**N. Jb. Geol. Paläont. Abh. 276/3 (2015)**, 229–265
Stuttgart, June 2015

**Article**

# Revision of the boselaphin bovid *Miotragocerus monacensis* Stromer, 1928 (Mammalia, Bovidae) at the Middle to Late Miocene transition in Central Europe

**Jochen Fuss, Jérôme Prieto, and Madelaine Böhme**

With 19 figures and 8 tables

**Abstract:** During excavations in 2011-2014, new fossil material of the boselaphin *Miotragocerus monacensis* Stromer, 1928 (Mammalia, Bovidae) was found at the locality Hammerschmiede (Bavaria, Germany), which is dated to ~11.6 Ma (Middle to Late Miocene transition). For the first time, both dentition and postcranial material can be studied on this species. These new findings complete a collection of casts stored in the Bavarian State Collection for Palaeontology and Geology. In addition, the holotype of *M. monacensis* from Oberföhring (Bavaria, Germany) and further unpublished material from Southern Germany and Lower Austria are newly described in this study. Important new taxonomic characters are emphasized improving our knowledge on the species which was originally described based on one single horn core. *M. monacensis* can be assigned to the basal Boselaphini based on the plesiomorphic features in the dentition and characters of the postcranial material. Intraspecific variabilities, ontogenetic changes and allometries are identified improving the differenciation to other basal boselaphins like *Miotragocerus pannoniae*, *Austroportax latifrons* and *Protagocerus chantrei*. An improved statement regarding the biostratigraphic range of basal Boselaphines from Central Europe is provided.

**Key words:** Taxonomy, Biostratigraphy, Boselaphini, *Miotragocerus monacensis*, Middle to Late Miocene transition, Central Paratethys, Southern Germany, Lower Austria.

## 1. Introduction

The locality Hammerschmiede (Bavaria, Germany) provides a rare insight into the European palaeoecosystem at the Middle to Late Miocene transition because of the wide taxonomic range of fossils excavated since decades (see Chapter 2 and references therein). Among them, the vertebrates play an important part, especially ectothermic forms and small mammals while larger mammals were until now poorly documented. The discovery of a new fossil-rich layer allows to fill this gap. Particularly, the excavated assemblage provides new insight into the bovid *Miotragocerus*.

The genus *Miotragocerus* Stromer, 1928 was one of the dominant taxa among the Boselaphini during the Late Miocene in terms of diversity and geographic distribution. It is known from Europe (e.g., Stromer 1928; Kretzoi 1941; Morales et al. 1999; Spassov & Geraads 2004; Kostopoulos 2006; Gentry & Kaiser 2009), Asia Minor (Köhler 1987; Kostopoulos 2005) and the Indo-Pakistani Siwaliks (Khan et al. 2009), as well as China (Zhang 2005) and sub-Saharan Africa (e.g., Bibi 2011). Currently, *Miotragocerus* includes the subgenera *M. (Pikermicerus)* Kretzoi, 1941 and *M. (Miotragocerus)* Stromer, 1928. Its relationship to *Tragoportax* is unclear and they have been used synonymously


DOI: 10.1127/njgpa/2015/0481
www.schweizerbart.de
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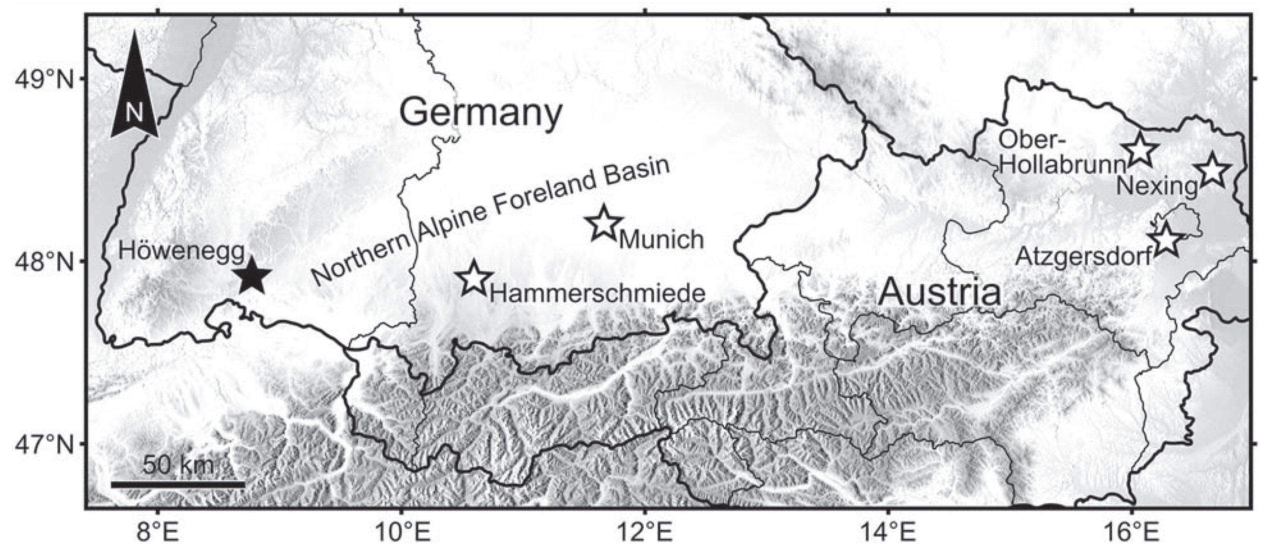



**Fig. 1.** Map of the localities with findings of *Miotragocerus monacensis* (white asterisks). The black asterisk marks the fossil site Höwenegg in Southern Germany, where *M. pannoniae* was found.

in some cases (Bibi et al. 2009; Bibi 2011). Hence, both genera were united in the tribe Tragoportacini (Bibi et al. 2009), implying that Boselaphini is a non-monophyletic group. *M. monacensis* Stromer 1928 is the type species of *Miotragocerus*. It is documented only from southern Germany and Lower Austria (Thenius 1948). A second species – *M. pannoniae* (Kretzoi, 1941) – appears in the northern alpine region of the Central Paratethys (Berg 1970; Romaggi 1987; Bechly et al. 2005; Swisher 1996).

This study presents a new description of the holotype material of *M. monacensis*, as well as the description of the newly excavated material from Hammerschmiede. Further, the first detailed description of the bovid material from Lower Austria is given. The fossils of *M. monacensis* are compared with *M. pannoniae* from Höwenegg (Baden-Württemberg, Germany), *Protragocerus chantrei* (La Grive, France), *Austroportax latifrons* (Lower Austria) and further related taxa. On this basis, assumptions on their taxonomy are proposed, particularly with regard to the ontogeny of *M. monacensis*.

## 2. Geology and stratigraphy of the studied localities

Hammerschmiede. – The fossil site Hammerschmiede from the Northern Alpine Foreland Basin is a clay pit located 300 m W of the settlement Hammerschmiede/Pforzen, and 4 km NNW of Kaufbeuren (Fig. 1; Bavaria, Germany; N47.9258, E11.080). The outcrop shows a ca. 20 m thick section of floodplain deposits consisting of clays, marls and sandstones of the Upper Freshwater Molasse (UFM). It contains a coal layer at the base and a few thin coaly beds at the top. This sedimentary sequence belongs to the youngest part of the UFM, called "Obere Serie"/ "Upper Series" (Doppler 1989; Doppler et al. 2005; Fig. 2).

The deposits provide a rich fossil fauna including molluscs (Mayr & Fahlbusch 1975; Schneider & Prieto 2011), fishes, ectothermic vertebrates and small mammals (Fahlbusch 1975; Fahlbusch & Mayr 1975; Mayr & Fahlbusch 1975; Schleich 1985; Bolliger 1999; Hugueney 1999; Böhme 2003; Böhme & Ilg 2003; Prieto & Rummel 2009; Klembara et al. 2010; Prieto et al. 2011; Prieto 2012; Prieto & van Dam 2012). In addition, a few large mammals were mentioned in Mayr & Fahlbusch (1975). Furthermore, the palaeoflora of Hammerschmiede has been studied by several authors (Meyer 1956; Jung & Mayr 1980; Gregor 1982; Seitner 1987).

A dominant part of the terrestrial vertebrates are small mammals, which confers a significant stratigraphic importance to the locality (Prieto & Rummel 2009; Prieto et al. 2011). According to this, the age of the Hammerschmiede sediments was set to the Middle to Late Miocene transition, not younger than 11.5 Ma (Prieto et al. 2011), slightly older than the locality Aumeister near Munich (see below; Prieto et al. 2011).

A correlation to the Late Sarmatian s.str. to earliest

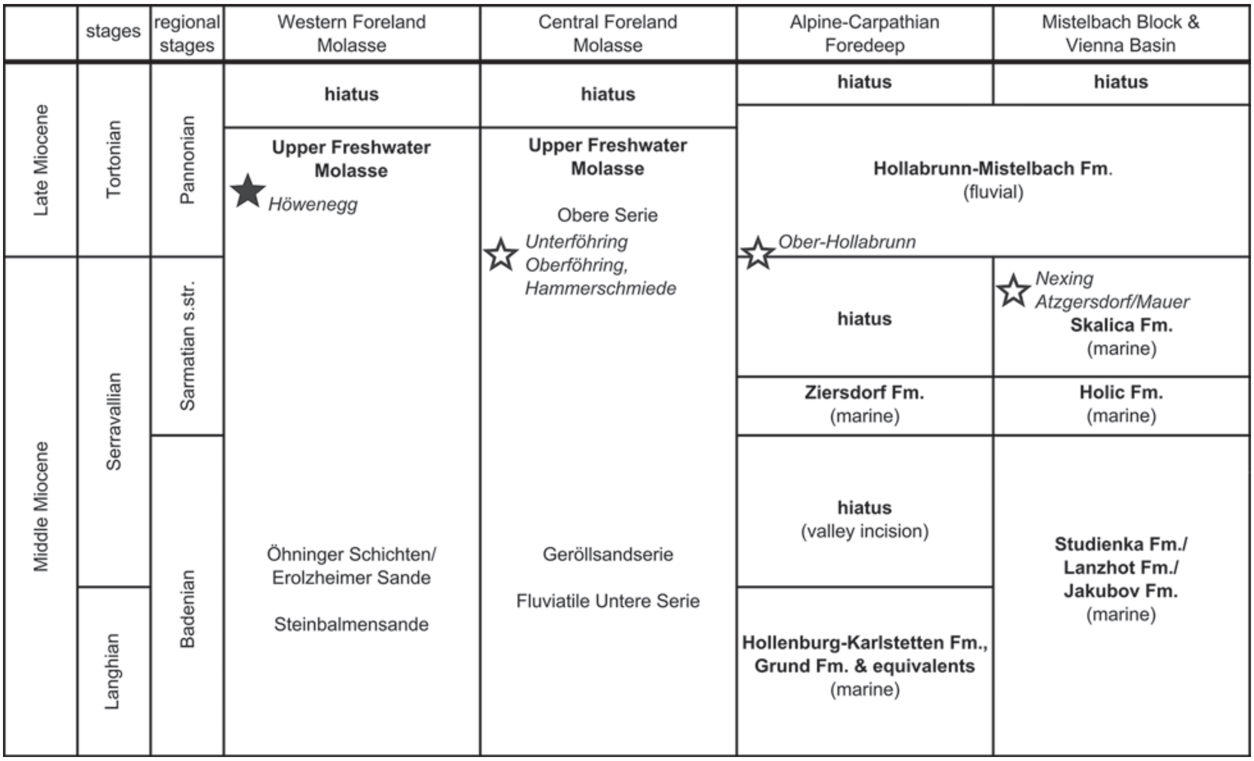



**Fig. 2.** Stratigraphy of Miocene Foreland basins (after Piller et al. 2004, Harzhauser & Piller 2004, and Schneider & Prieto 2011) and the stratigraphic position of important localities (White asterisks = *Miotragocerus monacensis*; grey asterisk = *M. pannoniae*).

Pannonian is further supported by the absence of hipparionin horses, which have their first appearance at 11.2 Ma in Austria (Daxner-Höck 1996; Rögl & Daxner-Höck 1996). Hence, Hammerschmiede is among the few localities representing the transition from Middle to Late Miocene, a time span poorly documented in the Northern Alpine Foreland Basin and Central/East Europe, in sharp contrast to the Iberian fossil record.

The locality Hammerschmiede is traditionally divided into three fossil-bearing layers (Mayr & Fahlbusch 1975; Böhme & Ilg 2003; Prieto & Rummel 2009; Prieto 2012). A fourth layer (here named Ham4) contains mostly small vertebrates and is characterized by well-preserved unionid bivalves (Schneider & Prieto 2011). The new findings of *M. monacensis* presented in this study come from a newly discovered fifth layer (Ham5). It may correlate with the previous layers Ham1-2 or even Ham3 (Mayr & Fahlbusch 1975). Because no detailed profile is available for the situation in the pit during the 70's/80's, a secure correlation between Ham3 to Ham5 is at present not possible. However, no biostratigraphical difference can be observed between the different layers (J. Prieto, pers. obs.). The layer of Ham5 (Fig. 3) represents deposits of an E-W directed channel which eroded into clays lying below. The lower part of the channel has a thickness of about one meter and is dominated by silty clay. Therein, three horizons are enriched in reworked pedogenic carbonate concretions as well as freshwater and terrestrial gastropods. Furthermore, this lower part provides remains of charophytes, unionid bivalves, fishes, turtles, small and large mammals. The sediments of the lower part can be followed laterally for several meters. The material of *M. monacensis* comes from the transition to the upper part. The upper part is dominated by fine sands in troughs of decimetre thickness. These cross-bedded sand bodies are intercalating with silty clay of smaller thickness. This part is significantly less rich in larger vertebrates. The sediment bodies are laterally restricted to a few meters.

The channel sediments suggest an allochthonous deposition of the fossils, which is supported by the dis-

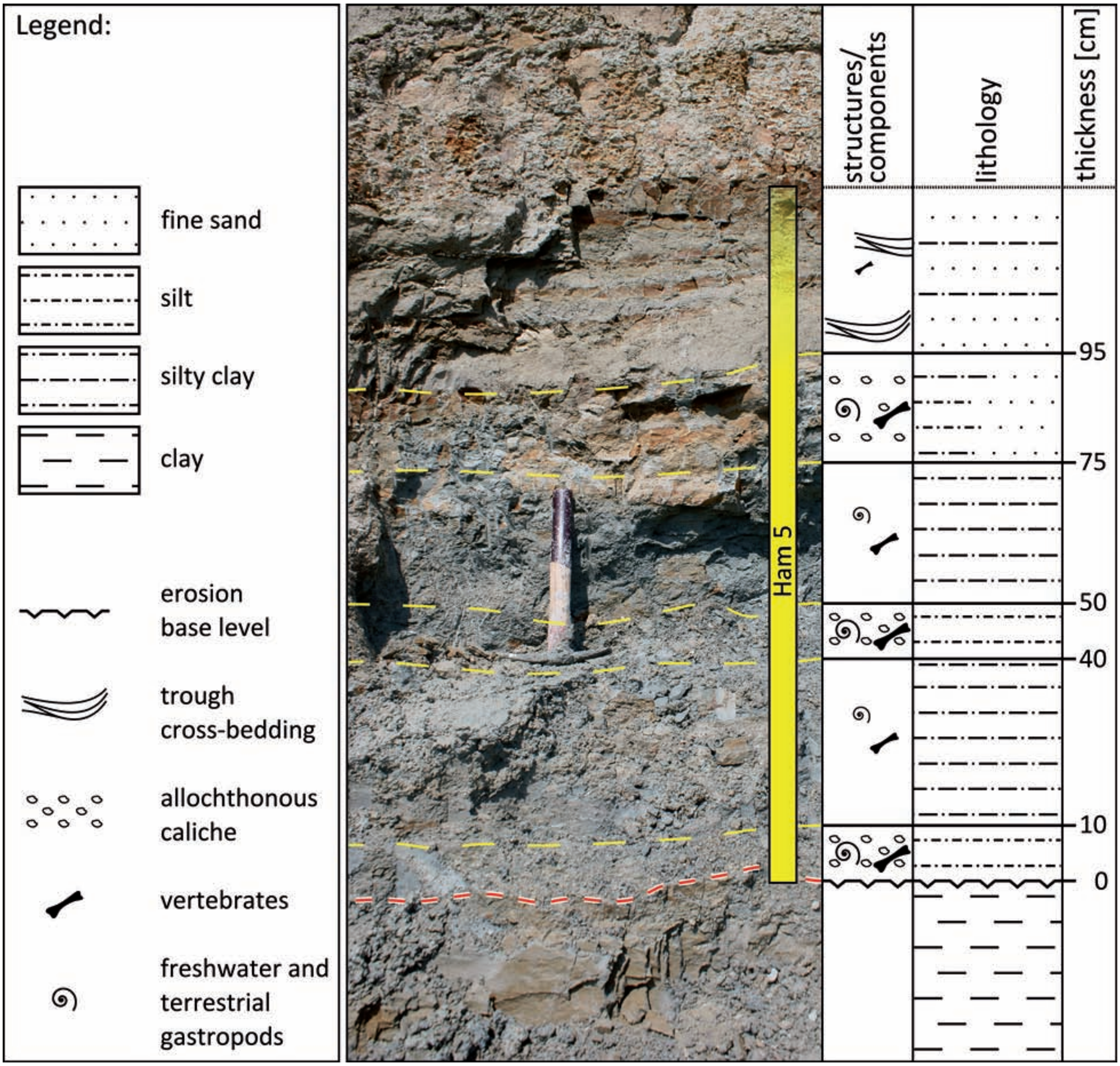
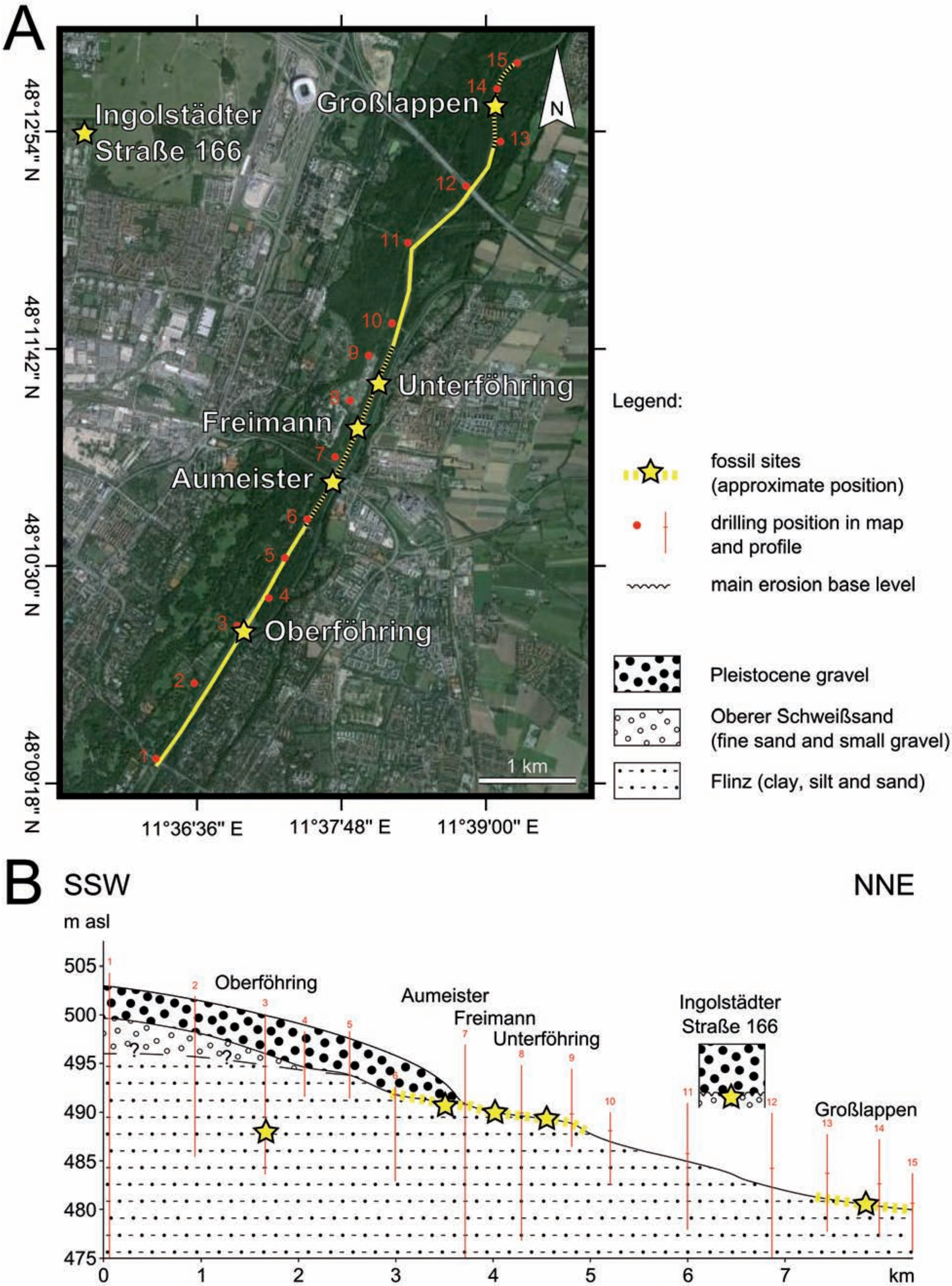



**Fig. 3.** Outcrop and schematic lithology of the channel Ham5. The thickness is measured from erosion base level. The abundance of the main components (ignoring small vertebrates) is indicated by the size of their symbols.

**Fig. 4. A** – Aerial photograph of the northern Munich with the fossil localities Oberföhring, Aumeister, Freimann, Unterföhring, Großlappen and Ingolstädter Straße 166 mentioned in Stromer (1928, 1937, 1938). **B** – Profile along the Isar river (marked with a yellow line in Fig. 4A) and the section of the former gravel pit Ingolstädter Straße 166 (Stromer 1937, 1938; Klein 1939). The lithology derived from literature is matched with drillings obtained from the Bavarian Environment Agency (LfU). However, the available drilling descriptions did not allow a consistent differentiation of *Flinz* and *Oberer Schweißsand*. (Drilling IDs: 1 = 7835BG000550; 2 = 7835BG008130; 3 = 7835BG008128; 4 = 7835BG001541; 5 = 7835BG001542; 6 = 7835BG011839; 7 = 7835BG000509; 8 = 7835BG002411; 9 = 7835BG002414; 10 = 7835BG001482; 11 = 7735BG001482; 12 = 7735BG001935; 13 = 7735BG015519; 14 = 7735BG015517; 15 = 7735BG015508).


A
48°12'54" N
48°11'42" N
48°10'30" N
48°09'18" N
11°36'36" E
11°37'48" E
11°39'00" E
Ingolstädter Straße 166
Großlappen
Unterföhring
Freimann
Aumeister
Oberföhring
N
1 km
Legend:
fossil sites (approximate position)
drilling position in map and profile
main erosion base level
Pleistocene gravel
Oberer Schweißsand (fine sand and small gravel)
Flinz (clay, silt and sand)
B
SSW
NNE
m asl
505
500
495
490
485
480
475
0
1
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4
5
6
7
km
Oberföhring
Aumeister
Freimann
Unterföhring
Ingolstädter Straße 166
Großlappen

**Fig. 4.**

articulation of the material. However, the fossil remains are mostly well preserved and only a few are intensively abraded by transport. This shows that the fossil material has not been transported over long distances and hence, they can be seen as semi-autochthonous. Besides, the presence of fine sands, silts and clays suggests a low energy and non-destructive transport.

Munich (Oberföhring, Aumeister, Unterföhring). – Intensive palaeontological investigations of the Munich region (Fig. 1) were done by Stromer (1928, 1937, 1938, 1940). The fossil-bearing lithologies mentioned in these studies are *Flinz* (greenish-grey silt and clay) and *Oberer Schweißsand* (mainly ferruginous sand and fine gravel). The lithology of the same region is investigated in detail by Klein (1937, 1938, 1939). Therein, further local lithostratigraphic terms were established. The lowermost unit is *Flinzmergel*, an aquiclude mainly consisting of greenish-grey silt and clay. The overlying *Flinzsand* is dominated by reddish or greenish sand and clay. Between the deposition of *Flinzmergel* and *Flinzsand* a minor hiatus is assumed due to the continuous coarsening-up and the lack of intense weathering horizons between both units (Klein 1939). The *Flinzsand* is followed by *Oberer Schweißsand*. A distinct weathering horizon can be observed between these two lithologies implying a major time of non-deposition (Klein 1939). All these Miocene deposits are widely covered with Pleistocene gravel, which intensively eroded the underlying sediments.

Supported by the studies of Klein (1939) and Stromer (1928, 1937), the lithostratigraphic position of the former fossil sites along the Isar River in Munich (Oberföhring, Aumeister, Freimann, Unterföhring and Großlappen; see Stromer 1928, 1937, 1940) can be approximated (Fig. 4). In general, all these localities are positioned in the *Flinz*. Aumeister, Freimann and Unterföhring are stratigraphically close to each other; Oberföhring and Großlappen lie stratigraphically below. The locality Ingolstädter Straße 166 (Fig. 4), which is located close to the fossil sites of the Isar river, shows *Oberer Schweißsand* below the Pleistocene gravels (Stromer 1937; Klein 1939). Further, an exposure of *Oberer Schweißsand* and *Flinzsand* is observed south of Freimann at an altitude of about 497 metres (Klein 1939). Consequently, *Oberer Schweißsand* could be preserved in the southern part of the profile.

Oberföhring (Munich). – The location Oberföhring (Fig. 4) was a temporary outcrop in the year 1923 during the construction of the water-power plant 'Mittlere Isar' (Stromer 1928). The excavation at the dam has achieved a depth of 12 m below the ground level and provided fine, ferruginous quartz sands of the UFM, belonging to the *Flinz*. In addition to the holotype of *Miotragocerus monacensis*, a few limb bones of a Rhinocerotidae were found at this site. Assuming nearly horizontal bedding, the location Aumeister (see below) lies stratigraphically slightly above Oberföhring (Fig. 4). Hence, Oberföhring could approximately coincide with the age of Hammerschmiede (Fig. 2), which is supposed to be slightly older than Aumeister (Prieto et al. 2011).

Aumeister (Munich). – The fossil findings of the locality Aumeister (Fig. 4) described by Stromer (1928) came from a small temporary outcrop at the riverside of the Isar in the year 1926. The site was located about 2 km downstream (NNE) from the locality Oberföhring. Molluscs, fishes, reptiles, birds as well as small and large mammals are known from the locality (e.g., Stromer 1928; Bolliger 1999; Prieto et al. 2011). Moreover, Stromer (1928) mentioned an upper P4 dextr., which he attributed to *Miotragocerus monacensis*. The sediments consist of greenish, silty fine sands of the UFM, belonging to the *Flinz*. They are supposed to be slightly younger than Hammerschmiede because of the evolutionary stage of the cricetid *Collimys* from Aumeister, which lies between *C. hiri* from Hammerschmiede and *C. longidens* from the Swiss locality Nebelbergweg (Prieto et al. 2011). However, this assumption needs to be confirmed by further findings (see details in Prieto et al. 2014: 149).

Unterföhring (Munich). – The site Unterföhring (Fig. 4) was located about 3 km downstream (NNE) from the locality Oberföhring at the riverside of the Isar. It also exhibited deposits which belong to the *Flinz*. The fossils described by Stromer (1928), were found in the year 1921 during the construction of the water-power plant 'Mittlere Isar'. The locality provided a horn core and the distal end of a humerus, both of them were attributed to *Miotragocerus monacensis* (Stromer, 1928). The stratigraphic level of Unterföhring is close to Aumeister, because both sites are at the level of the river bank, they are in close proximity to each other and there is no observable dip of the deposits (Fig. 4).

Lower Austria (Nexing, Atzgersdorf/Mauer, Ober-Hollabrunn). – In addition to the Southern German localities mentioned above, three Lower Austrian fossil sites (Nexing, Atzgersdorf/Mauer and Ober-Hollabrunn; Fig. 1) provided records of *M. monacensis* (Sickenberg

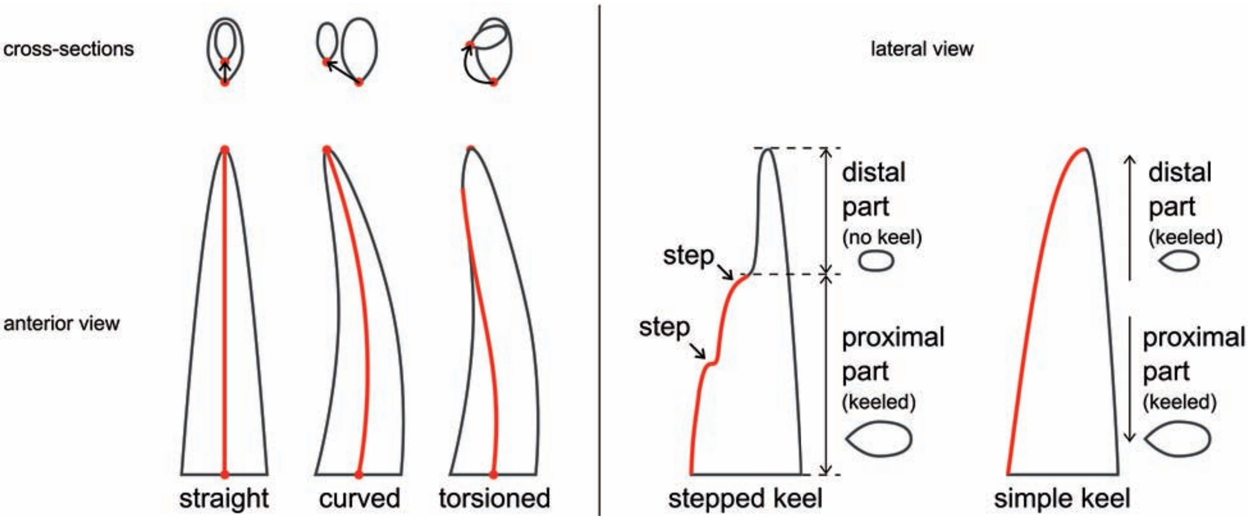


**Fig. 5.** Generalised drawing and used terminology of different tragoportacin horn core morphologies. The anterior keel is highlighted in red.

1929; Thenius 1948; Thenius 1956). However, there is no detailed description of these specimens in the literature.

The Lower Austrian localities are positioned in different geological settings: (1) An incised valley, which crosses the Alpine-Carpathian Foredeep (Ober-Hollabrunn), (2) the Mistelbach tectonic block (Nexing) and (3) the adjoining Vienna Basin (Atzgersdorf/Mauer). During the Middle to Late Badenian the Palaeo-Zaya River forms a W-E trending incised valley on the Alpine-Carpathian Foredeep and the Mistelbach block, which provides accommodation space for post-Badenian deposits (e.g. Gebhardt et al. 2009; Gebhardt & Roetzel 2013). The incised valley became flooded during an Early Sarmatian s.str. transgression, what partially eroded and reworked existing deposits. Afterwards, the Proto-Danube River refilled the valley with Upper Sarmatian s.str. to Pannonian deposits which were prograding into the Vienna Basin (Harzhauser & Piller 2007; Mandic et al. 2008; Gebhardt & Roetzel 2013).

The locality Atzgersdorf/Mauer (now Vienna city) was a quarry which was accessible till the year 1937 (Papp 1954). The section showed coastal marine sediments belonging to the Upper *Ervilia* biozone of the early Late Sarmatian s.str. (Papp 1954; Harzhauser & Piller 2004). Therefore, Atzgersdorf/Mauer documents the first appearance of *M. monacensis* at about 12.0 Ma. The fossil mammals of Nexing came either from the upper *Ervilia* biozone or the regressive part of the Upper Sarmatian s.str. (lowermost *Sarmatimactra* biozone; Grill 1968; Harzhauser & Piller 2009). Ober-Hollabrunn is an former gravel pit called Heilig. It provided fluvial sediments of the Palaeo-Danube which are deposited on the Alpine-Carpathian Foredeep and the Mistelbach block. The deposits belong to the Hollabrunn-Mistelbach Formation. Its correlation to the Upper Sarmatian s.str./lowermost Pannonian approximates the age of Ham5 and the Munich localities. Caused by a reactivation of the incised valley during the transition Sarmatian s.str./Pannonian, a reworking and faunal mixing due to fluvial accumulation is documented in the Hollabrunn-Mistelbach Formation (Harzhauser et al. 2011). However, the vertebrate-bearing deposits of Ober-Hollabrunn seem to be unaffected. This is indicated by the presence of typical Late Sarmatian s.str. large mammals (*Listriodon splendens*, *Anchitherium aurelianense*; Gross et al. 2014) and the absence of the typical Late Miocene hipparionin horses (Sickenberg 1929).

## 3. Materials and methods

The studied material comprises all specimens known from *M. monacensis* that are available in public collections. Comparative material comes from *M. pannoniae* (Höwenegg), *Austroportax latifrons* (Ober-Hollabrunn), *Protragocerus chantrei* (La Grive) and further related taxa. The material is housed in following collections:

– GPIT (palaeontological collection, University of Tuebingen): Hammerschmiede (Ham5).

– BSPG (Bayerische Staatssammlung für Paläontologie und Geologie, Munich): Munich and casts from Hammerschmiede (unknown layer, original material stored in private collection).
– NHMW (Natural History Museum, Vienna): Atzgersdorf/ Mauer and Ober-Hollabrunn.
– IPUW (Department of Palaeontology, University of Vienna): Ober-Hollabrunn and Nexing.
– SMNK (Staatliches Museum für Naturkunde, Karlsruhe): Höwenegg.
– SMNS (Staatliches Museum für Naturkunde, Stuttgart): Höwenegg.

The descriptive terminology for teeth follows Bärmann & Rössner (2011), for cranial and postcranial material the terminology of Nickel et al. (1961) is used. The terms used for the horn core descriptions are visually explained in Fig. 5.

The measurements on cranial and postcranial bones are performed as shown in the drawings of Figs. 6-12. The astragali are mainly measured following Degusta & Vrba (2003). All values are given in millimeters and rounded to one decimal. The specimens of *M. monacensis* are photographed and drawn. Drawings of cross-sections are generated by forming the bones with a 0.25 mm copper wire which is retraced afterwards.

## 4. Systematic palaeontology

Class Mammalia Linnaeus, 1758
Order Cetartiodactyla Montgelard, Catzeflis & Douzery, 1997
Family Bovidae Gray, 1821
Tribe Boselaphini Knottnerus-Meyer, 1907
Genus *Miotragocerus* Stromer, 1928
*Miotragocerus monacensis* Stromer, 1928
Figs. 6-12

1927 *Protragocerus chantrei* Deperét, 1887. – Abel, pp. 194-195, fig. 160.
1928 *Miotragocerus monacensis* Stromer, 1928. – Stromer, pp. 36-38, fig. 1.
1956 *Protragocerus chantrei* Deperét, 1887. – Thenius, pp. 308-318, fig. 3.

### 4.1. Oberföhring (Munich)

**Material:** Calvarium with left horn core [BSPG 1923 I 9] (holotype).

**Description:** The holotype of *Miotragocerus monacensis* is a well preserved partial calvarium with the main part of the left horn core and the basal part of the right pedicle (Fig. 6). The calvarium shows two very strong temporal ridges on the postcornual fronto-parietal area. They are running posteriorly from the horn cores in caudal direction and converge weakly medially. The surface of the postcornual fronto-parietal bones between the two ridges are very rough and depressed. The intercornual area of the frontal does not show any sagittal ridge but is slightly elevated on the whole. The sagittal suture and the coronal suture are closed, but still clearly visible, indicating that this specimen is not fully grown (compare with the specimen described in Chapter 4.4 Ober-Hollabrunn). The voluminous sinus frontalis invades the anterior part of the pedicle, but does not reach into the horn core itself. Further, the sinus runs into the elevated intercornual part of the frontal. The pedicles are attached right above the inconspicuous orbital rims. The posterior border of the horn core makes an angle of 35° with the dorsal fronto-parietal surface. The proximal part of the horn core shows a prominent anterior keel with a length of 70.7 mm, which extends onto the pedicle. The keel is nearly straight and shows no torsion. The basal horn core has an anteroposteriorly elongated ellipsoid cross-section with an index of 1.95 (index = 1 means circular). The distal part of the horn core has no keel and is nearly circular (index = 1.19).

### 4.2. Hammerschmiede

**Material (Ham5):** Cranial appendages: Almost completely preserved right horn core and a large fragment of the left horn core of the same individual [GPIT/MA/03483]. Dentition: Mandible dext. with p4-m3 [GPIT/MA/07196], M2/3? dext. [GPIT/MA/03484], M2/3? dext. [GPIT/MA/07199], P4 dext. [GPIT/MA/05740], fragmented P3 dext. [GPIT/MA/05741], P2 dext. [GPIT/MA/05743], m3 sin. [GPIT/MA/07197], m2 dext. [GPIT/MA/05745], m1 sin. [GPIT/MA/05744], m1 sin. [GPIT/MA/05746], p4 sin. [GPIT/MA/05742], p3 dext. [GPIT/MA/07198]. Postcranial material: Astragalus, dext. [GPIT/MA/03485], proximal and distal end of a right metacarpal [GPIT/MA/03486], phalanx proximalis [GPIT/MA/03487], distal end of a phalanx proximalis [GPIT/MA/07201], phalanx medialis [GPIT/MA/07200], distal end of a dextral humerus [GPIT/MA/07202], proximal end of a left ulna [GPIT/MA/05747].

**Material (unknown layer, casts):** Mandible dext. with p2-m3 [BSPG 1521], proximal end of a right metatarsal III+IV [BSPG 1519], proximal end of a metacarpal [BSPG 1523] astragalus, dext. [BSPG 1522], proximal end of a phalanx proximalis [BSPG 1527], proximal end of a phalanx medialis [BSPG 1520].

**Description:** Horn cores (Figs. 7-8): Proximally, the horn core is characterized by a prominent anterior keel, reaching a length of 62.5 mm in distal direction (right horn core). Thereby, the keel occupies nearly 1/3 of the total length of the horn core. In this proximal area the horn core possesses an anteroposteriorly elongated ellipsoid cross-section with an index of 2.28. The distal two third of the horn core form a 146 mm long curve. The cross-section of this part is oval to circular with indices of 1.23 to 1.20. The transition from the proximal to the distal area of the horn core is marked by a fast decline of the anterior-posterior diameter above the step. The transverse diameter remains relatively constant. This implies that the cross-section changes from elongated to circular. Furthermore, the horn core shows a marginal curvature in medial direction. The sinus frontalis (visible at the left horn core) is large, reaching up into the basal horn core.

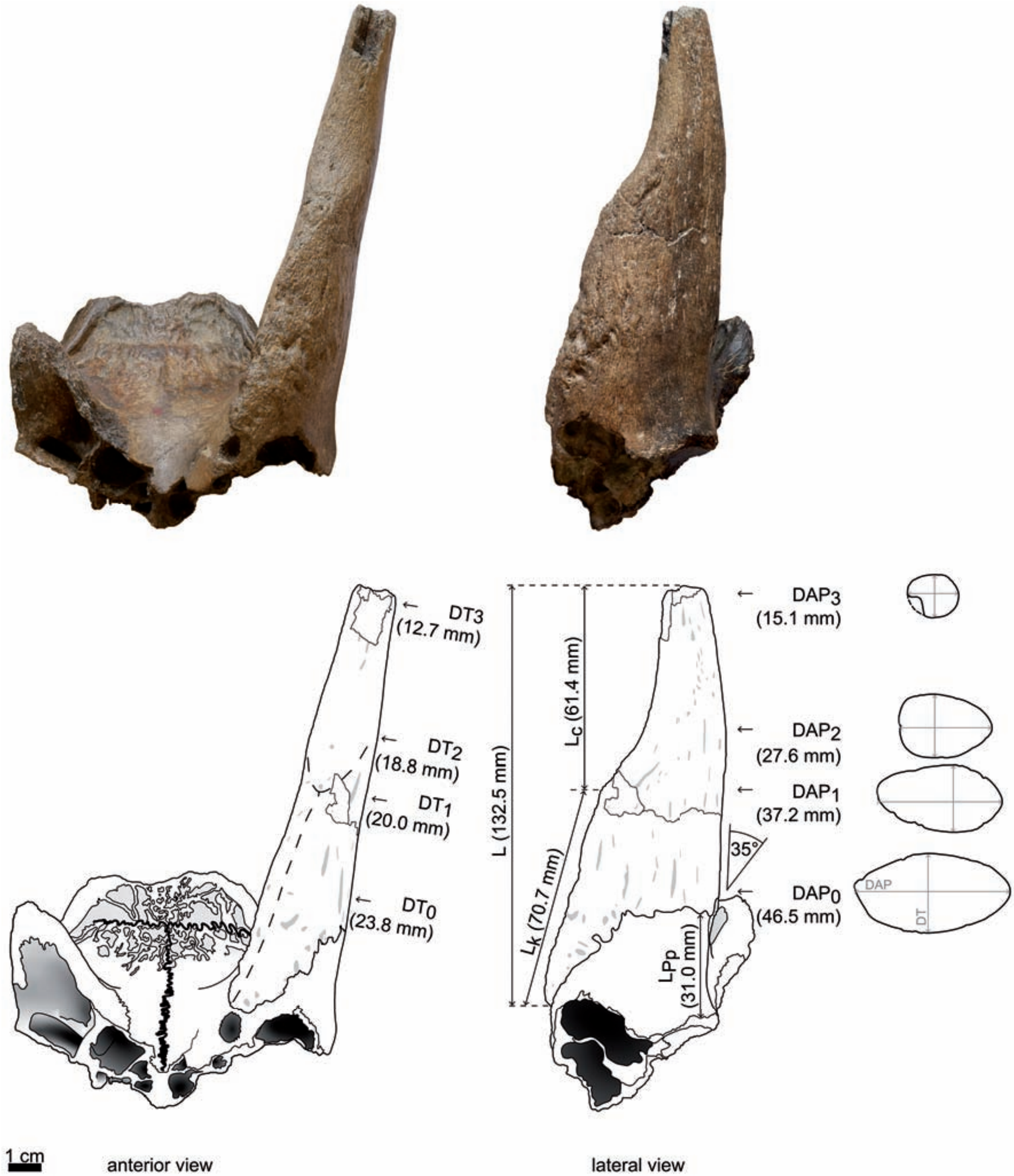


**Fig. 6.** Holotype of *Miotragocerus monacensis* from Oberföhring, calvarium with left horn core – BSPG 1923 I 9.

**Dentition** (Fig. 9): The teeth show the primitive morphology known from basal boselaphins. They are brachydont, the premolars are less molarized and have moderately thick and rugose enamel.

– Upper Molars: The M2/3 has a rather simple morphology. It is brachydont with a height/length ratio of ~0.84 and height/width ratio of ~0.78. The DTa is larger than the DTp. The metastyle is placed inward making the buccal wall slightly angled. Lingually, a weak entostyle can be present.

– Upper Premolars: The P4 is broad (DAP < DT) and has a triangular basal outline. It has small anterior and posterior styles, a central fold and a weak posterolingual cingulum. The P3 and P2 are elongated (DAP > DT). The prominent labial cone and the anterior style are narrow folds that are

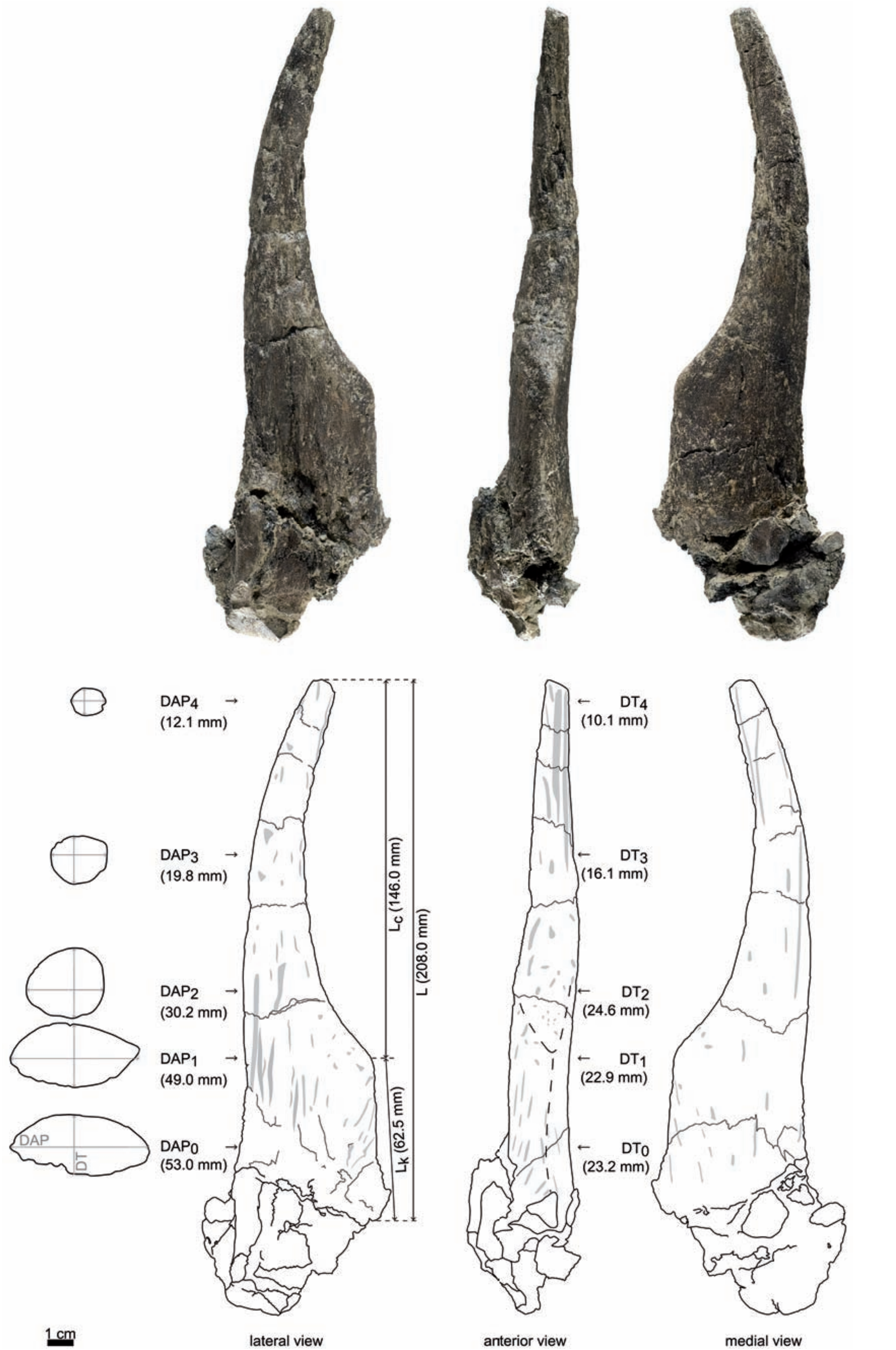


**Fig. 7.** Horn core, dext. of *Miotragocerus monacensis* from Hammerschmiede (Ham5) – GPIT/MA/3483.

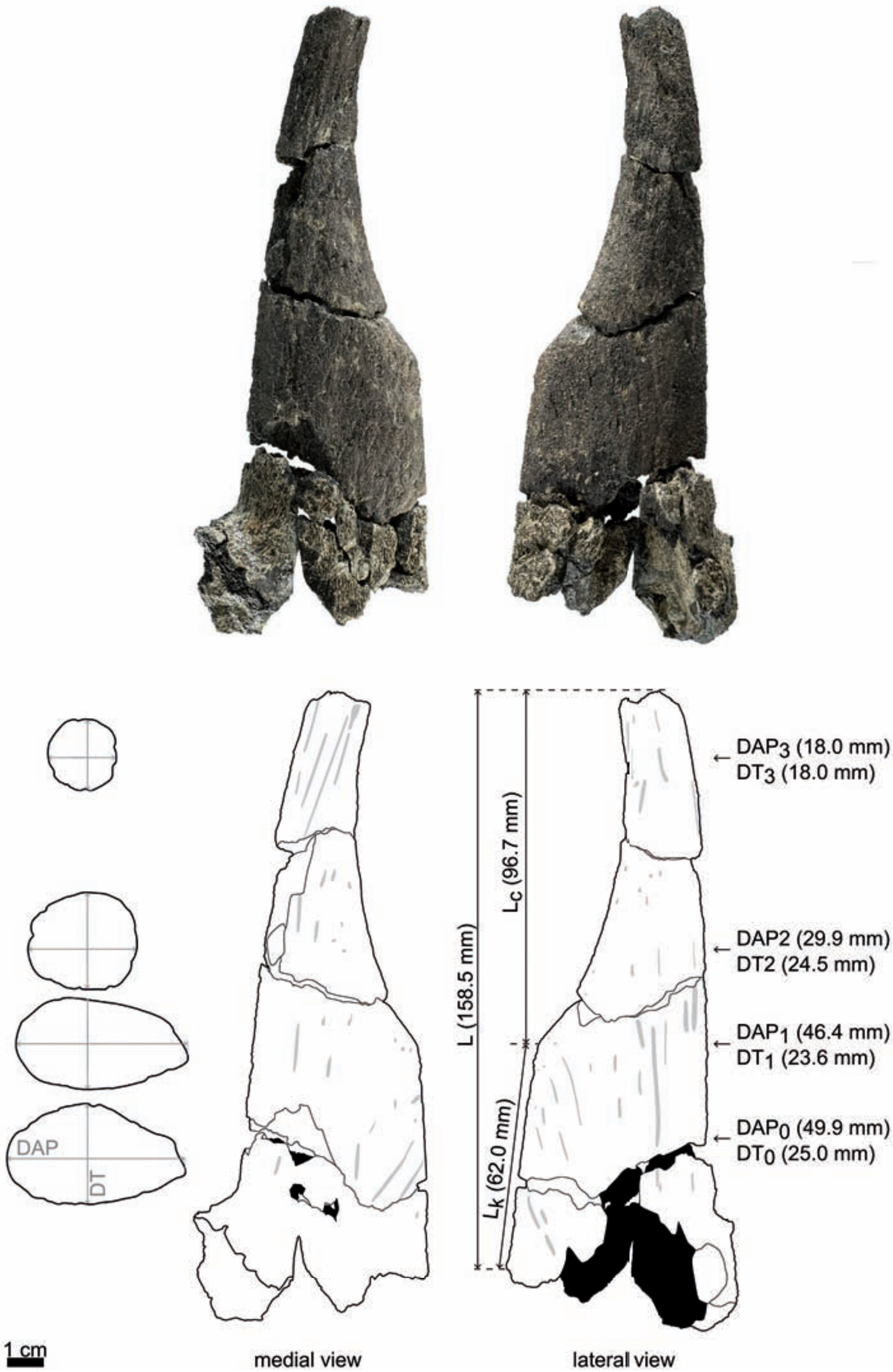


**Fig. 8.** Horn core, sin. of *Miotragocerus monacensis* from Hammerschmiede (Ham5) – GPIT/MA/3483.

very close to each other. The posterior style is not folded and ends as a sharp edge. The lingual wall is low compared to the high buccal wall. The P3 has a distinct fossa that is bordered by the anterolingual crista and the labial cone.

– Lower Molars: The buccal wall is deeply folded. The buccal lobes are sharply bent and slant towards posterior. Entoconid and metaconid are lingually slightly convex. The lingual side shows herring-bone enamel rugosities, which are also visible in other boselaphins. An ectostylid (basal pillar) is well developed. An unusual feature is a lingual cingulid at the lower molars (specimen BSPG 1521), likewise it is mentioned for some specimens referred to as *Tragoportax gaudryi* from

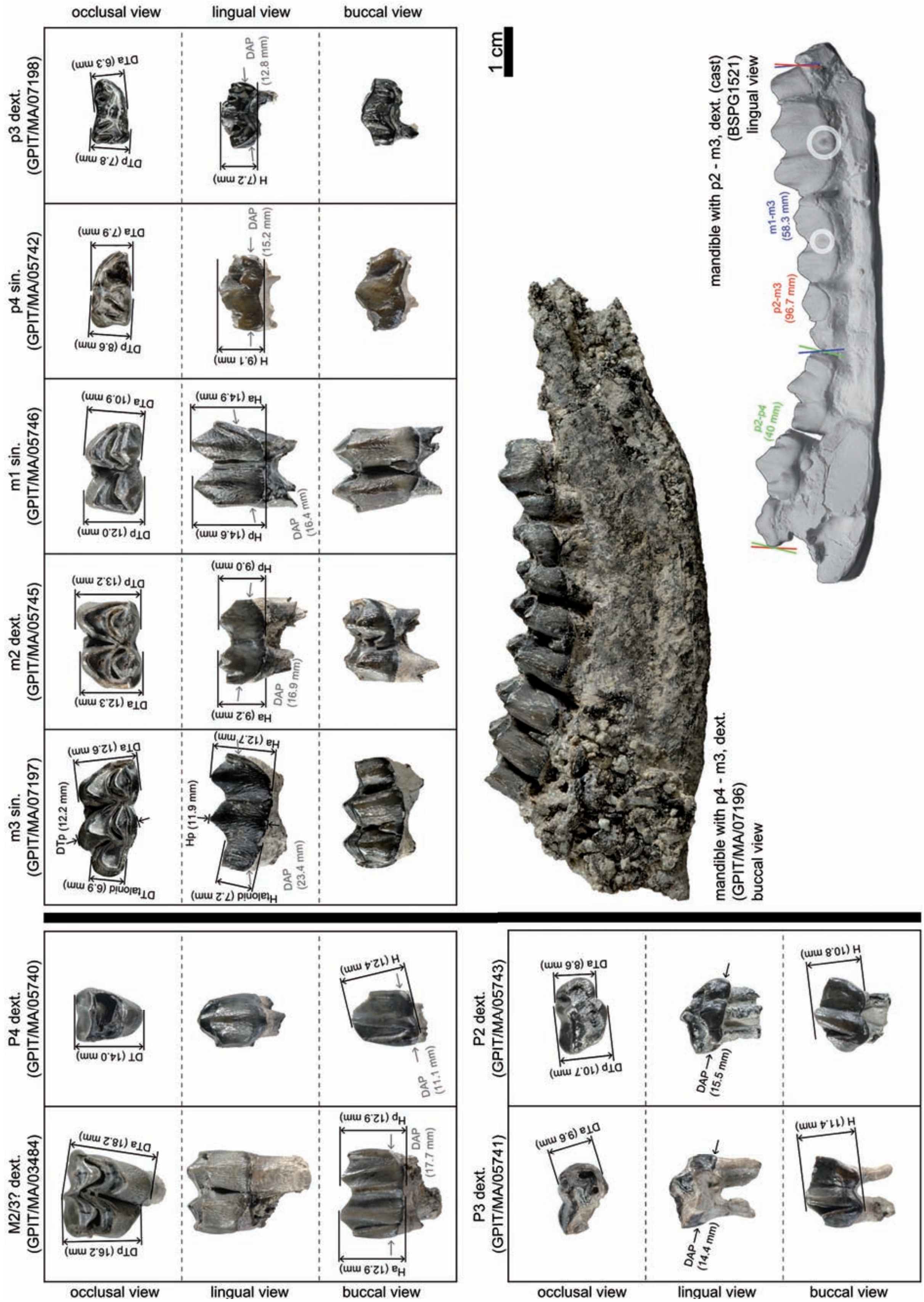
occlusal view
lingual view
buccal view
p3 dext. (GPIT/MA/07198)
DTa (6.3 mm)
DTp (7.8 mm)
DAP (12.8 mm)
H (7.2 mm)
p4 sin. (GPIT/MA/05742)
DTa (7.9 mm)
DTp (8.6 mm)
DAP (15.2 mm)
H (9.1 mm)
m1 sin. (GPIT/MA/05746)
DTa (10.9 mm)
DTp (12.0 mm)
Ha (14.9 mm)
Hp (14.6 mm)
DAP (16.4 mm)
m2 dext. (GPIT/MA/05745)
DTp (13.2 mm)
DTa (12.3 mm)
Hp (9.0 mm)
Ha (9.2 mm)
DAP (16.9 mm)
m3 sin. (GPIT/MA/07197)
DTa (12.6 mm)
DTp (12.2 mm)
DTtalonid (6.9 mm)
Ha (12.7 mm)
Hp (11.9 mm)
Htalonid (7.2 mm)
DAP (23.4 mm)
1 cm
mandible with p4 - m3, dext. (GPIT/MA/07196) buccal view
mandible with p2 - m3, dext. (cast) (BSPG1521) lingual view
p2-p4 (40 mm)
p2-m3 (96.7 mm)
m1-m3 (58.3 mm)
P4 dext. (GPIT/MA/05740)
DT (14.0 mm)
H (12.4 mm)
DAP (11.1 mm)
M2/3? dext. (GPIT/MA/03484)
DTa (18.2 mm)
DTp (16.2 mm)
Hp (12.9 mm)
Ha (12.9 mm)
DAP (17.7 mm)
P2 dext. (GPIT/MA/05743)
DTa (8.6 mm)
DTp (10.7 mm)
DAP (15.5 mm)
H (10.8 mm)
P3 dext. (GPIT/MA/05741)
DTa (9.6 mm)
DAP (14.4 mm)
H (11.4 mm)

**Fig. 9.**

Çorakyerler (Köhler 1987) and *Tragoportax rugosifrons* from Prochoma and Ravin des Zouaves n° 5 (Bouvrain 1994). The presence of this feature is assumed to be variable within the species, because Ham5 also provides lower molars which lack the lingual cingulid.

– Lower Premolars: The p4 shows almost no molarisation. The anterior part shows an anterior stylid, but a less developed anterior conid. The large anterior valley is confined by a distinct lingual cingulid. The posterolingual part of the tooth has three distinct folds (mesolingual conid, posterior cristid and posterior stylid) which enclose two narrow valleys (posterior and back valley). The mesolingual conid possesses a well-developed posterolingual cristid, but no anterolingual cristid. This plesiomorphic morphology resembles those of *Tragoportax gaudryi* from Çorakyerler (Köhler 1987) and *Miotragocerus* sp. (SMF-DD-4745) from Dorn-Dürkheim (Gentry & Kaiser 2009).

**Postcranial material** (Fig. 10): The astragalus is very large compared to those of the contemporaneous cervid *Euprox furcatus*. The size and morphology correspond very well with the astragali of *M. pannoniae* from Höwenegg. Its trochlear ridges are parallel, as well as the distal articular facets.

The proximal and distal ends of the right metacarpal presumably belong to the same individual. At the proximal articulation the synovial fossa between the two facets is deep and narrow incised on the posterior side. The ridge separating the two facets is long (~ 1/2 of $DAP_{pe}$) compared to the ridge of cervids (~ 1/3 of $DAP_{pe}$; Heintz 1970) and runs more sidewise along the lateral border of the incision. The distal metacarpal shows a well-defined sagittal groove on anterior side, which ends before the distal articulation. Generally, this feature appears more diminished in bovids, but is reminiscent of cervid metatarsals. A piercing channel goes through the anterior sagittal groove to the posterior side of the metacarpal.

The phalanges are robust. The phalanx proximalis has a rectangular proximal articulation. The anterior side of the shaft is slightly convex. The posterior surface is not preserved. The phalanx medialis is short and robust. Its proximal articulation has an approximately triangulated outline. The bulge anterior to the proximal articulation is very weak compared to cervids (Heintz 1970). Further, they are larger than phalanges of cervids from the same locality. Their dimensions fall within the lower part of the range of *M. pannoniae* from Höwenegg.

Considering the characters of bovid and cervid humeri described by Heintz (1970), the humerus fragment shows the following features on the distal articular facet. Cervid-like: the median gorge lies slightly above the external condyle. The external ridge is relatively sharp-edged and prominent. Bovid-like: the internal condyle rises hardly above the external ridge. Further, the internal condyle runs straight and is slightly inclined medially. Its transition to the median gorge is relatively abrupt.

The proximal ulna fragment is slender. The preserved upper shaft is narrow and presumably becomes rudimental distally, which is typical for bovids and cervids. Its size could correspond to *M. monacensis*. However, a clear attribution is not possible, due to the lack of taxonomically relevant characters.

**Taxonomic discussion:** The described horn core features coincide with the characters of the type of *M. monacensis* Stromer, 1928. Hence, an attribution to this species can be assured. Compared to the subadult holotype, the horn cores from Ham5 are longer and apparently belong to a full-grown individual. The described dentition and postcranial material show features of a medium sized basal boselaphin, and attributing this material to *M. monacensis* is very likely, most of the postcranial morphologies coinciding well with the supposed closely related *M. pannoniae*.

## 4.3. Unterföhring (Munich)

**Material:** Left horn core [BSPG 1921 I 34], distal end of a left humerus [BSPG 1921 I 501].

**Description:** Stromer (1928) already mentioned the specimen BSPG 1921 I 34 (Fig. 11), but did not describe it in detail. The horn core possesses the complete pedicle and parts of the orbital rim. It is moderately preserved due to fluvial transport and the distal end is lacking. The specimen has scars in the medioproximal part of the horn core. They are arranged in a row, suggesting that they could represent bite marks or other injuries formed during the life time. The horn core is positioned right above the orbit. The anterior keel runs anteriorly downward the pedicle, a characteristic feature of *Miotragocerus*. The straight keel of 107 mm in length is long in comparison to the horn cores described above. However, it is not very prominent. This is partially caused by its abrasion. Especially, the step in the keel is very weak. The basal cross-section is anteroposteriorly elongated (index = 1.75), the distal cross-section is rather rounded (index = 1.37). The sinus frontalis runs deep into the anterior part of the pedicle, up to the horn core basis.

The humerus fragment BSPG 1921 I 501 (Fig. 11) shows the same morphology as specimen GPIT/MA/07202 from Ham5 (see 4.2).

**Taxonomic discussion:** The horn core from Unterföhring shows some differences to the previously described specimens. The $DAP_0$ and $DAP_1$ of the horn cores of the holotype and Ham5 are slightly larger. However, the few differences can be interpreted as intraspecific variations, as mentioned by Stromer (1928). The fluvial abrasion blurred some characters, but the general morphology still fits to *M. monacensis*. Especially its narrow $DT_0$ differs from other Tragoportacini such as *M. pannoniae*. The humerus fragment from the same

**Fig. 9.** Dentition of *Miotragocerus monacensis* from Hammerschmiede. Isolated teeth (Ham5) – GPIT/Ma/03484, 05740-05743, 05745, 05746, 07197 and 07198; dextral mandible with p4-m3 – GPIT/MA/07196 and cast of a dextral mandible with p2-m3 (unknown layer) – BSPG 1521. BSPG 1521 is the only specimen that shows lingual cingulids on the m1 and m2 (marked with circles).

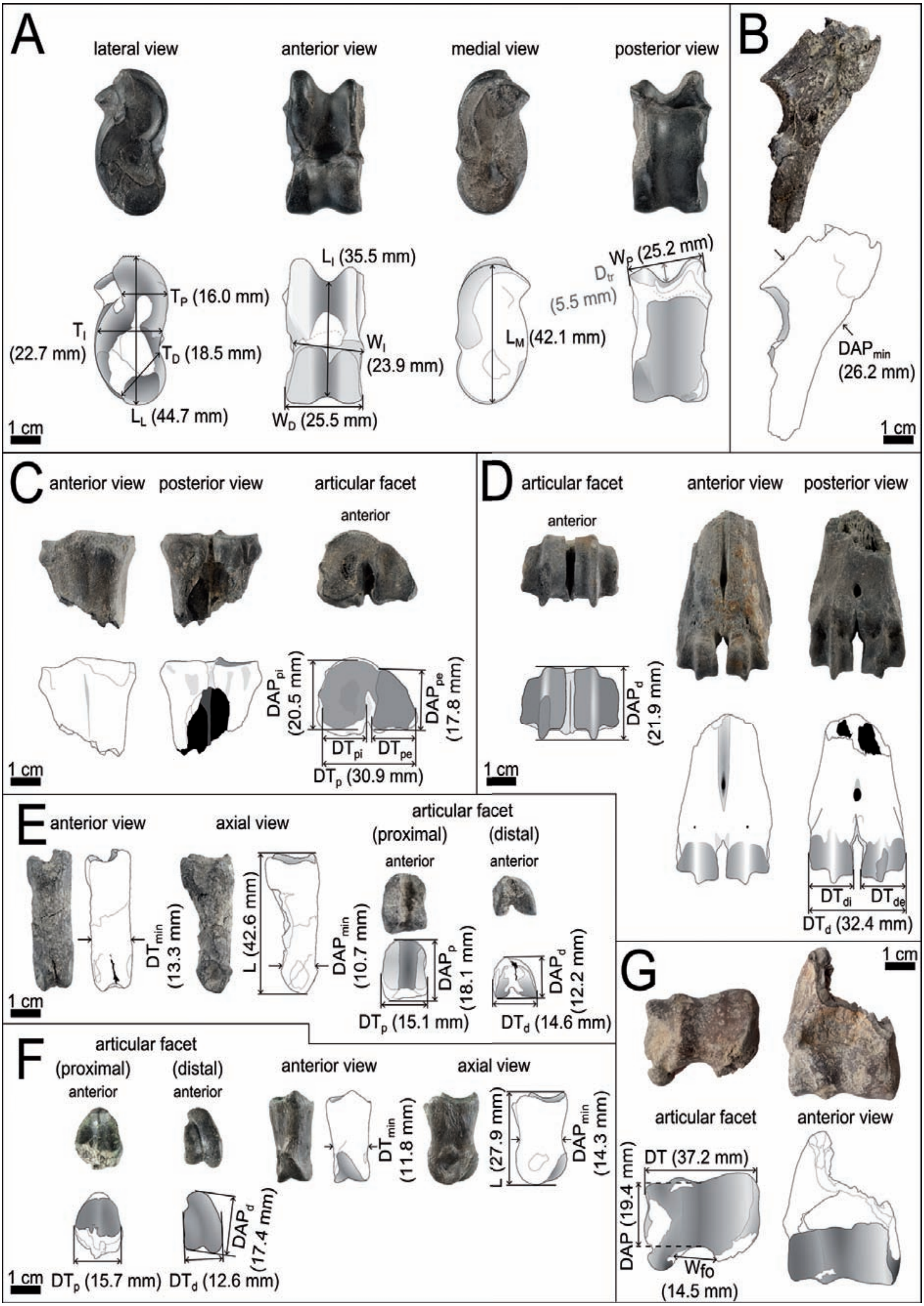
A
lateral view
anterior view
medial view
posterior view
L_l (35.5 mm)
T_P (16.0 mm)
T_l
(22.7 mm)
T_D (18.5 mm)
L_L (44.7 mm)
W_l
(23.9 mm)
W_D (25.5 mm)
L_M (42.1 mm)
W_P (25.2 mm)
D_tr
(5.5 mm)
1 cm
B
DAP_min
(26.2 mm)
1 cm
C
anterior view
posterior view
articular facet
anterior
DAP_pi
(20.5 mm)
DAP_pe
(17.8 mm)
DT_pi
DT_pe
DT_p (30.9 mm)
1 cm
D
articular facet
anterior
anterior view
posterior view
DAP_d
(21.9 mm)
1 cm
DT_di
DT_de
DT_d (32.4 mm)
E
anterior view
axial view
articular facet
(proximal)
(distal)
anterior
anterior
DT_min
(13.3 mm)
L (42.6 mm)
DAP_min
(10.7 mm)
DAP_p
(18.1 mm)
DAP_d
(12.2 mm)
DT_p (15.1 mm)
DT_d (14.6 mm)
1 cm
F
articular facet
(proximal)
(distal)
anterior
anterior
anterior view
axial view
DT_min
(11.8 mm)
L (27.9 mm)
DAP_min
(14.3 mm)
DAP_d
(17.4 mm)
1 cm
DT_p (15.7 mm)
DT_d (12.6 mm)
G
1 cm
articular facet
anterior view
DT (37.2 mm)
DAP (19.4 mm)
Wfo
(14.5 mm)

**Fig. 10.**

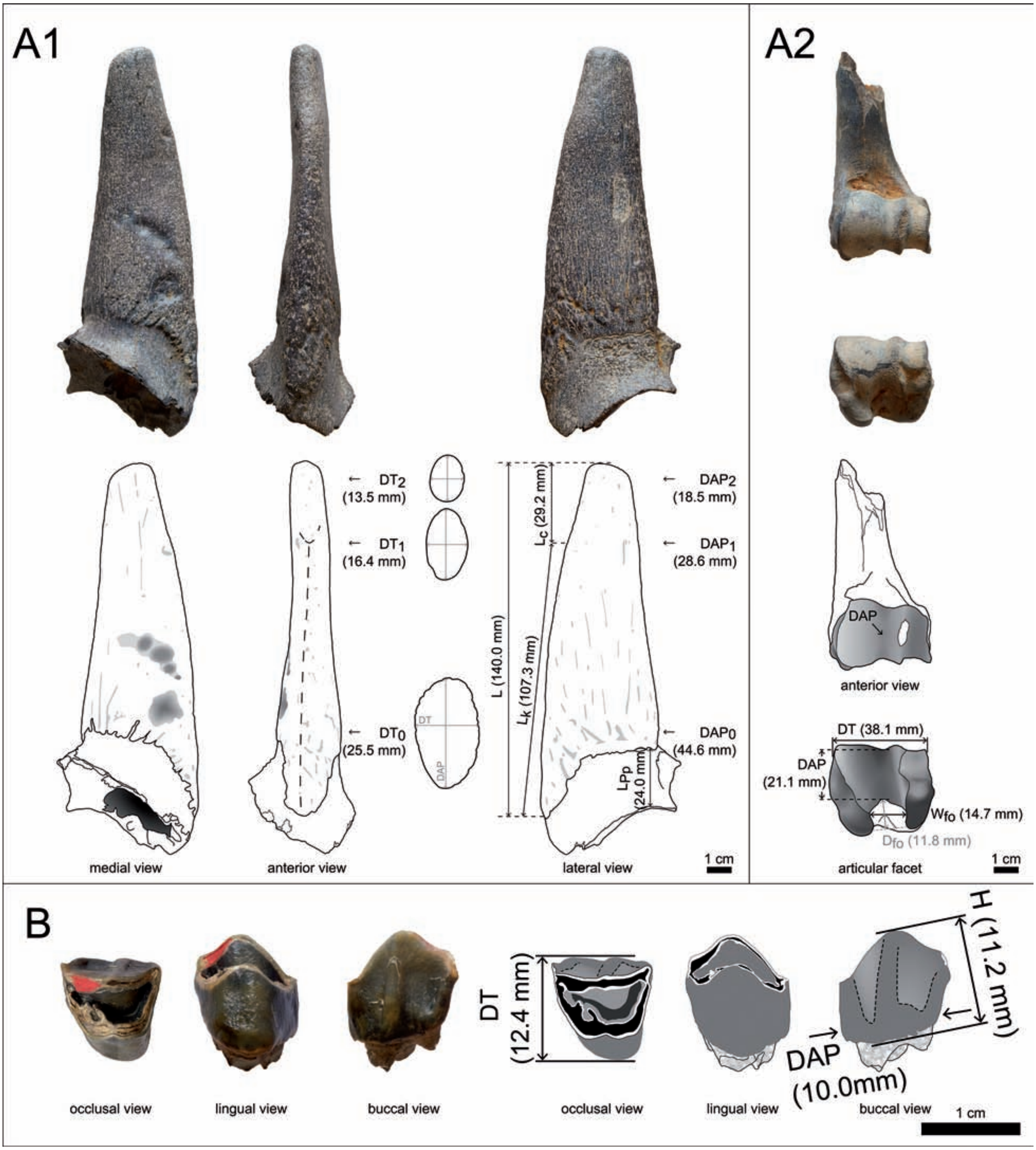


**Fig. 11. A1** – Horn core, sin. – BSPG 1921 I 54 and **A2** humerus, sin., distal end – BSPG 1921 I 501 of *Miotragocerus monacensis* from Unterföhring. **B** – P4 of Boselaphini indet. from Aumeister – BSPG 1926 V 34.

**Fig. 10.** Postcranial material of *Miotragocerus monacensis* from Hammerschmiede (HAM5). **A** – Astragalus, dext. – GPIT/MA/3485. **B** – Ulna, proximal end – GPIT/MA/05747. **C** – Metacarpal III+IV, dext., proximal end – GPIT/MA/3486. **D** – Metacarpal III+IV, dext., distal end – GPIT/MA/3486. **E** – Phalanx proximalis – GPIT/MA/3487. **F** – Phalanx medialis – GPIT/MA/07200; (G) Humerus, dext., distal end – GPIT/MA/07202.

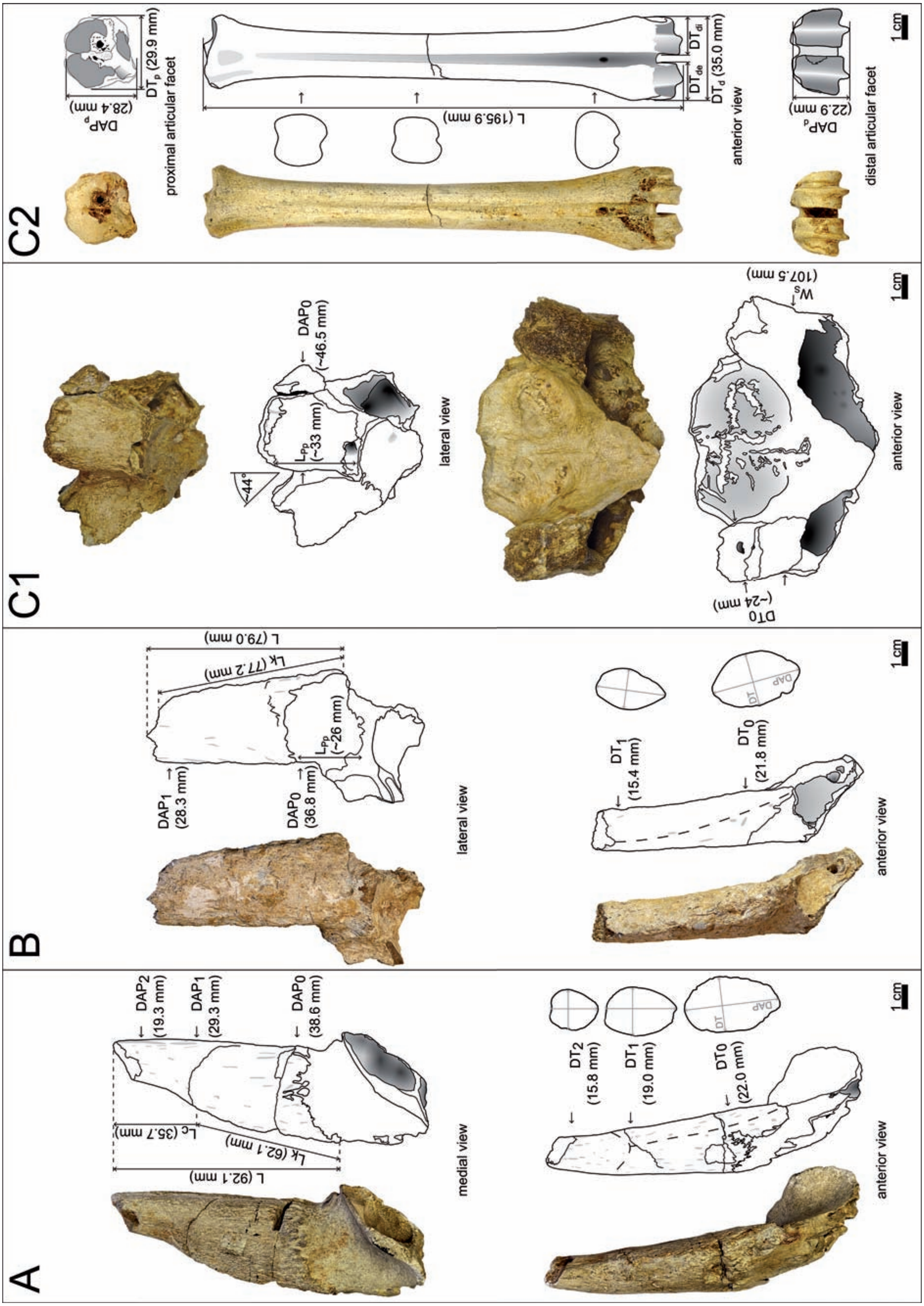
A
L (92.1 mm)
Lc (35.7 mm)
Lk (62.1 mm)
DAP2 (19.3 mm)
DAP1 (29.3 mm)
DAP0 (38.6 mm)
medial view
DT2 (15.8 mm)
DT1 (19.0 mm)
DT0 (22.0 mm)
DT
DAP
anterior view
1 cm
B
DAP1 (28.3 mm)
DAP0 (36.8 mm)
Lk (77.2 mm)
L (79.0 mm)
Lpp (~26 mm)
lateral view
DT1 (15.4 mm)
DT0 (21.8 mm)
anterior view
1 cm
C1
44°
Lpp (~33 mm)
DAP0 (~46.5 mm)
lateral view
DT0 (~24 mm)
Ws (107.5 mm)
anterior view
1 cm
C2
DAPp (28.4 mm)
DTp (29.9 mm)
proximal articular facet
L (195.9 mm)
DTde
DTdi
DTd (35.0 mm)
anterior view
DAPd (22.9 mm)
distal articular facet
1 cm

**Fig. 12.**

locality probably belongs to *M. monacensis*, too. It is smaller than the humeri of the related *M. pannoniae*, but its morphology coincides well.

### 4.4. Ober-Hollabrunn

**Material:** Calvarium with both pedicles [NHMW2014/0375/0001].

**Description and taxonomic discussion:** The calvarium (fig. 12C1) consists of the parietal bone and parts of the frontal with both pedicles. The transition to the horn core itself is just visible. As in the holotype from Oberföhring, the calvarium shows two very strong lateral ridges on the postcornual fronto-parietal, as well as a rough and depressed surface in between. The intercornual area of the frontal is elevated, as well. The sagittal suture and coronal suture are completely closed, indicating that this individual is full-grown. The sinus frontalis invades the basal horn core, where it is subdivided. Furthermore, the voluminous sinus invades the elevated intercornual frontal, in the same way as in the holotype. The pedicles are attached right above the inconspicuous orbital rims. Their posterior border is at an angle of ~44° with the dorsal fronto-parietal surface. The striking similarities in the morphology clearly attribute this specimen to *M. monacensis.* The dimensions of the holotype are identical or marginally smaller than the specimen from Ober-Hollabrunn (Table 1).

### 4.5. Nexing

**Material:** Right horn core with parts of the frontal [IPUW3193].

**Description and taxonomic discussion:** The specimen 3193 (Fig. 12B) consists of the proximal part of a right horn core with small parts of the frontal. The orbital rim is partially preserved. Its surface is weathered. The anterior keel is slightly torsioned and convex, whereas the posterior side is straight. The anterobasal keel extends far proximally. There is no step of the keel, probably because the distal part is missing. The frontal sinus reaches into the anterior part of the pedicles, but does not reach the horn core itself.

First, Thenius (1948) mentioned this specimen as *M. monacensis*, but later he described it as a young individual of *P. chantrei* (cf. Thenius 1956). This assumption has to be used with caution, because on one hand the species *P. chantrei* is not well defined and on another hand Thenius (1956) compared this specimen with other questionable horn cores from Lower Austria (see Chapters 4.6 and 5.1). However, its morphology could also fit to a smaller, probably subadult individual of *M. monacensis.* Therefore, we prefer to refer it as cf. *M. monacensis.*

### 4.6. Atzgersdorf/Mauer (Vienna)

**Material:** Right horn core [NHMW2014/0376/0001].

**Description:** The specimen NHMW2014/0376/0001 (Fig. 12A) consists of a well-preserved right horn core with the pedicle and parts of the frontal bone. The distal end of the horn core is not preserved. The proximal part of the horn core shows a characteristic anterior keel with a length of 62.1 mm. It is nearly straight, shows no torsion and extends anterobasal onto the pedicle. The basal cross-section is an anteroposteriorly elongated ellipsoid with an index of 1.75. The keel ends distally in a distinct step. Above this step, the cross-section becomes oval (index = 1.22) and the horn core slightly inclines medially. The sinus frontalis is narrow and invades the pedicle, but does not reach into the horn core. The intercornual frontal shows a minor elevation due to the less voluminous sinus frontalis.

**Taxonomic discussion:** The horn core morphology coincides with the holotype of *M. monacensis*, as already recognised by Stromer (1928). Its dimensions are slightly smaller than of the holotype. A largest difference is the narrow sinus frontalis in specimen NHMW2014/0376/0001 which was first considered by Thenius (1956). This feature led Thenius (1956) to attribute this specimen to *Protragocerus chantrei*, as was already done by Abel (1927). However, we confirm the identification of Stromer (1928) and interpret the differences in the frontal sinus volume as an intraspecific variation of *M. monacensis* depending on the ontogenetic stage of the individual (see General Discussion 5.1).

## 5. General discussion

The presence of the species *M. monacensis* in Hammerschmiede is definitely documented by the two horn cores. In general, the dentition and postcranial material is attributed to *M. monacensis* considering that this species is the only bovid documented in Hammerschmiede so far. Metrical (Table 7) and morphological similarities in the postcranial material with the closely related *M. pannoniae* from Höwenegg support this assumption. The morphology of horn cores, calvaria and/or dentition differentiates *M. monacensis* from the boselaphins *Protragocerus chantrei* Depéret, 1887 and *Austroportax latifrons* Sickenberg, 1929. Though, the horn core and frontal sinus of *M. monacensis* undergo major ontogenetic changes that have to be considered. Due to the scarce record of *P. chantrei* and *A. latifrons*, a differentiation based on postcranial characters is not possible yet.

**Fig. 12. A** – Horn core, dext. of *Miotragocerus monacensis* from Atzgersdorf/Mauer (Vienna) – NHMW2014/0376/0001. **B** – Horn core, dext. of cf. *M. monacensis* from Nexing – IPUW3193. **C1** – Calvarium of *M. monacensis* from Ober-Hollabrunn – NHMW2014/0375/0001 and **C2** metatarsal III+IV of ?*Austroportax latifrons* from Ober-Hollabrunn – IPUW (no sample-ID).

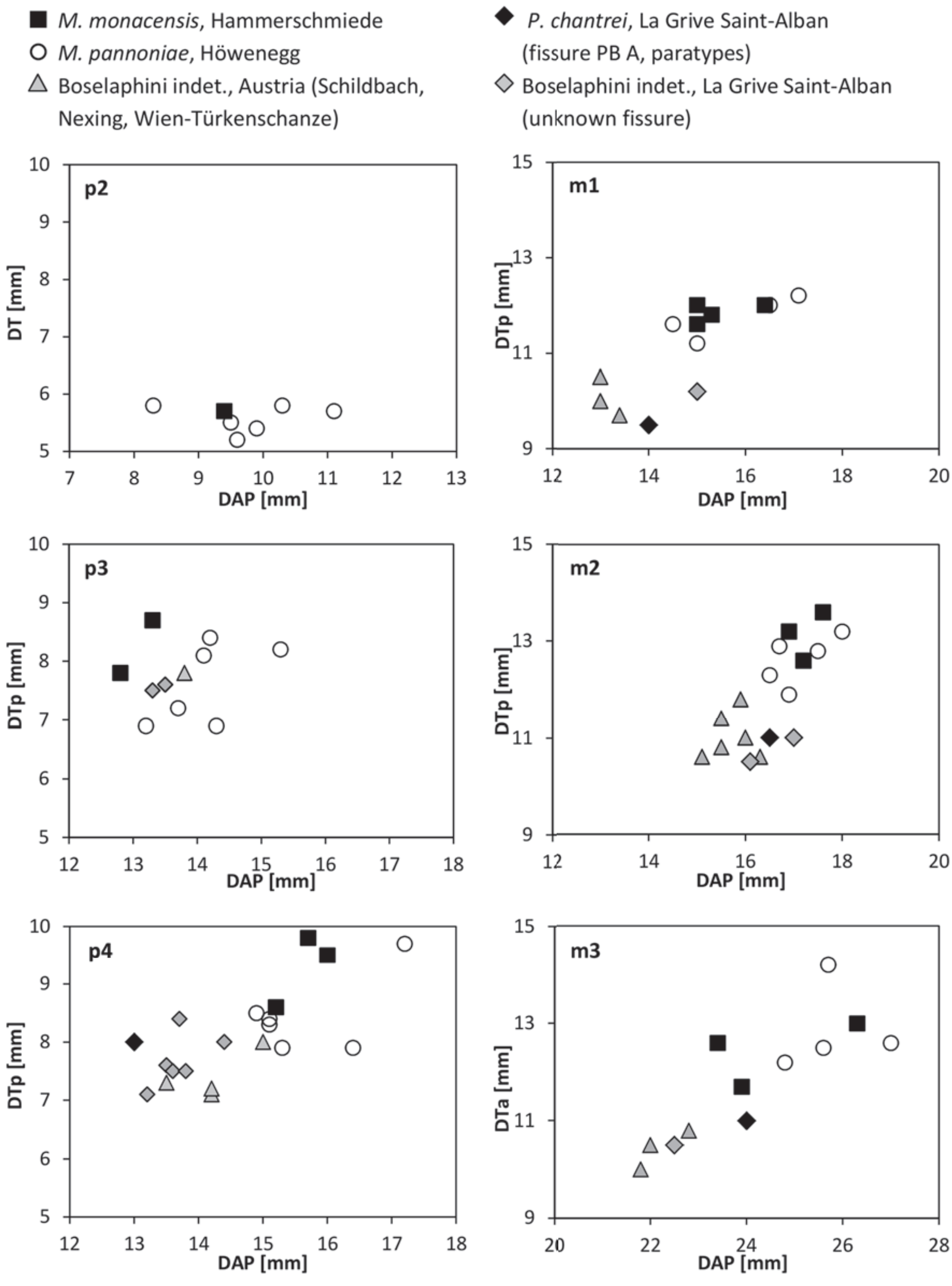


**Fig. 13.** Mandibular tooth dimensions of *Miotragocerus monacensis* (Hammerschmiede), *M. pannoniae* (Höwenegg), Boselaphini indet. (Schildbach, Nexing and Wien-Türkenschanze (Austria) from MOTTL 1961 and our own measurements) and *Protragocerus chantrei* from La Grive Saint-Alban (fissure PB A and unknown fissure, from MOYÀ-SOLÀ 1983 and ROMAGGI 1987).

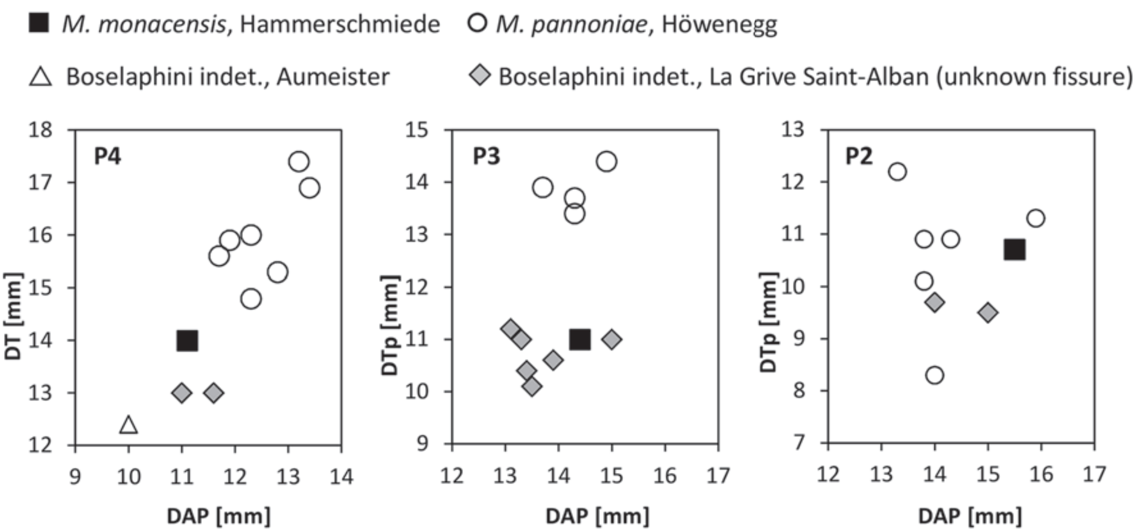


**Fig. 14.** Diameters of upper premolars (P2-P4) of *Miotragocerus monacensis* (Hammerschmiede), *M. pannoniae* (Höwenegg), Boselaphini indet. (Aumeister) and *Protragocerus chantrei* (La Grive Saint-Alban, unknown fissure, from Moyà-Solà 1983 and Romaggi 1987).

## 5.1. Comparison with *Protragocerus chantrei* Depéret, 1887

**Taxonomic discussion:** The species *Protragocerus chantrei* is based on a horn core from La Grive Saint-Alban (Isère, France), quarry Peyre et Beau, fissure PB A (Depéret 1887; Mein & Ginsburg 2002). However, the lack of taxonomically important characters of this specimen does not allow a satisfying definition of this species. The paratype material is an upper molar and a mandible with p4-m3 from the same fissure. The exact location of the additional specimens from La Grive attributed to *P. chantrei* (Moyà-Solà 1983; Romaggi 1987) is not stated. Depéret (1887) did not mention them and hence, they presumably come from later excavations in the quarry Lechartier, fissures L3 and L5 (Mein & Ginsburg 2002). Against the previous opinion, PB A seems to be older than L3 and L5. This is indicated by the appearance of *Deperetomys rhodanicus* in PB A (Depéret 1887; Mein & Ginsburg 2002; ?=*D. hagni*: De Bruijn et al. 1993; Prieto 2012). *D. hagni* has a short stratigraphic range in the middle Serravallian (Kälin & Kempf 2009; Prieto 2012). Instead, the *D. rhodanicus* is missing in the fissures L3 and L5, but *D. crusafonti* (taxonomy sensu van der Meulen et al. 2003) is documented (Mein & Ginsburg 2002). This points to a late Serravallian age (Casanovas-Villar et al. 2008). The proposed age differences between the assemblages, as well as the lack of distinct horn cores in L3+L5 make an evidence of *P. chantrei* in L3+L5 questionable. An attribution only based on dentition is problematic within boselaphins, so that the supposed L3+L5 material should be left as Boselaphini indet. When referring to *P. chantrei* only the holotype and paratype material from the fissure PB A is considered here. The teeth from Austria previously assigned to *P. chantrei* (Mottl 1961) are treated in the same way and called Boselaphini indet. The horn core specimens from Austria, previously assigned to *P. chantrei* (Thenius 1956) are assigned here to the species *M. monacensis*, cf. *M. monacensis*, cf. *A. latifrons* and ? *P. chantrei* (see below and Table 8).

**Comparison:** The description of Depéret (1887) and personal observations on a cast of the holotype of *P. chantrei* provide the following characters: the completely preserved horn core possesses an anterior keel and a weak posterior keel. Both keels are not stepped and are running from the base to top. The horn core is slightly curved medially. Its basal cross-section is rather oval and triangular compared to the transversally compressed cross-section in *M. monacensis.* The molar morphology is very similar to *M. monacensis.* Differences are observable in the p4 which shows a strong anterior conid that is not present in *M. monacensis.* A lingual cingulid is missing. The mandibular teeth dimensions (Fig. 13) of *P. chantrei* and of the unidentified boselaphins from La Grive (given by Moyá-Solá 1983; Romaggi 1987) and Austria (given by Mottl (1961) and our own measurements) are generally below *M. monacensis* and *M. pannoniae.* The dimensions of the upper teeth (Fig. 14) are close to each other, but *M. pannoniae* is rather larger-sized.

**Ontogeny:** Based on the horn core and the dentition of *P. chantrei*, its body size is slightly below that of *M. monacensis.* Accordingly, the holotype of *P. chantrei* shows some horn core features that fit to a juvenile *M. monacensis.* The horn core is keeled and the cross-section is slightly elongated. The sinus frontalis reaches neither into the horn core nor into the pedicle. This is why Abel (1927) and Thenius (1956) mistook the subadult *M. monacensis* from Atzgersdorf/ Mauer (NHMW2014/0376/0001) for *P. chantrei.* Stromer (1928) and Sickenberg (1929) attribute this specimen to a new species *M. monacensis*. Its horn core morphology clearly coincides with *M. monacensis*. However, differences in the frontal sinus of the holotype of *M. monacensis* and specimen NHMW2014/0376/0001 lead Thenius (1956) to determine it back to *P. chantrei*. Indeed, the difference of a very narrow frontal sinus in NHMW2014/0376/0001 compared to the voluminous frontal sinus in the holotype and the specimen from Ober-Hollabrunn is very significant (Fig. 15). However, after our observations these differences are based on ontogeny. An ontogenetic increase in frontal sinus volume is usual for many extant artiodactyls, even if sparsely treated in literature (Farke 2010; Badlangana et al. 2011). It is indicated that the growth can even continue during the adulthood (Farke 2010). An extension from the frontal into the pedicle or the horn core is very common. Some taxa even show a lateral and caudal extension up to the occipital region (e.g., Farke 2010; Badlangana et al. 2011). In bovids, it can be assumed that the frontal bone has to enlarge together with the attached horn cores in order to sustain their mechanical support. Consequently, there is more potential space for a frontal sinus. Its enlargement might be in order to reduce structural unnecessary bone and therefore cranial mass as it is assumed for several bovids (Farke 2010).

For *M. monacensis*, the holotype BSPG 1923I9 and the somewhat older individual from Ober-Hollabrunn (NHMW2014/0375/0001) clearly document that a slight increase in the frontal sinus volume does appear with age. Hence, the disputable specimen from Atzgersdorf/Mauer (NHMW2014/0376/0001) can join this ontogenetic series as a subadult individual of *M. monacensis*. Thereby, an enormous ontogenetic increase in the frontal sinus height of ~20 mm is documented (Fig. 15). Beside the narrow frontal sinus of specimen NHMW2014/0376/0001, the comparatively low dimensions of its horn core indicate the younger age of the individual. Beside the height of the frontal sinus, the ontogeny determines how deep the frontal sinus reaches into the pedicle and the horn core of *M. monacensis*. Hence, a large frontal sinus is not a characteristic feature for differentiating *M. monacensis* from *P. chantrei* as assumed by Thenius (1956).

In this respect, the determination of further related specimens from Lower Austria (NHMW2014/0373/0001, NHMW2014/0374/0001, IPUW1510; see Thenius 1956) is questionable. Therefore, the ontogenetic horn core development of *P. chantrei* described in Thenius (1956) remains unclear. The specimen NHMW2014/0373/0001 from Sommerein, figured in Thenius (1956) might fit to *P. chantrei*. It possesses a medially curved anterior keel without torsion and probably, without step. The apparent step rather seems to be damage. The distal part has a weak posterior edge. Its basal cross-section is rather oval and less elongated than in the specimens we assign to *M. monacensis*. The preserved distal part of the pedicle shows no intrusion of the frontal sinus. The specimen NHMW2014/0374/0001 (cast) from Ober-Hollabrunn is intensively abraded and no certain determination can be given yet. Its cross-section is oval and less elongated than the specimens we assign to *M. monacensis*. The anterior side has a weak keel and the posterobasal side is slightly compressed. A frontal sinus is present, despite the small size of the horn core. Specimen IPUW1510, figured in Thenius (1956) is close to *Austroportax latifrons* from the same locality (see Chapter 5.2). It shows an anterior keel, which is distinctly torsioned. This is an important similarity to *A. latifrons*. Its elongated and approximately triangulated basal cross-section supports the assignment. However, the distal step of the keel and the transition into an oval cross-section reminds of the morphology of *Miotragocerus*. Hence, this specimen is labeled as cf. *Austroportax latifrons*.

The determination of the Lower Austrian horn cores, previously attributed to *P. chantrei* (Thenius 1956) is questionable, because the horn cores are not well preserved, they lack taxonomically important characters or they even combine features of different taxa. However, the main problem is the unknown intraspecific horn core variability, especially in *A. latifrons* and *P. chantrei*. This problem is further enhanced by the definition of the species *P. chantrei* itself, whose holotype lack taxonomical important characters. Among the questionable horn cores, the specimen NHMW2014/0376/0001 from Atzgersdorf is an exception as it shows clear affinities to *M. monacensis*. Its narrow sinus frontalis is not a characteristic feature of *P. chantrei*, but a feature of young individuals of *M. monacensis*. The previous and revised taxonomic interpretations of the mentioned horn cores are summarised in Table 8.

## 5.2. Comparison with *Austroportax latifrons* Sickenberg, 1929

The skull and horn cores of *A. latifrons* are similar in size to those of *M. monacensis*. However, its cranium shows certain differences to *M. monacensis*. *A. latifrons* has a less pneumatized frontal and the intercornual area has a frontal sagittal ridge. *M. monacensis* is slightly elevated on the whole intercornual area and depressed in the parietal region. In contrast, *A. latifrons* shows two depressions laterally to the frontal ridge and has no depressed parietal. Its horn cores are proximally triangular and considerably compressed distally. The anterior keel has no step and shows a torsion.

A well-preserved metatarsal attributed to ?*A. latifrons* (Fig. 12C2) is known from Ober-Hollabrunn. Its determination is mainly based on its size and the absence of the lateral depression known from *M. pannoniae*. However, the metatarsal fragment of *M. monacensis* from Hammerschmiede has similar dimensions. Hence, an attribution to *M. monacensis* might be possible, which would challenge the relationship of *M. monacensis* with *M. pannoniae*.

## 5.3. Comparison with *Miotragocerus pannoniae* (Kretzoi, 1941) (Höwenegg)

A close relation of *M. monacensis* with *M. pannoniae* is supposed due to similarities in their skull and horn core morphology (Thenius 1948; Moyà-Solà 1983; Romaggi 1987).

Besides, a certain sexual dimorphism in *M. pannoniae* (keeled male horn cores and straight female horn cores without keel; Berg 1970; Romaggi 1987) should be taken into account. We restrict our comparison to male horn cores, since in *M. monacensis* only a keeled morphology is known. Characteristic features of the male horn cores shared by *M. monacensis* and *M. pannoniae* are: (1) The proximal part of the horn core is anteroposterior elongated and has a prominent keel; (2) The distal part of the horn core is oval to circular and

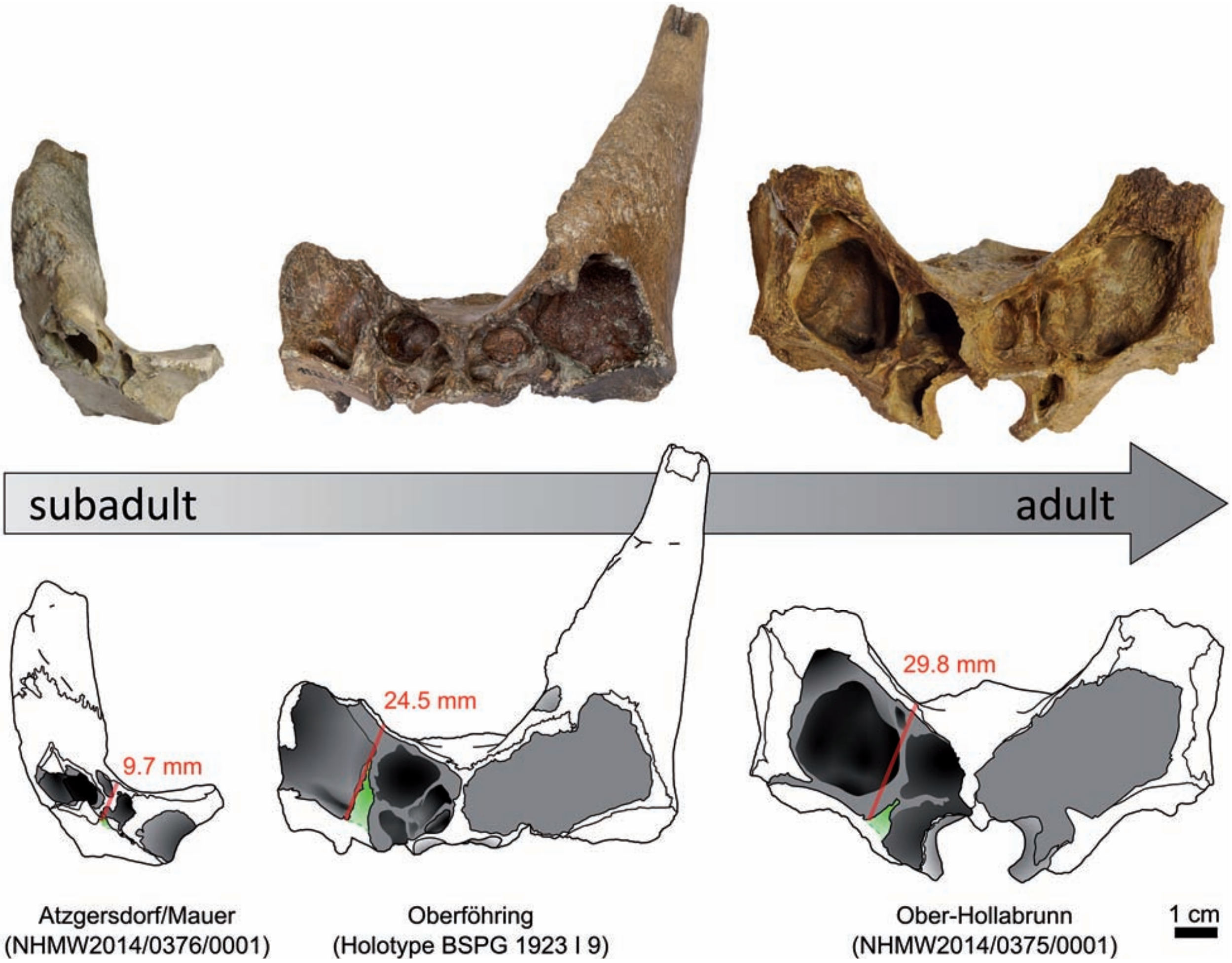


**Fig. 15.** Sinus frontalis in *Miotragocerus monacensis* from Atzgersdorf/Mauer (NHMW2014/0376/0001), Oberföhring (BSPG 1923 I 9) and Ober-Hollabrunn (NHMW2014/0375/0001). The height of the sinus frontalis is measured at the position of the supraorbital foramen (green).

is slightly curved forwards; (3) The horn cores are attached directly above the orbits.

When examining the horn cores of both taxa, it has to be considered that their morphology changes during ontogeny (THENIUS 1948). Hence, in juvenile specimens the characteristic anterior keel is not developed like in adults. These ontogenetic differences in morphology can be easily misinterpreted as interspecific differences. The following characters differentiate both taxa: the horn cores of *M. monacensis* are strongly inclined backward, their posterior border making an angle of 35-44° with the dorsal fronto-parietal surface; those of *M. pannoniae* are high angled with up to 70°. Lateral compressions of *M. pannoniae* at the distal part of the keel make the step sharp-edged and often more distinct than in *M. monacensis*. Hence, the transition to the circular part of the horn core appears to be swollen in *M. pannoniae*. The horn core of *M. monacensis* does not show any compressions at the distal part of the keel. Thereby, the keel reduces continuously above the step and the cross-section becomes circular. The distal part of the horn core of *M. monacensis* is more curved forward and shows smaller diameters. The distal cross-section is always nearly circular; in *M. pannoniae* it is oval or sometimes transversally compressed and more robust. Depending on the ontogenetic level, *M. pannoniae* can have several distinct steps (mostly 1-2) on the anterior keel, which are formed by anterobasal accumulation of bone. An accumulation of bone is observable in *M. monacensis*, too. However, the known specimens do not show any additional steps. Looking at the metrical differences between both taxa, the ontogeny of each specimen has to be considered, as well (THENIUS 1948). Especially, the basal diameters depend on the maturity of the individual (Fig. 16). However, the metric data indicate a different allometry of both taxa (Fig. 16). I.e. only $DAP_0$ increases and $DT_0$ remains relatively constant during the lifetime of *M. monacensis*, whereas in *M. pannoniae* both diameters increase noticeably.

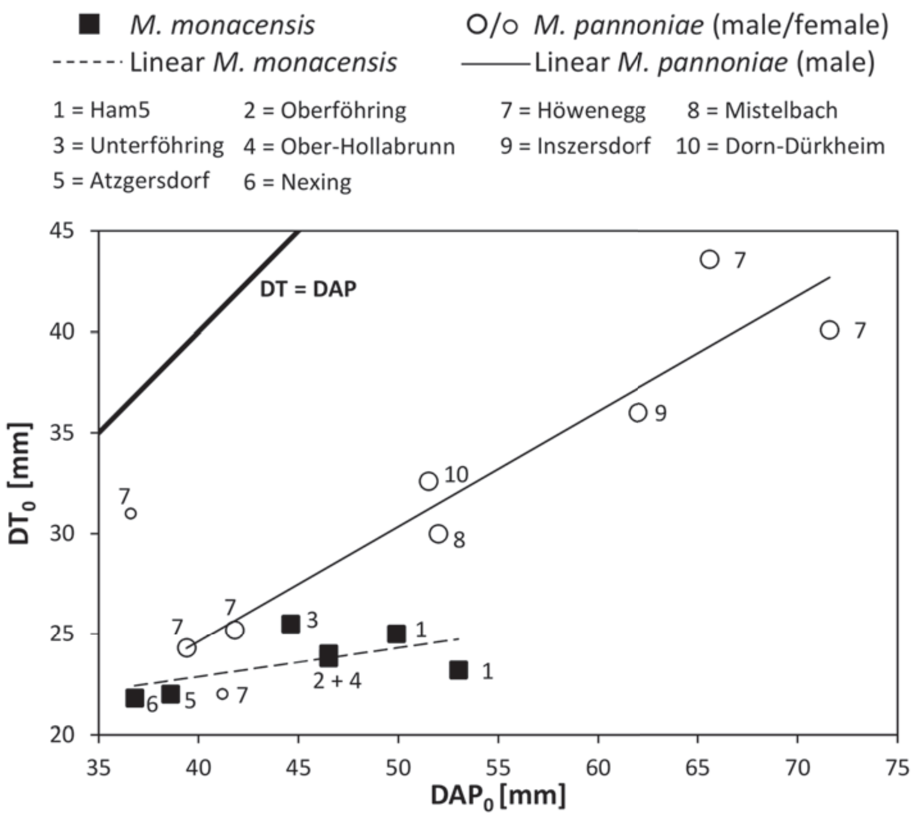


**Fig. 16.** Basal horn core diameters of *Miotragocerus monacensis*, cf. *M. monacensis*, *M. pannoniae* (from Thenius 1948a and our own measurements) and *Miotragocerus* sp. (from Gentry & Kaiser 2009). In order to simplify the graph, cf. *M. monacensis* (number 6) is assigned to *M. monacensis* and *Miotragocerus* sp. (number 10) is assigned to *M. pannoniae.* The allometry of each species is shown by linear regressions (DT on DAP). The ratio, where a circular cross-section (DT = DAP) is realized is plotted.

Consequently, *M. monacensis* cross-section of the proximal part of the horncore is more compressed ($DT_0 < 57\%$ of $DAP_0$) compared to the rather rounded cross-section in *M. pannoniae* ($DT_0 = 57\% – 67\%$ of $DAP_0$). Moreover, *M. monacensis* has rather lower $DAP_0$ than *M. pannoniae*. The highest $DAP_0$ measured for *M. monacensis* is 53 mm at the fully grown adult from Ham5. In contrast, *M. pannoniae* shows values up to ~72 mm (specimen SMNK-72/56 from Höwenegg). Overall, the horn cores of *M. monacensis* appear less robust than *M. pannoniae.*

In general, the dentition of *M. monacensis* is similar to those of *M. pannoniae* concerning the dimensions and the typical basal boselaphin morphology. The morphologies of the P3 and P4 of *M. monacensis* are identical to *M. pannoniae*. However, their dimensions (Fig. 14) are rather smaller. The size of the M2/3 is in the lower range of *M. pannoniae*, as well. Morphological differences are observable in the metaconule. In *M. pannoniae* the metaconule is well-rounded, similar to the shape of the protocone. In *M. monacensis* the base of the metaconule appears flattened. Hence, it is more angular than rounded. The dimensions (Fig. 13) and the morphology of

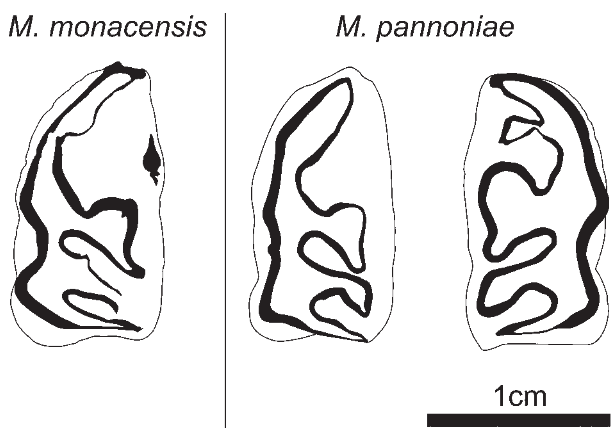


**Fig. 17.** Plesiomorphic occlusal surface of the p4 of *Miotragocerus monacensis* from Ham5 in comparison with the variable and sometimes more advanced molarisation of *M. pannoniae* from Höwenegg.

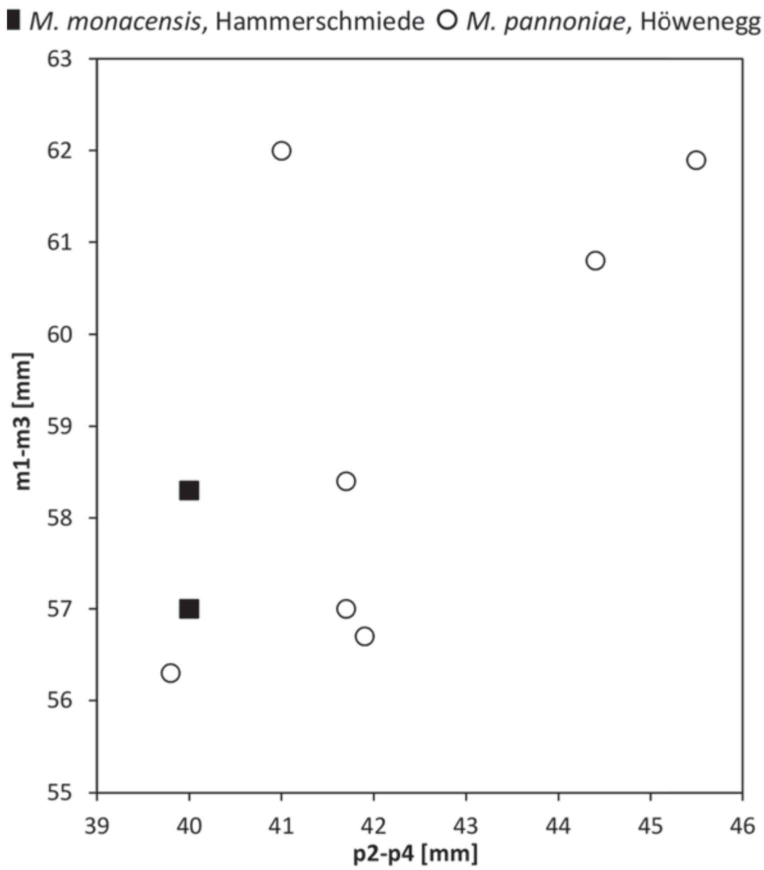


**Fig. 18.** Mandibular teeth proportions of *Miotragocerus monacensis* and *M. pannoniae* (from BERG 1970, and our own measurements).

the lower molars are similar to *M. pannoniae*. However, the lingual cingulids in *M. monacensis* can be well-developed or absent in all lower molars, whereas those of *M. pannoniae* are always absent. The dimensions of the lower premolars (Fig. 13) are very similar to *M. pannoniae*. However, there are some distinct morphological differences. *M. monacensis* p4 have a lingual cingulid, which is well-separated from the weakly developed anterior conid (Fig. 17). In contrast, there is no isolated lingual cingulid in *M. pannoniae*. The anterior conid of *M. pannoniae* is either well-developed and runs far lingually, or it is nearly absent like in the p4 of *M. monacensis* (Fig. 17). The mandibular tooth row dimensions (Fig. 18) of *M. monacensis* are in the lower range of *M. pannoniae*. In general, *M. monacensis* shows more plesiomorphic characters in dentition.

The metacarpal fragments of *M. monacensis* show only some minor differences to *M. pannoniae*. The cross-section of its proximal shaft is rather broadened compared to the V-shaped cross-section in *M. pannoniae* (Fig. 19). The cross-section of its distal shaft is rather compressed. Both species show an anterior sagittal groove on the distal shaft, which is more pronounced in *M. monacensis*. The astragals and the proximal and medial phalanges of both species are very similar and cannot be distinguished morphologically or metrically.

### 5.4. Further related specimen

Within the first description of *M. monacensis* by STROMER (1928), a dextral P4 [BSPG 1926 V 34] from Aumeister (Munich) is mentioned as paratype (Fig. 11). Its general morphology is similar to the P4 from Ham5. However, there are small differences in size. Considering the similar grade of the wear of both teeth, the P4 from Aumeister is slightly more brachydont. The DAP and DT are slightly smaller as well. Furthermore, the tooth is worn in different ways, particularly visible in the buccal view. Due to these differences and the fact that *M. monacensis* is not documented by a horn core in Aumeister, we prefer to label the specimen as Boselaphini indet.

Recently, HILLENBRAND et al. (2009) described isolated teeth and postcranial material as *Miotragocerus* sp. vel *Tethytragus* sp. from the locality Atzelsdorf (Lower Austria).

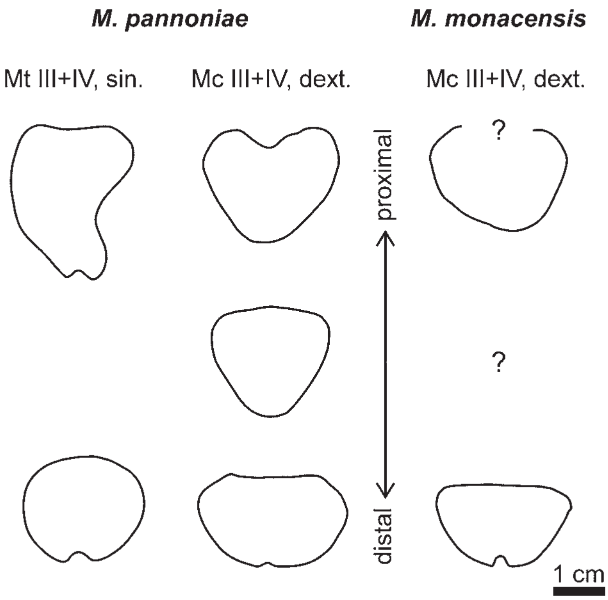


**Fig. 19.** Cross-sections of the metatarsal (SMNK-MI/9) and the metacarpal (SMNK-MI/42) of *Miotragocerus pannoniae* and the metacarpal of *M. monacensis* (GPIT/MA/03486). The proximal cross-section of the metatarsal of *M. pannoniae* shows the characteristic lateral depression.

Its deposits belong to the Hollabrunn-Mistelbach Formation and date to 11.2-11.1 Ma (Daxner-Höck & Göhlich 2009; Harzhauser 2009). These new findings are close to the geographical and stratigraphical appearance of *M. monacensis.* However, a reliable determination of this material was not possible yet. The type species of both genera (*Miotragocerus* and *Tethytragus*) are previously based mainly on horn cores. However, the bovid from Atzelsdorf is solely documented with dentition and postcranial material beside a small horn core fragment of less significance.

Now, the material of *M. monacensis* from Hammerschmiede makes a comparison of dentition and postcranial material possible. The dimensions of the postcranial elements (astragals, metacarpal) from Atzelsdorf are smaller than those of *M. monacensis* (Hammerschmiede) as well as *M. pannoniae* (Höwenegg; Table 7). Further, the morphometrics of the lower premolars and lower molars differ from *M. monacensis.* Their size is closer to the range of *P. chantrei* (La Grive) and Boselaphini indet. (La Grive and Lower Austria). The morphological differences are particularly visible in the p4. The anterior conid in the p4 from Atzelsdorf is well-developed in contrast to the very weak or absent anterior conid in *M. monacensis.* Due to these differences, an attribution of the bovid material of Atzelsdorf to *M. monacensis* can be excluded.

A specimen which has previously received little attention is a mandible fragment (p3-m2) of *Miotragocerus* sp. from the locality Tobel Oelhalde-Süd near Biberach (Baden-Württemberg, Germany) described by Sach (1999). The fossil was located beneath deposits containing evidences of the Nördlinger Ries meteoritic impact (Brockhorizont), which supposes an age of at least ~15 Ma (Abdul Aziz et al. 2010). An attribution to *Eotragus* is excluded based on morphometrical aspects (Sach 1999). As in other basal boselaphins, the enamel is rugose. Its morphology is similar to *M. pannoniae.* However, its dimensions (Table 5+6; Sach 1999) are slightly below *M. pannoniae* and *M. monacensis.*

A partially articulated skeleton of a further Middle to Late Miocene boselaphin comes from the location Tiefernitzgraben near Graz/Austria (collection museum Joanneum). Thenius (1952) described this specimen as *Tragocerus* sp. It shows similarities to *M. monacensis* concerning its tooth morphology and dimensions. In particular, its p4 resembles those of *M. monacensis* which shows a lingual cingulid and weak anterior conid. However, the horn cores differ significantly from other boselaphins. In particular, the medial side shows a depression which runs from the horn core base in distal direction. In general, the horn cores are anteroposterior elongated, low angled and curved backwards. The metatarsal does not possess the lateral depression known from *M. pannoniae.*

The mentioned fossils indicate the presence of further lineages of early bovids that are largely unknown yet. Thus, *Miotragocerus* sp. from Tobel Oelhalde-Süd might be a potential ancestor of *M. monacensis* or *M. pannoniae.* Furthermore, there seem to exist some contemporaneous boselaphins of similar size as indicated by the specimens of Aumeister and Tiefernitzgraben.

### 5.3. Stratigraphic significance

The presence of *M. monacensis* is stratigraphically restricted to a very short period, which makes this species interesting for biostratigraphy. The earliest record of *M. monacensis* comes from the Upper *Ervilia* biozone (early Late Sarmatian s.str.) of Atzgersdorf/Mauer (Vienna) and can be correlated to about 12.0 Ma (Harzhauser & Piller 2004). The locality Nexing shows deposits of the Upper *Ervilia* and the lowermost *Sarmatimactra* biozone (Grill 1968; Harzhauser & Piller 2009), but the exact stratigraphic position of the bovid material is unclear.

The last occurrence of *M. monacensis* is around the Sarmatian s.str.-Pannonian boundary at about 11.6 Ma, documented in the localities Hammerschmiede, Munich (Oberföhring and Unterföhring) and Ober-Hollabrunn. The disappearance of *M. monacensis* is accompanied with the disappearance of further large mammals like *Listriodon splendens.* Shortly thereafter, *M. pannoniae* and *Hippotherium primigenium* appear in the northern alpine region (Bechly et al. 2005; Daxner-Höck 1996; Rögl & Daxner-Höck 1996) indicating a major faunal change.

## 6. Conclusions

### 6.1. Taxonomic and stratigraphic implication

*Miotragocerus monacensis* is well-documented in the Southern German localities Oberföhring, Unterföhring and Hammerschmiede as well as in the Lower Austrian localities Ober-Hollabrunn, Atzgersdorf/Mauer and probably Nexing. Furthermore, Ober-Hollabrunn provides the holotype of *Austroportax latifrons*. The presence of *Protragocerus chantrei* in the Sarmatian s.str. of Austria is probably documented by a single horn core in Sommerein (Thenius 1956). Further evidences of *P. chantrei* are only based on dentition (Mottl 1961). Hence, the teeth from Nexing, Wien-Türkenschanze and Schildbach are rather labelled as Boselaphini indet. The other horn cores mentioned by Thenius (1956) rather belong to *M. monacensis* (Atzgersdorf/Mauer), cf. *M. monacensis* (Nexing) and ?*A. latifrons* (Ober-Hollabrunn).

The studied taxa show typical characters of basal boselaphins, which often resemble the morphology of cervids. In *M. monacensis*, these are particularly the less molarized premolars, the brachydonty and some plesiomorphic features in the preserved limb bones.

The observed cranial characters clearly distinguish *M. monacensis* from *P. chantrei* and the contemporaneous *A. latifrons*. However, a differentiation on postcranial material is still difficult due to the scarce record of the Middle Miocene boselaphins.

Likewise, the assumed close relation of *M. monacensis* to *M. pannoniae* is mainly based on their male skull and horn cores. The female horn core morphology, known in *M. pannoniae* (Berg 1970; Romaggi 1987), remains unknown in *M. monacensis*. Despite several similarities in the horn cores of the males, there are clear differences, as well. Further, the lower premolars of both taxa show major differences. Hence, their relation at the genus level remains disputable unless *M. monacensis* does show an evidence for the characteristic lateral depression in the metatarsal known from *M. pannoniae* (Thenius 1948b; Tobien 1953). Such an exceptional character is not known in any extant or fossil taxa.

Considering the rare record of *M. monacensis* and the Middle Miocene boselaphins in general, the new findings of *M. monacensis* from Hammerschmiede and the reinterpreted specimens from Lower Austria offer an important enlargement of the knowledge. Hence, the current revision of *M. monacensis* does not only improve the taxonomy. Furthermore, the newly described material improves our knowledge about the temporal range of this taxon. For *M. monacensis* only a short appearance is documented. Its first evidence comes from the upper Sarmatian s.str. (Upper *Ervilia* biozone) of Atzgersdorf/Mauer and probably Nexing (Upper *Ervilia* or *Sarmatimactra* biozone). Its last occurrence is during the Sarmatian s.str.-Pannonian boundary at about 11.6 Ma, documented in Hammerschmiede, the Munich localities and Ober-Hollabrunn. At the transition from the Middle to Late Miocene *M. monacensis* disappears and is replaced by the more evolved *M. pannoniae*. This faunal turnover seems to have biostratigraphic significance.

### 6.2. Ontogeny and sexual dimorphism of *Miotragocerus*

The ontogenetic development of the male horn core of *M. pannoniae* is well-documented since Thenius (1948). In juvenile specimens the characteristic anterior keel is not as pronounced as in adults. During the ontogenetic development *M. pannoniae* builds up several anterior steps on the keel due to anterobasal accumulation of bone. In contrast, the supposed adult *M. monacensis* from Hammerschmiede has only a single step. Additionally, an inter-specific allometry of the basal horn core is indicated between *M. monacensis* and *M. pannoniae*: *M. pannoniae* shows a significant horn core growth in the $DAP_0$ as well as in $DT_0$. In contrast, the $DT_0$ in *M. monacensis* remains small, while the $DAP_0$ is increasing. Further, *M. monacensis* does not achieve the high diameters of adult *M. pannoniae*. Another ontogenetic change is documented in the enormous volume growth of the frontal sinus in *M. monacensis*. The sinus height reaches from 9.7 mm in a subadult to 29.8 mm in an adult individual.

A distinct sexual dimorphism in *Miotragocerus* is shown by the horn cores of *M. pannoniae* from Höwenegg (Berg 1970; Romaggi 1987). The female horn cores are straight and have no anterior keel. They are mostly circular in cross-section. Few specimens are laterally depressed, but probably this is caused by sedimentary load. This horn core type can clearly be attributed to females, because complete individuals with foetus are known. Remarkably, apart from Höwenegg no other location has ever provided further specimens of female *M. pannoniae*. Likewise, there is no sexual dimorphism documented for *M. monacensis* yet. All known horn cores are attributed to male specimens, due to their keeled morphology known from the males of *M. pannoniae*. It is possible that a female individual is among the questionable boselaphin specimens from Austria, or the females are hornless at all.

The pronounced sexual dimorphism in *M. pannoniae* and in particular the presence of well-horned females suggests a complex social behaviour. An adaptation to inter- and intraspecific competition as well as the usage as defensive weapon as it is documented in several extant taxa (Packer 1983; Bubenik 1990) can be assumed.

### 6.3. Emended diagnoses

The emended diagnosis of *Miotragocerus monacensis* is based on the holotype from Oberföhring and the referred specimens from Southern Germany and Lower Austria. It extents the observations of Stromer (1928), Moyà-Solà (1983), and Romaggi (1987). The species-diagnosis of *Miotragocerus pannoniae* repeats the results of Kretzoi (1941), Berg (1970) and partially Romaggi (1987), and is implemented with our own observations on specimens from Höwenegg. The postcranial features described above (except those of the metatarsal in *M. pannoniae*) were excluded from the diagnoses due to their uncertain importance for taxonomy.

**Diagnosis of *Miotragocerus monacensis* Stromer, 1928:** *Miotragocerus monacensis* is a bovid (boselaphin) of intermediate size, close to that of a fallow deer. Its orbital rims are hardly protruding. The horn cores are attached on a short pedicle directly above the orbits and are strongly inclined backwards, their posterior edge making an angle of 35-44° with the dorsal fronto-parietal surface. They diverge moderately in the proximal half and slightly converge in the distal half. Proximally, the male horn cores show an anteroposterior elongated ellipsoid cross-section due to a prominent anterior keel. The anterior keel shows anterobasal accumulation of bone, which extends onto the anterior pedicle. The distal part of the horn core is nearly circular and curved forwards. The sinus frontalis invades the pedicle and the elevated intercornual part of the frontal. Depending on the ontogeny, the height of the sinus frontalis at the canalis supraorbitalis can be <10 mm or up to ~30 mm. The depressed postcornual fronto-parietal area is rugose and bordered by strong lateral ridges. The dentition is rather primitive, resembling that of cervids. The teeth are brachydont and have rugose enamel. The lower molars show herring-bone enamel rugosities on lingual side. The p4 is weakly molarized due to a weak anterior conid and the presence of a distinct lingual cingulid.

**Diagnosis of *Miotragocerus pannoniae* (Kretzoi, 1941):** The robust male horn cores are slightly inclined backward, their posterior edge making an angle up to 70° with the dorsal fronto-parietal surface. They have lateral compressions in the upper part of the keel making the distal step sharp-edged. The distal part of the horn core is hardly curved forwards and mostly oval in cross-section. Rare specimens can have a compressed distal cross-section. Depending on the ontogenetic stage, the anterobasal accumulation of bone can form several distinct steps (mostly 1-2) on the anterior keel. Female horn cores are straight and not keeled. They are mostly circular in cross-section. The p4 has no lingual cingulid, the anterior conid can be weak or well developed. The metatarsal is very characteristic due to a noticeable depression on the proximal lateral side.

**Differential diagnosis of *Miotragocerus monacensis* Stromer, 1928:** Further boselaphins of similar size are *Protragocerus chantrei* Depéret, 1887 and the contemporaneous *Austroportax latifrons* Sickenberg, 1929.

– *M. monacensis* is slightly larger than *P. chantrei*. Its horn cores are basally more compressed compared to the rather oval-triangulated horn core cross-section of *P. chantrei*. The horn cores of *M. monacensis* have only an anterior keel, in contrast to the horn core of *P. chantrei*, which is keeled on anterior and posterior sides. The keel of *M. monacensis* terminates distally in a distinct step, whereas both keels in *P. chantrei* are running from the base to top without any step.

– *M. monacensis* differs from *A. latifrons* in the basal horn core cross-sections. They are transversally compressed in contrast to the elongated-triangulated basal cross-sections of *A. latifrons*. The distal cross-sections in *M. monacensis* are circular in contrast to those of *A. latifrons*, which are considerably compressed. *M. monacensis* shows a distinct step in the anterior keel, which is not present in *A. latifrons*. The keel is nearly straight compared to the pronounced torsion in the keel of *A. latifrons*. In contrast to *Miotragocerus*, the intercornual area of *A. latifrons* has a frontal sagittal ridge. In *Miotragocerus* the whole intercornual area is slightly elevated and the postcornual fronto-parietal area is depressed. The latter area is bordered by distinct lateral ridges. In contrast, *A. latifrons* shows two depressions laterally to the frontal sagittal ridge. Its postcornual fronto-parietal area is neither depressed nor bordered by lateral ridges.

### Acknowledgements

The authors are indebted to Gertrud Rössner (BSPG), Ursula Göhlich (NHMW), Karl Rauscher and Doris Nagel (both IPUW), Eberhard Frey and Wolfgang Munk (both SMNK), Reinhard Ziegler (SMNS), Franz Dreyer (local museum of Immendingen), Philipe Havlik (GPIT), Erich Weber and Jürgen Rösinger (both University of Tuebingen, Zoological Collection) for access to the collections. For access to the Hammerschmiede pit, we cordially thank Ludwig Saur (Geiger Group). Many thanks to Davit Vasilyan and Manuela Aiglstorfer (both GPIT) for all kinds of support during the fieldwork, and, to the students from Tuebingen for the good work during the excavations. We acknowledge Henrik Stöhr and Regina Ellenbracht (both GPIT), who assisted during fieldwork and prepared the finds. For taking photographs, we are grateful to WOLFGANG GERBER (GPIT). Special thanks go to the reviewers DENIS GERAADS (Paris) and DIMITRIS S. KOSTOPOULOS (Thessaloniki) as well as to NIKOLAI SPASSOV (Sofia) and GERHARD DOPPLER (LfU) for helpful discussions. This research received financial support from the German Research Foundation (DFG, project B01550/16).

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Manuscript received: November 4th, 2014.
Revised version accepted by the Stuttgart editor: January 14th, 2015.

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## Appendix

**Table 1.** Horn core dimensions (in mm) of *Miotragocerus monacensis* (Hammerschmiede, Oberföhring, Unterföhring, Atzgersdorf/Mauer, Ober-Hollabrunn), cf. *M. monacensis* (Nexing), Boselaphini indet., cf. *Austroportax latifrons* and *A. latifrons* (all from Ober-Hollabrunn), ?*Protragocerus chantrei* (Sommerein), *Miotragocerus* sp. (Dorn-Dürkheim) and *M. pannoniae* (Höwenegg, Mistelbach, Inzersdorf, Altmannsdorf, Sopron). The citations of data sources are added within the table.

| Sample ID | description | L | $L_k$ | $L_c$ (preserved) | $DAP_0$ | $DT_0$ | $DAP_1$ | $DT_1$ | $DAP_2$ | $DT_2$ | $DAP_3$ | $DT_3$ | $DAP_4$ | $DT_4$ | horn core distance, antero-basal | horn core distance, postero-basal | angle between horn core and calvarium | $L_{Pp}$ | $L_{Pa}$ | $W_{fs}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***M. monacensis*, Ham 5 (GPIT), our measurements** | | | | | | | | | | | | | | | | | | | | |
| GPIT/MA/03483 | horn core, dextr. | 208.0 | 62.5 | 146.0 | 53.0 | 23.2 | 49.0 | 22.9 | 30.2 | 24.6 | 19.8 | 16.1 | 12.1 | 10.1 | - | - | - | - | - | - |
| GPIT/MA/03483 | horn core, sin. | 158.5 | 62.0 | 96.7 | 49.9 | 25.0 | 46.4 | 23.6 | 29.9 | 24.5 | 18.0 | 18.0 | - | - | - | - | - | - | - | - |
| ***M. monacensis*, Oberföhring (BSPG), our measurements** | | | | | | | | | | | | | | | | | | | | |
| BSPG 1923 I 9 | horn core, sin. | 132.5 | 70.7 | 61.4 | 46.5 | 23.8 | 37.2 | 20.0 | 27.6 | 18.8 | 15.1 | 12.7 | - | - | ~42,5 | ~76,3 | 35° | 31.0 | | 24.5 |
| ***M. monacensis*, Unterföhring (BSPG), our measurements** | | | | | | | | | | | | | | | | | | | | |
| BSPG 1921 I 34 | horn core, sin. | 140.0 | 107.3 | 29.2 | 44.6 | 25.5 | 28.6 | 16.4 | 18.5 | 13.5 | - | - | - | - | - | - | - | 24.0 | 22.2 | - |
| ***M. monacensis*, Atzgersdorf/Mauer (NHMW), our measurements** | | | | | | | | | | | | | | | | | | | | |
| 2014/0376/0001 | horn core, dext. | 92.1 | 62.1 | 35.7 | 38.6 | 22.0 | 29.3 | 19.0 | 19.3 | 15.8 | - | - | - | - | - | - | - | - | - | 9.7 |
| ***M. monacensis*, Ober-Hollabrunn (NHMW), our measurements** | | | | | | | | | | | | | | | | | | | | |
| 2014/0375/0001 | pedicles, dext.+ sin. | - | - | - | ~46.5 | ~24.0 | - | - | - | - | - | - | - | - | - | - | ~44° | ~33 | - | 29.8 |
| **cf. *M. monacensis*, Nexing (IPUW), our measurements** | | | | | | | | | | | | | | | | | | | | |
| 3193 | horn core, dext. | 79 | 77.2 | - | 36.8 | 21.8 | 28.3 | 15.4 | - | - | - | - | - | - | - | - | - | ~26 | - | - |
| **Boselaphini indet., Ober-Hollabrunn (NHMW), our measurements** | | | | | | | | | | | | | | | | | | | | |
| 2014/0374/0001 | horn core, dext. | 70.0 | - | - | 30.5 | 23.7 | 22.3 | 15.8 | - | - | - | - | - | - | - | - | - | - | - | - |
| **cf. *A. latifrons*, Ober-Hollabrunn (IPUW), our measurements** | | | | | | | | | | | | | | | | | | | | |
| 1510 | horn core, dext. | 120.0 | - | - | 39.8 | 24.2 | 33.4 | 21.0 | 16.7 | 15.2 | - | - | - | - | - | - | - | - | - | - |
| ***A. latifrons* (cast), Ober-Hollabrunn (NHMW), our measurements** | | | | | | | | | | | | | | | | | | | | |
| 2014/0377/0001 | horn core, dext. | - | 150.0 | - | 49.2 | 26.2 | - | - | - | - | - | - | 22.8 | 9.6 | - | - | 60° | - | - | - |
| **? *P. chantrei*, Sommerein (NHMW), our measurements** | | | | | | | | | | | | | | | | | | | | |
| 2014/0373/0001 | horn core, dext. | 82.0 | 33.0 | 53.0 | 37.6 | 24.2 | 32.0 | 21.3 | 23.3 | 16.7 | - | - | - | - | - | - | - | - | - | - |
| ***M. pannoniae*, Höwenegg (SMNK), our measurements** | | | | | | | | | | | | | | | | | | | | |
| U/44 | horn core, dext. | 241.0 | 159.0 | 87.0 | 65.6 | 43.6 | 37.5 | 22.3 | 30.2 | 22.7 | 21.9 | 17.8 | 17.0 | 14.7 | 5.4 | 77 | ~50° | 38.9 | ~29 | - |
| S/56 | horn core, dext. (juvenile) | 137.0 | - | - | 39.4 | 24.3 | $= DAP_0$ | $= DT_0$ | - | - | 27.6 | 19.8 | 14.5 | 6.3 | 12.2 | 54.4 | ~50° | 34.1 | - | - |
| S/56 | horn core, sin. (juvenile) | 133.0 | - | - | 41.8 | 25.2 | $= DAP_0$ | $= DT_0$ | - | - | 29.0 | 19.9 | 15.1 | 7.3 | - | - | - | 34.8 | 31.5 | - |
| 72/56 | horn core, dext. | 320.0 | 180.0 | 135.0 | 71.6 | 40.1 | 42.1 | 28.9 | 30.2 | 26.9 | 22.7 | 18.2 | 15.0 | 11.2 | - | - | - | 28.3 | 38.5 | - |
| 99/89 | horn core (female) | 195.0 | - | - | 36.6 | 31.0 | - | - | - | - | - | - | 18.3 | 19.3 | - | - | - | - | - | - |
| ***M. pannoniae*, Höwenegg (local museum Immendingen), our measurements** | | | | | | | | | | | | | | | | | | | | |
| W58 | horn core (female) | 269.0 | - | - | 41.2 | 22.0 | - | - | - | - | - | - | 12.6 | 6.9 | 7.5 | 52.9 | ~65° | 32.0 | 33.3 | - |
| ***M. pannoniae*, Höwenegg (SMNS), our measurements** | | | | | | | | | | | | | | | | | | | | |
| 47279a | horn core, dext. | 350.0 | ~170 | ~85 | - | - | - | - | - | - | - | - | - | - | 22.4 | - | - | 83.7 | 62.5 | - |
| ***Miotragocerus* sp., Dorn-Dürkheim 1, GENTRY & KAISER (2009)** | | | | | | | | | | | | | | | | | | | | |
| SMF-DD-2345 | horn core, dext. | 75.0 | - | - | 51.5 | 32.6 | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| ***M. pannoniae*, several localities, THENIUS (1948)** | | | | | | | | | | | | | | | | | | | | |
| Mistelbach | horn core, sin. | - | - | - | 52.0 | 30.0 | 47.2 | 26.2 | - | - | - | - | 26.0 | 24.5 | - | - | - | - | - | - |
| Inzersdorf | horn core, sin. | - | - | - | 62.0 | 36.0 | 40.0 | 27.0 | - | - | - | - | 25.0 | 23.0 | - | - | - | - | - | - |
| Altmannsdorf | horn core, sin. (juvenile) | - | - | - | $= DAP_1$ | $= DT_1$ | 47.8 | 23.6 | - | - | - | - | 20.8 | 20.0 | - | - | - | - | - | - |
| Sopron | horn core | - | - | - | $= DAP_1$ | $= DT_1$ | ~50,0 | 34.0 | - | - | - | - | 20.0 | 21.0 | - | - | - | - | - | - |

**Table 2.** Tooth row measurements (in mm) in *Miotragocerus monacensis* (Hammerschmiede), *M. pannoniae* (Höwenegg), *Protragocerus chantrei* (La Grive) and Boselaphini indet. (Tiefernitzgraben).

| Sample-ID | Lower tooth row | | | Upper tooth row | | |
|---|---|---|---|---|---|---|
| | p2-m3 | m1-m3 | p2-p4 | P2-M3 | M1-M3 | P2-P4 |
| ***Miotragocerus monacensis*** **, Ham5 (GPIT), our measurement** | | | | | | |
| GPIT/MA/07196 | ~97 | 57.0 | ~40 | - | - | - |
| ***Miotragocerus monacensis*** **, Hammerschmiede (BSPG), our measurement** | | | | | | |
| BSPG 1521 | 96.7 | 58.3 | 40.0 | - | - | - |
| ***Miotragocerus pannoniae*** **, Höwenegg (SMNK), BERG 1970** | | | | | | |
| II | 105.1 | 60.8 | 44.4 | 102.0 | 54.0 | 46.2 |
| L | - | 65.0 | - | 107.0 | 56.0 | 51.0 |
| Q | 105.0 | 62.0 | 41.0 | 93.0 | 53.4 | 42.2 |
| U | 100.8 | 58.4 | 41.7 | 93.0 | 50.1 | 41.5 |
| W | 95.2 | 56.3 | 39.8 | 90.0 | 51.0 | 42.0 |
| 56/20 | - | - | - | 90.0 | 50.0 | 40.0 |
| 436 | - | - | - | 92.5 | 52.0 | 42.0 |
| ***Miotragocerus pannoniae*** **, Höwenegg (SMNK), our measurement** | | | | | | |
| 100/59 | - | 57.0 | 41.7 | - | - | - |
| ***Miotragocerus pannoniae*** **, Höwenegg (local museum Immendingen), our measurement** | | | | | | |
| W58 | 97.9 | 56.7 | 41.9 | 93.8 | 53.2 | 58.9 |
| ***Miotragocerus pannoniae*** **, Höwenegg (SMNS), our measurement** | | | | | | |
| 47279a | 107.2 | 61.9 | 45.5 | - | - | - |
| ***Protragocerus chantrei*** **, La Grive (Museum Lyon), DEPÉRET (1887)** | | | | | | |
| Lgr471 | - | 55.0 | - | - | - | - |
| **Boselaphini indet. (one individual), Tiefernitzgraben near Graz (Museum Joanneum Graz), our measurement** | | | | | | |
| - (dextral) | 96.9 | 57.8 | 39.1 | - | - | 45.8 |
| - (sinistral) | 96.9 | 57 | 40.6 | - | ? ~47.2 | ~44.8 |

**Table 3.** Measurements (in mm) of upper molars in *Miotragocerus monacensis* (Hammerschmiede) and *M. pannoniae* (Höwenegg).

| Sample-ID | Tooth position | $H_a$ | $H_p$ | DAP | $DT_a$ | $DT_p$ |
|---|---|---|---|---|---|---|
| ***Miotragocerus monacensis*** **, Ham5 (GPIT), our measurement** | | | | | | |
| GPIT/MA/03484 | M2/3?, dext. | 12.9 | 12.9 | 17.7 | 18.2 | 16.2 |
| GPIT/MA/07199 | M2/3?, dext. | 14.2 | 14.2 | 17.0 | 18.1 | 15.8 |
| ***Miotragocerus pannoniae*** **, Höwenegg (SMNK), our measurement** | | | | | | |
| 122 | M1, sin. | 10.3 | 12.1 | 15.3 | 17.4 | 16.6 |
| U/44 | M1, dext. | - | - | 13.7 | 17.2 | 17.5 |
| U/44 | M2, dext. | - | - | 17.4 | 20.2 | 18.9 |
| U/44 | M3, dext. | - | - | 18.7 | 19.2 | 16.3 |
| Q1955 | M1, dext. | - | - | 14.9 | 17.9 | 17.9 |
| Q1955 | M2, dext. | - | - | 17.4 | 20.7 | 20.1 |
| Q1955 | M3, dext. | - | - | 19.6 | 20.7 | 17.9 |
| ***Miotragocerus pannoniae*** **, Höwenegg (SMNK), BERG (1970), supplemented with our own measurements** | | | | | | |
| II | M2, sin. | - | - | 18.2 | 20.8 | 19.2 |
| II | M3, sin. | - | - | 18.5 | 19.9 | 18.3 |
| R | M1, sin. | - | - | 13.5 | 15.1 | 16.2 |
| S | M1, dext. | - | - | 15.2 | 15.9 | - |
| S | M2, dext. | - | - | 15.0 | 17.5 | 16.5 |
| W58 | M1, sin. | 9.3 | 9.9 | 14.5 | 16.3 | 16.2 |
| W58 | M2, sin. | 12.4 | 12.6 | 16.1 | 18.6 | 17.1 |
| W58 | M3, sin. | 12.3 | 12.5 | 18.5 | 18.5 | 17.0 |
| 56/20 | M1, dext. | - | - | 14.3 | 19.8 | 19.5 |
| 56/20 | M2, dext. | - | - | 17.4 | 21.6 | 20.0 |
| 56/20 | M3, dext. | - | - | 18.2 | 20.1 | 18.0 |
| 431 | M2/3?, dext. | - | - | 16.5 | - | 19.7 |
| 431 | M3/2?, dext. | - | - | 18.1 | 20.4 | 19.1 |
| 431 | M1, sin. | - | - | 14.0 | - | 17.3 |
| 431 | M2, sin. | - | - | 16.2 | - | 19.3 |
| 431 | M3, sin. | - | - | 17.8 | 20.3 | 18.4 |
| 436 | M1 | - | - | 14.5 | 17.8 | 17.5 |
| 436 | M2 | - | - | 17.7 | 20.2 | 19.7 |
| 436 | M3 | - | - | 18.4 | 19.0 | 17.7 |

**Table 4.** Measurements (in mm) of upper premolars in *Miotragocerus monacensis* (Hammerschmiede), Boselaphini indet. (Aumeister, La Grive and Tiefernitzgraben) and *M. pannoniae* (Höwenegg).

| Sample-ID | Tooth position | H | DAP | DT | $DT_a$ | $DT_p$ |
|---|---|---|---|---|---|---|
| ***Miotragocerus monacensis*, Ham5 (GPIT), our measurement** | | | | | | |
| GPIT/MA/05740 | P4, dext. | 12.4 | 11.1 | 14.0 | - | - |
| GPIT/MA/05741 | P3, dext. | 11.4 | 14.4 | - | 9.6 | (~11) |
| GPIT/MA/05743 | P2, dext. | 10.8 | 15.5 | - | 8.6 | 10.7 |
| **Boselaphini indet., Aumeister (BSPG), our measurement** | | | | | | |
| BSPG 1926 V 34 | P4, dext. | 11.2 | 10.0 | 12.4 | - | - |
| ***Miotragocerus pannoniae*, Höwenegg (SMNK), our measurement** | | | | | | |
| 122 | P4, sin. | 12.4 | 12.3 | 16.0 | - | - |
| 122 | P3, sin. | 12.1 | 14.3 | - | 10.5 | 13.4 |
| U/44 | P4, dext. | - | 11.7 | 15.6 | - | - |
| U/44 | P3, dext. | - | 13.7 | - | 10.3 | 13.9 |
| Q1955 | P4, dext. | - | 12.3 | 14.8 | - | - |
| Q1955 | P3, dext. | - | 14.9 | - | 11.6 | 14.4 |
| Q1955 | P2, dext. | - | 14.3 | - | 10.0 | 10.9 |
| ***Miotragocerus pannoniae*, Höwenegg (SMNK), BERG (1970), supplemented with our own measurements** | | | | | | |
| II | P4, sin. | - | 13.4 | 16.9 | - | - |
| R | P2, sin. | - | 14.0 | 8.3 | - | - |
| W58 | P2, sin. | - | 13.8 | - | 9.9 | 10.9 |
| W58 | P3, sin. | - | 14.3 | - | 12.7 | 13.7 |
| W58 | P4, sin. | - | 12.8 | 15.3 | - | - |
| 56/20 | P2, dext. | - | 13.3 | 12.2 | - | - |
| 56/20 | P4, dext. | - | 13.2 | 17.4 | - | - |
| 431 | P2, dext. | - | 13.8 | 10.1 | - | - |
| 436 | P2 | - | 15.9 | 11.3 | - | - |
| 436 | P4 | - | 11.9 | 15.9 | - | - |
| **Boselaphini indet., La Grive (Museum Lyon), ROMAGGI (1987)** | | | | | | |
| Lgr 474 | P4 | - | 11 | 13 | - | - |
| Lgr 475 | P4 | - | 11.6 | 13 | - | - |
| Lgr 479 | P3 | - | 13.5 | 10.1 | - | - |
| Lgr 476 | P3 | - | 15 | 11 | - | - |
| Lgr 478 | P2 | - | 15 | 9.5 | - | - |
| **Boselaphini indet., La Grive (Museum Lyon), MOYÀ-SOLÀ (1983)** | | | | | | |
| - | P3 | - | 13.1 | 11.2 | - | - |
| - | P3 | - | 13.9 | 10.6 | - | - |
| - | P3 | - | 13.4 | 10.4 | - | - |
| - | P3 | - | 13.3 | 11 | - | - |
| - | P2 | - | 14 | 9.7 | - | - |
| **Boselaphini indet. (one individual), Tiefernitzgraben near Graz (Museum Joanneum Graz), our measurement** | | | | | | |
| 1399 | P2, dext. | - | 16.1 | - | 10.1 | 12 |
| 1399 | P3, dext. | - | 16.1 | - | 10.7 | 12.5 |
| 1399 | P4, dext. | - | ~12.7 | - | - | - |
| 1400 | P4, sin. | - | 13.2 | - | - | - |

**Table 5.** Measurements (in mm) of lower molars in *Miotragocerus monacensis* (Hammerschmiede), *M. pannoniae* (Höwenegg), Boselaphini indet. (Tiefernitzgraben, Nexing, Schildbach and Wien-Türkenschanze) and *Miotragocerus sp.* (Tobel Oelhalde-Süd).

| Sample-ID | Tooth position | $H_a$ | $H_p$ | $H_{talonid}$ | DAP | $DT_a$ | $DT_p$ | $DT_{talonid}$ |
|---|---|---|---|---|---|---|---|---|
| ***Miotragocerus monacensis*, Ham5 (GPIT), our measurement** | | | | | | | | |
| GPIT/MA/05744 | m1, sin. | 9.7 | 9.2 | - | 15.3 | 10.9 | 11.8 | |
| GPIT/MA/05745 | m2, dext. | 9.2 | 9 | - | 16.9 | 12.3 | 13.2 | |
| GPIT/MA/05746 | m1, sin. | 14.9 | 14.6 | - | 16.4 | 10.9 | 12 | |
| GPIT/MA/07197 | m3, sin. | 12.7 | 11.9 | 7.2 | 23.4 | 12.6 | 12.2 | 6.9 |
| GPIT/MA/07196 | m1, dext. | 8.9 | 7.6 | - | 15.0 | 10.3 | 11.6 | |
| GPIT/MA/07196 | m2, dext. | 12.3 | 11.5 | - | 17.2 | 12.0 | 12.6 | |
| GPIT/MA/07196 | m3, dext. | 14.5 | 12.8 | 7.5 | 23.9 | 11.7 | 11.5 | 6.6 |
| ***Miotragocerus monacensis*, Hammerschmiede (BSPG), our measurement** | | | | | | | | |
| BSPG 1521 | m1, dext. | - | 6.3 | - | 15.0 | 10.4 | 12.0 | |
| BSPG 1521 | m2, dext. | 9.2 | 8.6 | - | 17.6 | 13.2 | 13.6 | |
| BSPG 1521 | m3, dext. | 13.4 | 12.4 | 7.6 | 26.3 | 13.0 | 12.3 | 6.9 |
| ***Miotragocerus pannoniae*, Höwenegg (SMNK), Berg (1970)** | | | | | | | | |
| II | m1, sin. | - | - | - | 17.1 | 12.1 | 12.2 | |
| II | m2, sin. | - | - | - | 18.0 | 13.0 | 13.2 | |
| II | m3, sin. | - | - | - | 25.7 | 14.2 | 13.0 | - |
| Q | m1, sin. | - | - | - | 16.5 | 11.2 | 12.0 | |
| Q | m2, sin. | - | - | - | 17.5 | 13.0 | 12.8 | |
| Q | m3, sin. | - | - | - | 27.0 | 12.6 | 12.0 | 7.3 |
| U | m1, dext. | - | - | - | 15.0 | 10.3 | 11.2 | |
| U | m2, dext. | - | - | - | 16.7 | 12.6 | 12.9 | |
| U | m3, dext. | - | - | - | 25.6 | 12.5 | 12.2 | 7.2 |
| W58 | m1 | - | - | - | 14.5 | 11.2 | 11.6 | |
| W58 | m2 | - | - | - | 16.5 | 12.1 | 11.9 | |
| W58 | m3 | - | - | - | 24.8 | 12.2 | 11.5 | 6.8 |
| 432 | m2, dext. | - | - | - | 16.9 | 12.0 | 12.3 | |
| 432 | m3, dext. | - | - | - | 25.2 | - | 11.8 | 6.9 |
| **Boselaphini indet. (one individual), Tiefernitzgraben near Graz (Museum Joanneum Graz), our measurement** | | | | | | | | |
| 1399 | m1, dext. | - | - | - | 14.3 | 9.9 | 10.8 | |
| 1399 | m2, dext. | - | - | - | 17.2 | 12.2 | 12.1 | |
| 1399 | m3, dext. | - | - | - | 25 | 12.1 | 11.5 | 6.5 |
| 1400 | m3, sin. | - | - | - | 25.1 | 12.3 | 11.6 | 6.9 |
| ***Miotragocerus* sp., Tobel Oelhalde-Süd, near Biberach (SMNS), Sach (1999)** | | | | | | | | |
| 46656 | m1, dext. | - | - | - | ~14.5 | 9.4 | - | |
| 46656 | m2, dext. | - | - | - | 16.4 | 11.4 | 11.4 | |
| **Boselaphini indet., Nexing (NHMW), our measurement** | | | | | | | | |
| 2003z0089/0045 (Collection Lienhart) | m1, sin. | - | - | - | 12 | - | - | |
| 2003z0089/0045 (Collection Lienhart) | m2, sin. | - | - | - | 15.5 | 9.4 | 10.8 | |
| 2003z0089/0046 (Collection Lienhart) | m2, sin. | - | - | - | 15.1 | 10.2 | 10.6 | |
| 2003z0089/0047 (Collection Lienhart) | m3, sin. | - | - | - | 21.8 | 10 | 9.5 | 6.8 |
| 2014/0372/0001 | m1, sin. (cast) | - | - | - | 13 | 9.1 | 10.5 | |
| 2014/0372/0001 | m2, sin. (cast) | - | - | - | 15.5 | 10.3 | 11.4 | |
| **Boselaphini indet., Nexing (NHMW), Mottl (1961)** | | | | | | | | |
| ? (Collection Zapfe) | m1 | - | - | - | 13.4 | - | 9.7 | |
| ? (Collection Zapfe) | m2 | - | - | - | 16.3 | - | 10.6 | |
| **Boselaphini indet., Schildbach (NHMW), Mottl (1961)** | | | | | | | | |
| ? | m1 | - | - | - | 13.0 | - | 10.0 | |
| ? | m2 | - | - | - | 16.0 | - | 11.0 | |
| ? | m3 | - | - | - | 22.0 | 10.5 | - | |
| **Boselaphini indet., Wien-Türkenschanze (NHMW), Mottl (1961)** | | | | | | | | |
| ? | m2 | - | - | - | 15.9 | | 11.8 | |
| ? | m3 | - | - | - | 22.8 | 10.8 | - | |

**Table 6.** Measurements (in mm) of lower premolars in *Miotragocerus monacensis* (Hammerschmiede), *M. pannoniae* (Höwenegg), Boselaphini indet. (Tiefernitzgraben, Nexing and Schildbach) and *Miotragocerus sp.* (Tobel Oelhalde-Süd).

| Sample-ID | Tooth position | H | DAP | DT | $DT_a$ | $DT_p$ |
|---|---|---|---|---|---|---|
| ***Miotragocerus monacensis*, Ham5 (GPIT), our measurement** | | | | | | |
| GPIT/MA/05742 | p4, sin. | 9.1 | 15.2 | - | 7.9 | 8.6 |
| GPIT/MA/07196 | p4, dext. | 9.9 | 16.0 | - | 8.5 | 9.5 |
| GPIT/MA/07198 | p3, dext. | 7.2 | 12.8 | - | 6.3 | 7.8 |
| ***Miotragocerus monacensis*, Hammerschmiede (BSPG), our measurement** | | | | | | |
| BSPG 1521 | p2, dext. | 6.5 | 9.4 | 5.7 | - | - |
| BSPG 1521 | p3, dext. | 10.3 | 13.3 | - | 6.7 | 8.7 |
| BSPG 1521 | p4, dext. | 9.5 | 15.7 | - | 8.3 | 9.8 |
| ***Miotragocerus pannoniae*, Höwenegg (SMNK), our measurement** | | | | | | |
| U/45 | p4, sin | 8.8 | 14.9 | - | 8.1 | 8.5 |
| ***Miotragocerus pannoniae*, Höwenegg (SMNK), BERG (1970)** | | | | | | |
| II | p2, sin. | - | 10.3 | 5.8 | - | - |
| II | p3, sin. | - | 15.3 | 8.2 | - | - |
| II | p4, sin. | - | 17.2 | 9.7 | - | - |
| L | p2, sin. | - | 9.6 | 5.2 | - | - |
| Q | p2, sin. | - | 9.9 | 5.4 | - | - |
| Q | p3, sin. | - | 14.3 | 6.9 | - | - |
| Q | p4, sin. | - | 15.3 | 7.9 | - | - |
| U | p2, dext. | - | 9.5 | 5.5 | - | - |
| U | p3, dext. | - | 13.7 | 7.2 | - | - |
| U | p4, dext. | - | 15.1 | 8.3 | - | - |
| W58 | p2 | - | 8.3 | 5.8 | - | - |
| W58 | p3 | - | 13.2 | 6.9 | - | - |
| W58 | p4 | 11.1 | 15.1 | - | 7.8 | 8.4 |
| 432 | p3, dext. | - | 14.1 | 8.1 | - | - |
| ***Miotragocerus pannoniae*, Höwenegg (SMNS), our measurement** | | | | | | |
| 47279a | p2 | 7.1 | 11.1 | 5.7 | - | - |
| 47279a | p3 | 10.8 | 14.2 | 8.4 | - | - |
| 47279a | p4 | 10.8 | 16.4 | 7.9 | - | - |
| **Boselaphini indet. (one individual), Tiefernitzgraben near Graz (Museum Joanneum Graz), our measurement** | | | | | | |
| 1399 | p2, dext. | | 9.8 | 5.8 | - | - |
| 1400 | p2, sin. | | 10.5 | 5.8 | - | - |
| 1399 | p3, dext. | | 14.3 | | 6.9 | 8.2 |
| 1400 | p3, sin. | | 14.2 | | 6.3 | 8.1 |
| 1399 | p4, dext. | | 15.5 | | 8.2 | 9.1 |
| 1400 | p4, sin. | | 16 | | 7.6 | 9.4 |
| ***Miotragocerus* sp., Tobel Oelhalde-Süd, near Biberach (SMNS), SACH (1999)** | | | | | | |
| 46656 | p3, dext. | - | 12.5 | - | - | 8.0 |
| 46656 | p4, dext. | - | 13.9 | - | - | 8.5 |
| **Boselaphini indet., Nexing (NHMW), our measurement** | | | | | | |
| 2014/0372/0001 | p3, sin. (cast) | - | 13.8 | - | - | 7.8 |
| 2014/0372/0001 | p4, sin. (cast) | - | 15 | - | - | 8 |
| 2003z0089/0045 (Collection Lienhart) | p4, sin. | - | 13.5 | - | - | 7.3 |
| **Boselaphini indet., Nexing (NHMW), MOTTL (1961)** | | | | | | |
| ? (Collection Zapfe) | p4 | - | 14.2 | - | - | 7.2 |
| **Boselaphini indet., Schildbach (NHMW), MOTTL (1961)** | | | | | | |
| ? | p4 | - | 14.2 | - | - | 7.1 |

**Table 7.** Measurements of humeri, phalanges, astragali and metacarpals/metatarsals III+IV of *Miotragocerus monacensis* (Hammerschmiede and Unterföhring), *Protragocerus chantrei* (La Grive) and ? *Austroportax latifrons* (Ober-Hollabrunn).

Humeri

| Sample ID | description | DAP | DT | $W_{fo}$ | $D_{fo}$ |
|---|---|---|---|---|---|
| ***Miotragocerus monacensis*, Ham 5 (GPIT), our measurement** | | | | | |
| GPIT/MA/07202 | humerus, dext., distal end | 19.4 | 37.2 | 14.5 | - |
| ***Miotragocerus monacensis*, Unterföhring (BSPG), our measurement** | | | | | |
| BSPG 1921 I 501 | humerus, sin., distal end | 21.1 | 38.1 | 14.7 | 11.8 |
| ***Miotragocerus pannoniae*, Höwenegg (SMNS), our measurement** | | | | | |
| Höw 06/127 | humerus, dext., distal end | 22.5 | 39.8 | 16.2 | 16.5 |
| 47279a | humerus, sin. | ~22,5 | ~53,8 | - | - |

Phalanges

| Sample ID | description | L | $DAP_{min}$ | $DT_{min}$ | $DAP_p$ | $DT_p$ | $DAP_d$ | $DT_d$ |
|---|---|---|---|---|---|---|---|---|
| ***Miotragocerus monacensis*, Ham 5 (GPIT), our measurement** | | | | | | | | |
| GPIT/MA/03487 | phalanx proximalis | 42.6 | 10.7 | 13.3 | 18.1 | 15.1 | 12.2 | 14.6 |
| GPIT/MA/07201 | phalanx proximalis, distal end | - | - | - | - | - | 13.1 | 14.4 |
| GPIT/MA/07200 | phalanx medialis | 27.9 | 14.3 | 11.8 | - | 15.7 | 17.4 | 12.6 |
| ***Miotragocerus monacensis*, Hammerschmiede (BSPG), our measurement** | | | | | | | | |
| BSPG 1527 | phalanx proximalis, prox. end | - | - | - | 19.1 | ~15,9 | - | - |
| BSPG 1520 | phalanx medialis, prox. end | - | - | - | 20.3 | 15.9 | - | - |
| ***Miotragocerus pannoniae*, Höwenegg (SMNK), our measurement** | | | | | | | | |
| D54/D33 | phalanx proximalis | 38.0 | 11.1 | 13.6 | 17.9 | 16.3 | 12.4 | 13.9 |
| D54/D36 | phalanx proximalis | 39.2 | 11.5 | 14.7 | 18.4 | 15.1 | 12.2 | 13.5 |
| 787 | phalanx proximalis | 46.0 | 12.6 | 15.6 | 19.2 | 17.9 | 14.3 | 15.3 |
| 52 | phalanx proximalis | 47.0 | 12.5 | 15.4 | 20.7 | 17.7 | 13.9 | 14.5 |
| 772 | phalanx proximalis | 45.0 | 13.3 | 14.0 | 21.2 | 16.8 | 14.2 | 14.8 |

Astragali

| Sample ID | description | $L_L$ | $T_l$ | $T_P$ | $T_D$ | $L_l$ | $W_l$ | $W_D$ | $W_P$ | $D_{tr}$ | $L_M$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Miotragocerus monacensis*, Ham 5 (GPIT), our measurement** | | | | | | | | | | | |
| GPIT/MA/03485 | astragalus, dext. | 44.7 | 22.7 | 16.0 | 18.5 | 35.5 | 23.9 | 25.5 | 25.2 | 5.5 | 42.1 |
| ***Miotragocerus monacensis*, Hammerschmiede (BSPG), our measurement** | | | | | | | | | | | |
| BSPG 1522 | astragalus, dext. | - | 21.6 | - | 18.4 | ~35,1 | 23.1 | 25.1 | - | - | 40.2 |
| ***Miotragocerus pannoniae*, Höwenegg (SMNK), our measurement** | | | | | | | | | | | |
| 58/55 | astragalus, dext. | 41.9 | 21.7 | 16.9 | 17.5 | 33.1 | 24.4 | 27.1 | 27.1 | 5.3 | 39.6 |
| 459 | astragalus, dext. | 45.0 | 24.5 | 17.4 | 20.0 | 35.8 | 26.3 | 29.4 | 29.5 | 5.6 | 42.9 |
| 813/59 | astragalus, dext. | 41.8 | 22.4 | 15.6 | 19.4 | 33.0 | 23.5 | 25.1 | 25.4 | 5.3 | 38.5 |
| ***Protragocerus chantrei*, La Grive (Museum Lyon), Depéret 1887** | | | | | | | | | | | |
| - | astragalus | 40.0 | - | - | - | - | - | 25.0 | - | - | - |

Metacarpal/Metatarsal III+IV

| Sample ID | description | L | $DAP_{min}$ | $DT_{min}$ | $DAP_{pe}$ | $DAP_{pi}$ | $DT_p$ | $DT_{pe}$ | $DT_{pi}$ | $DAP_d$ | $DT_d$ | $DT_{de}$ | $DT_{di}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Miotragocerus monacensis*, Ham 5 (GPIT), our measurement** | | | | | | | | | | | | | |
| GPIT/MA/03486 | metacarpal, dext., prox. end | - | - | - | 17.8 | 20.5 | 30.9 | 14.3 | 14.3 | - | - | - | - |
| GPIT/MA/03486 | metacarpal, dext., distal end | - | - | - | - | - | - | - | - | 21.9 | 32.4 | 14.7 | 14.9 |
| ***Miotragocerus monacensis*, Hammerschmiede (BSPG), our measurement** | | | | | | | | | | | | | |
| BSPG 1523 | metacarpal, distal end | - | - | - | - | - | - | - | - | 19.8 | ~31,7 | 15,3 ($DT_{di}$?) | - |
| BSPG 1519 | metatarsal, dext., prox. end | - | - | - | - | 26.1 | 30.3 | - | - | - | - | - | - |
| ***Miotragocerus pannoniae*, Höwenegg (SMNK), our measurement** | | | | | | | | | | | | | |
| MI/42 | metacarpal, dext. | 196.0 | 16.1 | 22.7 | 18.6 | 23.3 | 34.6 | 16.0 | 16.2 | 23.2 | 34.7 | 15.9 | 15.6 |
| D54/D13 | metacarpal, sin. | 198.0 | 17.1 | 21.4 | 16.9 | 20.6 | 32.7 | 12.6 | 14.2 | 22.2 | 31.2 | 14.0 | 13.2 |
| U78 | metacarpal, sin. | 209.0 | 16.0 | 21.4 | 17.4 | 20.3 | 33.1 | 13.3 | 16.2 | 23.1 | 33.0 | 15.3 | 15.4 |
| MI/9 | metatarsal, sin. | 208.0 | 17.5 | 14.5 | 28.1 | 29.4 | 30.8 | - | - | 23.3 | 35.1 | 16.5 | 15.6 |
| **? *Austroportax latifrons*, Oberhollabrunn (IPUW), our measurement** | | | | | | | | | | | | | |
| - | metatarsal, dext. | 195.9 | 16.6 | 18.5 | 26.5 | 28.4 | 29.9 | - | - | 22.9 | 35.0 | 15.7 | 15.7 |
| ***Protragocerus chantrei*, La Grive (Museum Lyon), Depéret 1887** | | | | | | | | | | | | | |
| - | metacarpal | - | - | - | - | - | 29.0 | - | - | - | - | - | - |
| - | metatarsal | - | - | - | - | - | 28.0 | - | - | - | - | - | - |

**Table 8.** Investigated boselaphin horn core specimens with previous and revised identifications. The specimens used in this study, but assigned to *M. pannoniae* are excluded here.

| Sample ID | Location | Identifications | |
|---|---|---|---|
| BSPG 1923 I 9 | Oberföhring (Munich) | ***Miotragocerus monacensis*** (holotype) | **Stromer (1928)** |
| BSPG 1921 I 34 | Unterföhring (Munich) | *Miotragocerus monacensis* | Stromer (1928) |
| | | ***Miotragocerus monacensis*** | **this study** |
| GPIT/MA/03483 | Hammerschmiede | ***Miotragocerus monacensis*** | **this study** |
| NHMW2014/0376/0001 | Atzgersdorf/Mauer | *Protragocerus chantrei* | Abel(1927) |
| | | *Miotragocerus monacensis* | Stromer (1928) |
| | | *Protragocerus chantrei* | Thenius (1956) |
| | | ***Miotragocerus monacensis*** | **this study** |
| IPUW 3193 | Nexing | *Miotragocerus monacensis* | Thenius (1948) |
| | | *Protragocerus chantrei* | Thenius (1956) |
| | | **cf. *Miotragocerus monacensis*** | **this study** |
| NHMW2014/0375/0001 | Ober-Hollabrunn | *Miotragocerus monacensis* | Sickenberg (1929) |
| | | ***Miotragocerus monacensis*** | **this study** |
| NHMW2014/0374/0001 | Ober-Hollabrunn | **Boselaphini indet.** | **this study** |
| NHMW2014/0377/0001 | Ober-Hollabrunn | ***Austroportax latifrons*** (cast of the holotype) | **Sickenberg (1929)** |
| IPUW 1510 | Ober-Hollabrunn | *Protragocerus chantrei* | Thenius (1956) |
| | | **cf. *Austroportax latifrons*** | **this study** |
| IPUW 1480 | La Grive, fissure PB A | ***Protragocerus chantrei*** (cast of the holotype) | **Depéret (1887)** |
| NHMW2014/0373/0001 | Sommerein | *Protragocerus chantrei* | Thenius (1956) |
| | | **? *Protragocerus chantrei*** | **this study** |