mayr, G., Lechner, T. & Böhme, M. (2020b): A skull of a very large crane from the late Miocene of Southern Germany, with notes on the phylogenetic interrelationships of extant Gruinae. – Journal of Ornithology, **161** (4): 923–933. doi: 10.1007/s10336-020-01799-0.

Meyer, H. von (1846): Über die fossilen Reste von Wirbeltieren welche die Herren von Schlagintweit von ihren Reisen aus Indien und Hochasien mitgebracht haben. – Palaeontographica, **15**: 1–40.

Milne-Edwards, A. (1864): Recherches anatomiques, zoologiques et paléontologiques sur la famille des chevrotains. – Annales des Sciences Naturelles, **5**: 49–167.

Morales, J., Sánchez, I.M. & Quiralte, V. (2012): Les Tragulidae (Artiodactyla) de Sansan. – In: Peigné, S. & Sen, S. (eds.): Mammifères de Sansan: 225–247; Paris (Muséum d'Histoire Naturelle de Paris).

Owen, R. (1848): Description of teeth and portions of jaws of two extinct anthracotherioid quadrupeds (*Hyopotamus vectianus* and *Hyop. bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits on the N.W. coast of the Isle of Wight; with an attempt to develop Cuvier's idea of the classification of pachyderms by the number of their toes. – Quarterly Journal of the Geological Society of London, **4**: 103–141. doi: 10.1144/GSL.JGS.1848.004.01-02.21

Pickford, M. (2012): Les Suoidea (Artiodactyla) de Sansan: systématique, paléoécologie, biogéographie et biochronologie. – In: Peigné, S. & Sen, S. (eds.): Mammifères de Sansan: 249–278; Paris (Muséum d'Histoire Naturelle de Paris).

Prieto, J. & Mayr, C. (2017): New Miocene record of the suid *Listriodon* near Munich. – Zitteliana, **89**: 355–357.

Rössner, G.E. & Heissig, K. (1999): The Miocene Land Mammals of Europe. – 515 pp.; Munich (Verlag Dr. Friedrich Pfeil).

Rössner, G.E. & Heissig, K. (2013): New records of *Dorcatherium guntianum* (Tragulidae), stratigraphical framework, and diphyletic origin of Miocene European tragulids. – Swiss Journal of Geosciences, **106** (2): 335–347. doi: 10.1007/s00015-013-0132-x.

Schäfer, I. & Berlinger, A. (1954): 100 Jahre Ziegelwerk Lämmle in Markt Rettenbach/Schwaben 1854–1954: 1–24; Markt Rettenbach (Ziegelwerk Joh. Lämmle).

Scopoli, G.A. (1777): Introductio ad Historiam naturalem, sistens genera Lapidum, Plantarum et Animalium hactenus detecta, caracteribus essentialibus donata, in tribus divisa, subinde ad leges Naturae. Praha, Czech Republic (Gerle). doi: 10.5962/bhl.title.10827

Stromer von Reichenbach, E. (1928): Wirbeltiere im obermiocänen Flinz Münchens. – Abhandlungen der Bayerischen Akademie der Wissenschaften, **32** (1): 1–74.

Stromer von Reichenbach, E. (1930): Neue Funde fossiler Säugetiere im Obermiozän bayerisch Schwabens. – Berichte des Naturwissenschaftlichen Vereins für Schwaben und Neuburg, **48**: 29–31.

Suraprasit, K., Chaimanee, Y., Chavasseau, O. & Jaeger, J.-J. (2013): Middle Miocene Bovidae from Mae Moh Basin, Northern Thailand: the first record of the genus *Eotragus* from Southeast Asia. – Acta Palaeontologica Polonica, **60** (1): 67–78. doi: 10.4202/app.2012.0061.

Thenius, E. (1948): Zur Kenntnis der fossilen Hirsche des Wiener Beckens, unter besonderer Berücksichtigung ihrer stratigraphischen Bedeutung. – Annalen des Naturhistorischen Museums in Wien, **56**: 262–308.

Thenius, E. (1956): Zur Entwicklung des Knochenzapfens von *Protragocerus* Depéret aus dem Miozän. – Geologie, **5** (3): 308–318.

Tütken, T., Vennemann, T.W., Janz, H. & Heizmann, E.P.J. (2006): Palaeoenvironment and palaeoclimate of the Middle Miocene lake in the Steinheim Basin, SW Germany: A reconstruction from C, O, and Sr isotopes of fossil remains. – Palaeogeography, Palaeoclimatology, Palaeoecology, **241** (3–4): 457–491. doi: 10.1016/j.palaeo.2006.04.007.

van der Made, J. (1996): Listriodontinae (Suidae, Mammalia), their evolution, systematics and distribution in time and space. – Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie, **33** (1/4): 3–254.

van der Made, J. (1998): The first described listriodont remains. – Bulletin de la Société Neuchâteloise de Sciences Naturelles, **121**: 40–44.

van der Made, J. (2010): The pigs and "Old World peccaries" (Suidae and Palaeochoeridae, Suoidea, Artiodactyla) from the Miocene of Sandelzhausen (southern Germany): phylogeny and an updated classification of the Hyotheriinae and Palaeochoeridae. – Paläontologische Zeitschrift, **84**: 43–121. doi: 10.1007/s12542-010-0051-3

van der Made, J. (2012): *Eotragus clavatus* (Artiodactyla, Bovidae, Boselaphini) de Sansan. – In: Peigné, S. & Sen, S. (eds.): Mammifères de Sansan: 145–199; Paris (Mémoires du Muséum National d'Histoire Naturelle).

van der Made, J., Prieto, J., Aiglstorfer, M., Böhme, M. & Gross, M. (2014): Taxonomic study of the pigs (Suidae, Mammalia) from the late Middle Miocene of Gratkorn (Austria, Styria). – Palaeobiodiversity and Palaeoenvironments, **94** (4): 595–617. doi: 10.1007/s12549-014-0152-1.

Wang, K.-M. (1928): Die obermiozänen Rhinocerotiden von Bayern. – Paläontologische Zeitschrift, **10** (2): 184–212. doi: 10.1007/BF03041571.

Wang, K.-M. (1929): Die fossilen Rhinocerotiden des Wiener Beckens. – Academia Sinica National Research Institute of Geology Memoir, **7**: 53–59.

Wessel, P., Smith, W.H.F., Scharroo, R., Luis, J. & Wobbe, F. (2013): Generic Mapping Tools: Improved Version Released. – EOS, **94** (45): 409–410. doi: 10.1002/2013EO450001

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