

New cranial material of *Miotragocerus monacensis* (Mammalia: Bovidae) from the late Miocene hominid locality Hammerschmiede (Germany)

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With 8 figures and 1 table

Abstract: Here we report on a partial skull and isolated horn core material of the boselaphin bovid *Miotragocerus monacensis* STROMER VON REICHENBACH, 1928 from the late Miocene hominid locality Hammerschmiede in southern Germany (HAM). The partial skull comprises the most complete cranial remains of *M. monacensis* so far. Using μ CT analysis, we demonstrate the unique morphology of the basicranium of *M. monacensis*, compared to closely related boselaphin bovids like *M. pannoniae* KRETZOI, 1941, *M. valenciennesi* GAUDRY, 1861 and *Tragoportax rugosifrons* SCHLOSSER, 1904, all from the late Miocene. In addition, the μ CT data of the cranium provide insight into the morphology of the cornual diverticulum (frontal sinus) supporting the presence of frontal sinuses within basal bovids. Besides the cranium, we describe further isolated horn core material from both the HAM 5 horizon (11.62 Ma) and for the first time the HAM 4 horizon (11.44 Ma), being the stratigraphic youngest record of this species.

Key words: Bovidae, Boselaphini, basicranium, frontal sinus, taxonomy, late Miocene.

1. Introduction

Extant bovids comprise the largest and most successful ruminants. They inhabit various types of habitats from mountain environments to woodlands, savannas, swamps, rainforests and even the Sahara Desert. According to BIBI *et al.* 2009, the earliest members of bovids are *Eotragus artensis* GINSBURG & HEINTZ, 1968 (France, MN4 in GENTRY 1999), *E. noyei* SOLOUNIAS *et al.*, 1995 (Pakistan, ca. 18 Ma) and *E. minus* GINSBURG *et al.*, 2001 (Pakistan, early Miocene). Bovids comprise Bovinae (including Bovini, Tragelaphini and Boselaphini) and Antilopinae (with the tribes Reduncini, Antilopini, *Aepyceros melampus*, Alcelaphini, Hippotragini and Caprini) (BIBI *et al.* 2009). This classification into tribes was established by SIMPSON (1945) and the number of accepted tribes varies around ten (BIBI *et al.* 2009; BIBI 2013). The tribe Boselaphini KNOTTNERNUS-MEYER, 1907 com-

prises the extant *Boselaphus tragocamelus*, *Tetracerus quadricornis* from India and all fossil relatives. The fossil record shows that Boselaphini once were more diverse than today (e.g., SPASSOV & GERAADS 2004; KOSTOPOULOS 2009), but its internal taxonomy is still a matter of discussion, because, species delimitation is intricate due to multiple and sometimes misleading nomenclatures.

One boselaphin species, *Miotragocerus monacensis*, was first described by STROMER VON REICHENBACH (1928) from the so called Flinz sediments (lithostratigraphic unit “Obere Serie” in the Upper Freshwater Molasse Group at the border of the Middle to Upper Miocene) in the Isar river bed near Oberföhring, Munich, Germany and is the type species of the genus *Miotragocerus*. The holotype is a frontlet comprising the fronto-parietal surface with a nearly complete preserved horn core. According to SPASSOV & GERAADS (2004), *Miotragocerus* includes two subgenera

M. (Pikermicerus) KRETZOI, 1941 and *M. (Miotragocerus) STROMER*, 1928 and the junior synonyms *Tragocerus (partim)*, *Graecoryx*, *Sivaceros*, *Pikermicerus* and *Dystychoceras* (KOSTOPOULOS 2005). The genus mainly comprises three species: *Miotragocerus monacensis* STROMER, 1928, *M. pannoniae* KRETZOI, 1941, and *M. valenciennesi* GAUDRY, 1861, which is the youngest species, known from the Turolian. KOSTOPOULOS (2005) furthermore discussed the synonymy of *M. valenciennesi* and *M. gaudryi* and stated that *M. gaudryi* is the junior synonym of *M. valenciennesi*.

The distribution of *Miotragocerus* is mainly western and central European as it is known from Hungary (KRETZOI 1941; SPASSOV & GERAADS 2004), Austria (THENIUS 1948; VISLOBOKOVA 2005; VISLOBOKOVA 2007; FUSS et al. 2015), Germany (STROMER VON REICHENBACH 1928; TOBIEN 1953; ROMAGGI 1987; FUSS et al. 2015), Spain (MOYA-SOLA 1983), Turkey and Iran (KÖHLER 1987), Bulgaria (SPASSOV & GERAADS 2004), Ukraine, Moldova and Georgia (LUNGU 1984; PEVZNERET et al. 1987; KOROTKEVICH 1988). *Miotragocerus* was present from the Astaracian to Vallesian and survived into the Turolian (SPASSOV & GERAADS 2004; GENTRY & KAISER 2009). The genus is well-known from the Turolian, especially in Greek localities like Samos and Pikermi (KOSTOPOULOS 2005; KOSTOPOULOS 2006; KOSTOPOULOS 2009; GENTRY & KAISER 2009). The species *M. monacensis* is assumed to be closely related to *Miotragocerus pannoniae* from Sopron, Hungary (KRETZOI 1941, Pannonian B in KIRSCHER et al. 2016), which is also present in Höwenegg, Germany (10.4 Ma, recalibrated after SWISHER 1996) by articulated specimens.

This study focuses on the description of the so far most complete skull of the boselaphin bovid *Miotragocerus monacensis* from the HAM 5 horizon of the late Miocene (11.67–11.44 Ma; KIRSCHER et al. 2016) Hammerschmiede locality, Germany previously exclusively known from HAM 5 (FUSS et al. 2015). Additionally, for the first time we report on new isolated *M. monacensis* horn core material from the younger horizon of HAM 4.

2. Geological setting

The Hammerschmiede is located in southern Germany (Allgäu, Bavaria) in the Northern Alpine Foreland Basin close to the town of Pforzen and 4 km NNW of Kaufbeuren. The locality is an actively mined clay pit.

It comprises floodplain deposits from the youngest part (“Obere Serie”/“Upper Series”, DEHM 1951; DOPPLER 1989, DOPPLER et al. 2006) of the Upper Freshwater Molasse (UFM). Within these sediments the two fossil bearing horizons HAM 5 and HAM 4 (ordered stratigraphically from oldest to youngest, 11.62 and 11.44 Ma respectively, KIRSCHER et al. 2016) have received great attention, because of the discovery of remains of the hominid *Danuvius guggenmosi* (BÖHME et al. 2019).

The layers of the Hammerschmiede contain a rich fossil fauna including bivalves and gastropods (MAYR & FAHLBUSCH 1975; SCHNEIDER & PRIETO 2011), fishes, amphibians, reptiles, small mammals (FAHLBUSCH 1975; FAHLBUSCH & MAYR 1975; SCHLEICH 1985; BOLLIGER 1999; HUGUENEY 1999; BÖHME 2003; PRIETO & RUMMEL 2009; KLEMBARA et al. 2010; PRIETO et al. 2011; PRIETO 2012; PRIETO & VAN DAM 2012), large mammals (FAHLBUSCH 1975; FUSS et al. 2015; KIRSCHER et al. 2016; BÖHME et al. 2019; BÖHME et al. 2020) and birds (MAYR et al. 2020a, 2020b). A detailed list of vertebrate taxa from the HAM 5 sediments was provided by BÖHME et al. (2019).

The fossiliferous horizons HAM 5 and HAM 4 are alluvial channel deposits. The deposits of the HAM 4 indicate a river of approximately 50 m width and flow direction from SW to NE (MAYR et al. 2020b). In contrast, the HAM 5 channel represents a rivulet of approximately 4–5 m width and S–N flow direction (BÖHME et al. 2019). The sediments of the Hammerschmiede consist of interbedded, unconsolidated clays, marls, silts and sands, whereas the HAM 5 has a high content of clayey and the HAM 4 of sandy and silty sediments.

3. Material and methods

The studied material comprises one cranium from the HAM 5 and two horn cores from HAM 4, as well as one horn core from HAM 5. The fossils from the HAM 4 and HAM 5 were collected during excavations of the Eberhard Karls University of Tübingen, Germany, in 2015–2019. The specimens are stored in the Palaeontological collection of the University of Tübingen (GPIT).

The cranium GPIT/MA/13480 was scanned with the Phoenix v/tomex/s μ CT scanner (GE) at the Institute of Geosciences at the University of Bonn, Germany. The scanner was calibrated to operate at a voltage of 160 kV and a current of 300 μ A. A voxel size of 97 μ m was used. Images were segmented using VG Studio Max, and the reconstruction was performed with Avizo 9.0.1. The resulting

Table 1. Horn core measurements [mm] of *M. monacensis* (Hammerschmiede HAM 5 and HAM 4, [Fuss et al. 2015](#) and authors measurements). DAP: anterior-posterior diameter (length), DT: transverse diameter (width), L: length (Lk and Lc), Lc: length of convex part above the step, Lk: length of keel, Lp: length of pedicle.

| <i>M. monacensis</i> (HAM 5), Fuss et al. (2015) | | | | | | | | | | |
|--|-------------------|-----------------------------------|-----------------------------------|-----------------------------------|-----------------------------------|-----------------------------------|-------|------|-------|------|
| Description | Collection number | DAP ₀ /DT ₀ | DAP ₁ /DT ₁ | DAP ₂ /DT ₂ | DAP ₃ /DT ₃ | DAP ₄ /DT ₄ | L | Lk | Lc | Lp |
| Horn core, dex. | GPIT/MA/03483 | 53.0/23.2 | 49.0/22.9 | 30.2/24.6 | 19.8/16.1 | 12.1/10.1 | 208.0 | 62.5 | 146.0 | - |
| Horn core, sin. | GPIT/MA/03483 | 49.9/25.0 | 46.4/23.6 | 29.9/24.5 | 18.0/18.0 | -/- | 158.5 | 62.0 | 96.7 | - |
| <i>M. monacensis</i> (HAM 5), authors measurements | | | | | | | | | | |
| Horn core, sin. | GPIT/MA/09981 | 48.0/23.9 | -/- | -/- | -/- | -/- | 26.1 | - | - | 17.7 |
| Horn core, dex. | GPIT/MA/13480 | 30.8/16.7 | -/- | -/- | -/- | -/- | 65.5 | - | - | - |
| Horn core, sin. | GPIT/MA/13480 | 39.8/21.4 | 31.5/18.7 | 23.5/12.8 | 13.2/12.3 | -/- | 114.5 | 90.0 | 24.5 | 6.7 |
| <i>M. monacensis</i> (HAM 4), authors measurements | | | | | | | | | | |
| Horn core, sin. | GPIT/MA/16736 | 36.5/22.4 | 32.2/20.7 | 20.2/17.6 | 16.7/15.6 | 10.2/8.9 | 113.5 | 22.5 | 90.9 | - |
| Horn core, dex. | GPIT/MA/17024 | 32.0/22.2 | 17.3/20.9 | -/- | -/- | -/- | 48.8 | - | - | 12.8 |
| <i>M. monacensis</i> , holotype (STROMER VON REICHENBACH 1928), authors measurements | | | | | | | | | | |
| Horn core, sin. | BSPG 1923 I 9 | 46.0/24.2 | 38.8/22.1 | 26.5/19.0 | 15.0/13.2 | -/- | 133.0 | 71.3 | 60.6 | 30.7 |

3D model of the cranium was then used to reconstruct the basicranium of *Miotragocerus monacensis*. The terminology for the description of the frontal sinus follows [FARKE \(2010a, 2007\)](#). The description of the basicranium follows [SPASSOV & GERAADS \(2004\)](#).

The horn core terminology and the measurements follow [Fuss et al. \(2015\)](#) using a 0.25 mm copper wire, which was traced afterwards. The antero-posterior diameter (DAP) and transverse diameter (DT) are displayed in Table 1. The measuring levels also follow [Fuss et al. \(2015\)](#) to ensure comparability with previous investigations on horn cores from the Hammerschmiede locality. The first measuring level (DAP₀ and DT₀) is at the base of each horn core, above the pedicle. If the horn core base is not preserved, a new measuring point has been established named DAP_{0,1} and DT_{0,1}. It is closest to the base, but does not match the original base diameters. The second one (DAP₁ and DT₁) cuts through the step of the anterior keel ([Fuss et al. 2015](#)). Depending on the total length of the horn core, two or three measuring points were chosen towards the tip. The DAP₂ and DT₂ follow approximately two centimeters after the step. The third and fourth points proceed towards the tip every five centimeters.

4. Systematic palaeontology

Class Mammalia LINNAEUS, 1758
 Order Cetartiodactyla MONTGERALD, CATZEFLIS &
 DOUZERY, 1997
 Family Bovidae GRAY, 1821
 Tribe Boselaphini KNOTTERNUS-MEYER, 1907
 Genus *Miotragocerus* STROMER VON REICHENBACH,
 1928

Miotragocerus monacensis
 STROMER VON REICHENBACH, 1928
 Figs. 1–7

Referred material: A partial skull GPIT/MA/13480 (Figs. 1–4), as well as three isolated horn cores GPIT/MA/09981, 16736, 17024 (Figs. 5–7). The referred materials (cranium and the isolated horn cores) are assigned to *M. monacensis*, because of the oval base cross-section of the horn cores and their metrics, and, where preserved, the single step and a prominent anterior keel.

Description and comparisons:

Cranium: The cranium GPIT/MA/13480 consists of the skull roof with two attached horn cores and the basicranial region (Fig. 1A–C). The sinistral horn core shows a single step at 9 mm from the horn core base. A prominent anterior keel proceeds from the proximal–most part of the horn core base towards the step. Furthermore, a short pedicle is visible at the medial site of the sinistral horn core (Fig. 1C). Based on the horn core morphology GPIT/MA/13480 is assigned to *M. monacensis*. The dextral horn core is broken off proximal to the step but the longitudinal half of the distal part was found in close association with the skull. The sinistral horn core is partially split near the proximal part, but was still attached to the skull. The horn core diameters are strongly

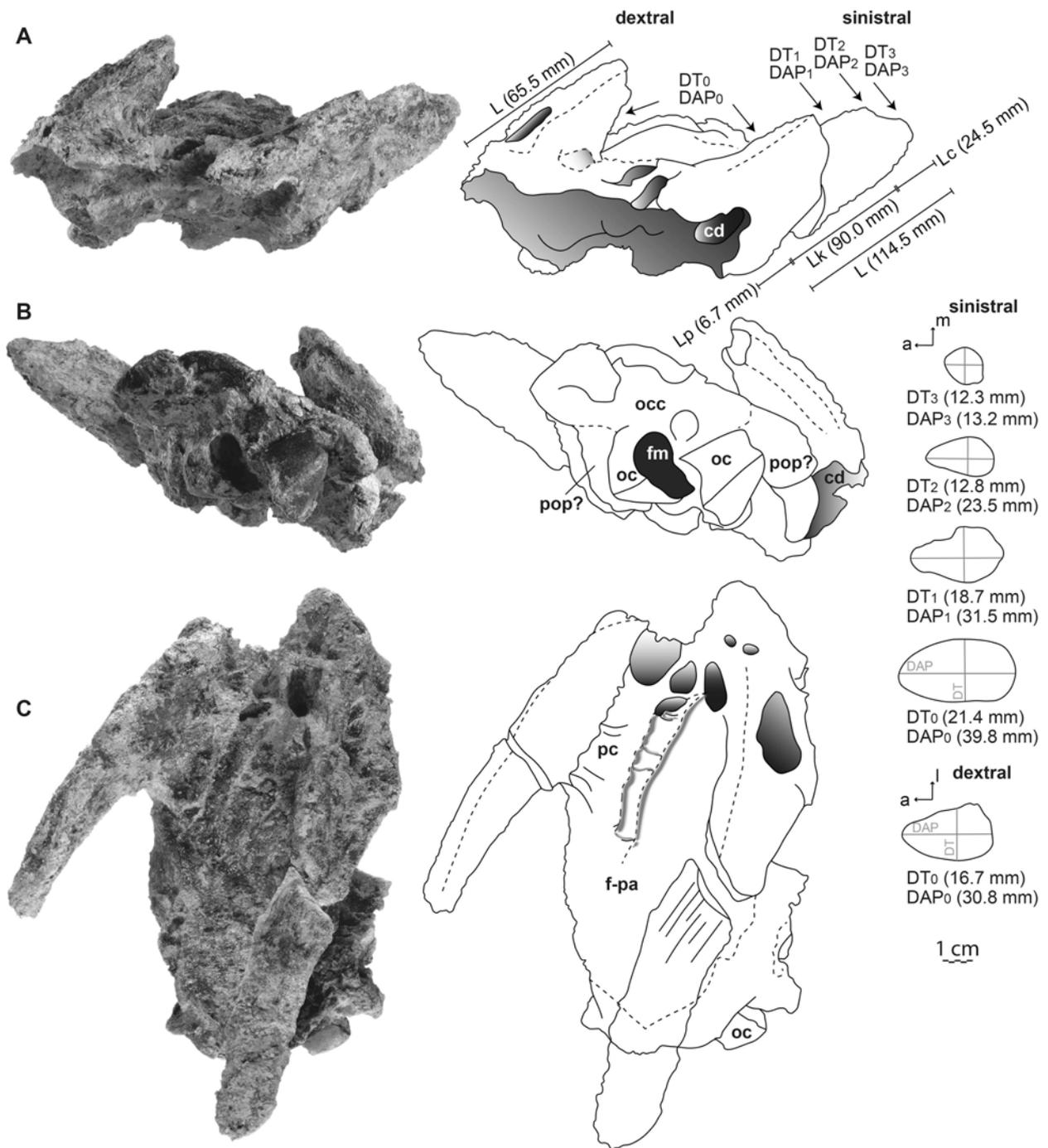


Fig. 1. GPIT/MA/13480. Cranium of *Miotragocerus monacensis* from the HAM 5 horizon with horn core diameters. **A** – Anterior view. **B** – Posterior view. **C** – Dorsal view. DAP: anterior-posterior diameter (length), DT: transverse diameter (width), L: length (Lk and Lc), Lc: length of convex part above the step, Lk: length of keel, Lp: length of pedicle, cd: cornual diverticulum, fm: foramen magnum, f-pa: fronto-parietal, oc: occipital condyle, occ: occiput, pc: pedicle, pop?: paroccipital process.

affected by deformation and abrasion of the skull. However, the sinistral horn core is comparable to other *M. monacensis* specimen as its base remains almost intact.

The horn cores have nearly oval cross sections and become circular towards the distal part (Fig. 1C). The skull roof itself is crushed, dorso-ventrally flattened and laterally distorted. The skull roof comprises the fronto-parietal surface. The suture between the frontal bone and the parietal is not visible. The fronto-parietal surface is posteriorly confined by two bony ridges. A rugose surface behind the horn core bases, as visible in the holotype (STROMER VON REICHENBACH 1928), is not present in this specimen. Anterior to the horn core basis, the collapsed sinus cavities are visible, which show a high degree of pneumatization of the frontal bone. The same arrangement of the frontal sinus cavities also occurs in the extant boselaphin bovid *Boselaphus tragocamelus* (FARKE 2010a). The cornual diverticulum, the extension of the frontal sinus, which penetrates the horn cores, proceeds far into the horn core itself, occupying almost one half of it. The opening of the two cornual diverticula are visible, but filled with sediment (Figs. 1A, 2A). The occipital region can be differentiated into occiput and occipital condyles (Fig. 1B). The foramen magnum is preserved, but dorso-ventrally compressed. The ventral view shows a crushed but well preserved basicranium.

Basicranium: The basicranium is diagnostic in fossil Boselaphini as demonstrated by SPASSOV & GERAADS (2004) and thus is discussed in detail below. Because no skulls of contemporaneous boselaphin taxa like *Protragocerus chantrei* DEPERÉT, 1887 and *Austroportax latifrons* SICKENBERG, 1929 are available, the closely related *Tragoportax rugosifrons* SCHLOSSER, 1904 (from Hadjidimovo, Bulgaria, early–middle Turolian), *Miotragocerus valenciennesi* GAUDRY, 1861 (from both Hadjidimovo, Bulgaria, early–middle Turolian, in SPASSOV & GERAADS (2004) referred to as *Miotragocerus (Pikermicerus) gaudryi* and Akkaşdağı, Turkey, middle Turolian (KOSTOPOULOS 2005)) and *Miotragocerus pannoniae* KRETZOI, 1941 (Höwenegg, Germany, local museum Immendingen, Vallesian) were used for comparison.

The basicranium of GPIT/MA/13480 is crushed and distorted. It comprises the occipital condyles, the basioccipital and the basisphenoid (Fig. 2A, B). The basioccipital is suspended posteriorly into the occipital condyles. The posterior tuberosities are comparably small; anterior tuberosities are not present. A striated ridge proceeds from the posterior tuberosities to the anterior-most part of the basioccipital (Fig. 2B). At the proximal basioccipital, two small foramina are situated at both sides of the ridge. The ridge is only present at the basioccipital and does not continue to the basisphenoid. The basisphenoid shows a completely smooth and slightly concave surface (Fig. 2A), which tapers anteriorly. The entire basicranium appears triangular and hourglass-shaped, with a broad posterior part at the occipital condyles.

Despite of the deformation, the basicranium reveals a unique morphology (Fig. 3) and shows marked differences to *Tragoportax rugosifrons*, *Miotragocerus valenciennesi* (compare BOUVRAIN 1994; KOSTOPOULOS 2009; SPASSOV & GERAADS 2004), and *Miotragocerus pannoniae* (pers. obs. male specimen at the local museum Immendingen, Germany) in the following characters: *T. rugosifrons* shows a

groove running from the foramen magnum to the basisphenoid, cutting through the entire basioccipital. This groove furthermore contains a weak, central, sagittal keel, which levels out anteriorly and merges with the basisphenoid. The groove disappears at both sides of the basisphenoid. In contrast, GPIT/MA/13480 shows a flat, evenly shaped, plateau-like basioccipital with a faint, striated keel at the center. It appears hourglass-shaped, a feature that is not visible in *T. rugosifrons*. In comparison to *M. valenciennesi*, the basioccipital keel of *M. monacensis* is striated and not visible at the basisphenoid. Furthermore, the keel in GPIT/MA/13480 becomes laterally broader towards the posterior part of the basioccipital. In contrast, *M. valenciennesi* shows a continuous, straight and uniform keel at the basioccipital. The keel is replaced at the basisphenoid by a narrow groove. The basicranium of *M. valenciennesi* appears more hourglass-shaped, without the prominent groove, seen in *T. rugosifrons*. Instead, it shows a weak and smooth depression anterior to the posterior tuberosities, proceeding along the entire length of the basioccipital.

The posterior tuberosities are shared by all three species, but they are more prominent in *T. rugosifrons*. *M. monacensis* shows more similarities with the basicranium of *M. valenciennesi* than with *T. rugosifrons*. In contrast to *M. monacensis*, *M. pannoniae* possesses strong anterior and posterior tuberosities. The basioccipital contains a uniform, non-striated ridge, which continues at the basisphenoid. The ridge is well-developed at the basisphenoid and the anterior tuberosities form two crests lateral to this ridge. *M. valenciennesi* and *M. pannoniae* bear more similarities to each other than to *M. monacensis*.

Frontal sinus: Remains of the cranial sinus are restricted to the dextral and sinistral cornual diverticula, which are part of the frontal sinus extending into the horn core. Furthermore, pneumatization chambers of the frontal sinus are exposed (Fig. 4). The cornual diverticulum extends deep into the horn core (Fig. 4) penetrating almost half of it. However, no statement about the size, volume and complexity of the frontal sinus can be made, because the frontal sinus is only fragmentarily preserved. Compared with extant Boselaphini (*Boselaphus tragocamelus* and *Tetracerus quadricornis*) studied by FARKE (2010a), the cornual diverticulum in this specimen invades the horn core more extensively. The frontal sinus of *Boselaphus tragocamelus* shows a maximum penetration depth of up to a quarter of the horn core. In *Tetracerus quadricornis*, the diverticulum reaches the base of the horn core and proceeds only into the pedicle. Accordingly, extant Boselaphini have solid horn cores (PROTHERO & FOSS 2007). However, although the cornual diverticulum is small in extant taxa, the frontal sinus is huge. This cannot be confirmed for GPIT/MA/13480, as the frontal sinus remains of the specimen are restricted to few pneumatization chambers within the fronto-parietal. These chambers are exposed due to the crushing of the skull roof. The midline strut and the supraorbital strut are not preserved.

Horn cores:

– GPIT/MA/09981 (HAM5): The sinistral horn core is still attached to the frontal bone. The horn core is relatively massive and shows the beginning of an anterior keel (Fig. 5). It is inclined backwards with an angle of 40° between the

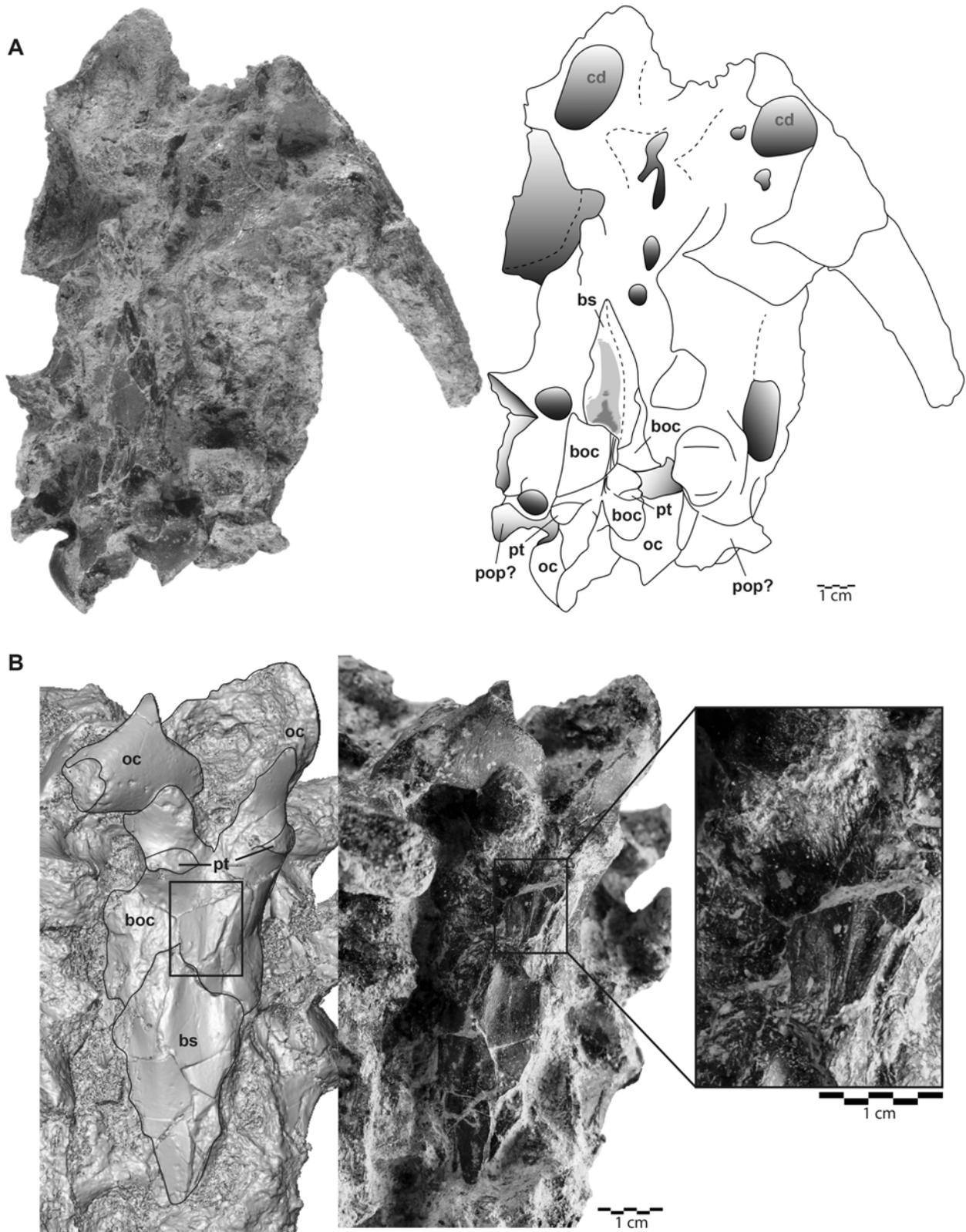


Fig. 2. GPIT/MA/13480. Cranium of *Miotragocerus monacensis* from the HAM 5 with preserved basicranium. **A** – Ventral view with drawing. **B** – Detail view of the basicranium (central and close-up (right)) with surface model (left). cd: cornual diverticulum, boc: basioccipital, bs: basisphenoid, oc: occipital condyle, pop?: paroccipital process, pt: posterior tuberosity.

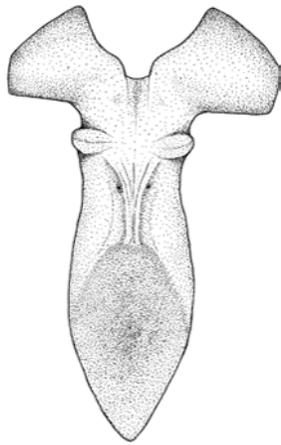


Fig. 3. Reconstruction of the basicranium of *Miotragocerus monacensis* (GPIT/MA/13480 HAM 5).

horn core and the dorsal surface of the frontal bone. It thus lies within the range of 35–44° of *M. monacensis* examined by [Fuss et al. \(2015\)](#). The horn core is broken off above the base. The total length is 26.1 mm. Due to the preservation, the differentiation between the pedicle and the horn core base is only hardly recognizable. The DAP_0 is 48.0 mm and the DT_0 is 23.9 mm, which fits the range of horn core dimensions of *M. monacensis* ([Fuss et al. 2015](#): fig. 16). The cross section is in general oval and the antero-posterior diameter at the base (DAP_0) is approximately twice the size of the transverse diameter at the base (DT_0). Furthermore, the cornual diverticulum extends into the horn core cavity and is visible from the anterior and lateral view (Fig. 5). The sinus height is usually measured at the position of the supraorbital foramen (see [Fuss et al. 2015](#)), which is unfortunately not well-preserved in GPIT/MA/09981.

– GPIT/MA/16736 (HAM4): The sinistral horn core shows a keeled step at the proximal part and is bent anteriorly at the tip (Fig. 6). It furthermore contains a prominent, continuous, posterior groove extending from the broken proximal end towards the distal part. It occupies nearly two-thirds of the entire horn core length, but disappears at 25.0 mm above the step. The groove is asymmetric, oriented postero-medially and flattened at the tip. The horn core-cross-section is oval and laterally compressed at the base. It is more circular distally up to nearly symmetric at the tip. The transverse and antero-posterior diameters decrease quickly towards the distal end, resulting in a pointed tip.

– GPIT/MA/17024 (HAM 4): The dextral horn core is still attached to the fronto-parietal surface. It is inclined backwards with an angle of 37° (Fig. 7), which is close to the typical angle of *M. monacensis* ([Fuss et al. 2015](#)). The anterior keel and the step known from *M. monacensis* are missing due to the incomplete preservation of the fossil. The DAP_0 (32.0 mm) and DT_0 (22.2 mm) are relatively small compared to other specimens of *M. monacensis* (e.g., [Fuss et al. 2015](#)), where the average DAP_0 is about 45.0 mm and the average DT_0 is about 24.0 mm. The sinus height is

19.8 mm, which indicates a subadult age ([Fuss et al. 2015](#)). The specimen preserves the cornual diverticulum extending far into the horn core and the dextral cavity of the frontal sinus. The midline strut is not visible. The supraorbital foramen medial to the orbital rim is preserved.

Horn core metrics: The horn core metrics (Fig. 8) are given for the antero-posterior and transverse diameter at the base (DAP_0 and DT_0) because these are the only diameters preserved in all specimens (Table 1). Furthermore, measurements for *M. pannoniae* from Höwenegg provided by [Fuss et al. \(2015\)](#) and [Thenius \(1948\)](#) were also included.

The holotype of *M. monacensis* plots close to the HAM 5 horn cores already described by [Fuss et al. \(2015\)](#), specimen GPIT/MA/03483) and the herein described specimens GPIT/MA/09981 and GPIT/MA/13480, both also from HAM 5. The specimens almost show the same width and differ in length only by a maximum of 7 mm compared to the holotype. The DAP_0 varies in the HAM 5 specimens within the range of 10 mm (excluding the distorted dextral horn core of GPIT/MA/13480), being about 50 mm on average. The DT_0 ranges from 21–25 mm. The male specimens of *M. pannoniae* from Höwenegg measured by [Fuss et al. \(2015\)](#) show massive bases with a maximum DAP_0 of 71.6 mm and a maximum DT_0 of 43.6 mm. The female horn cores of *M. pannoniae* range from a DAP_0 of 36 mm and a DT_0 of 31 mm to a DAP_0 of 41 mm and a DT_0 of 22 mm. The smaller one (W58) is still oval and the larger one (99/89) becomes circular, which could be an ontogenetic feature. The juvenile specimen of *M. pannoniae* (S/56) plots close to the *M. monacensis* samples from HAM 5 and the holotype from Oberföhring. The specimens of *M. pannoniae* measured by [Thenius \(1948\)](#) from Mistelbach and Inzersdorf plot in alignment with the juvenile and the adult specimen of the same species and also with the holotype of *M. monacensis*. The horn core GPIT/MA/16736 from HAM 4 is relatively small with a DAP_0 of 37 mm and a DT_0 22 mm. It plots close to the two horn cores of the partial skull (GPIT/MA/13480) from HAM 5. GPIT/MA/17024 shows a smaller DAP but nearly the same DT as GPIT/MA/16736.

Comparative horn core morphology: The three boselaphin taxa *Miotragocerus pannoniae* [Kretzoi, 1941](#), *Protragocerus chantrei* [Deperét, 1887](#), and *Austroportax latifrons* [Sickenberg, 1929](#) are almost contemporaneous to *M. monacensis*. As *P. chantrei* and *A. latifrons* are mainly known by horn cores a detailed comparison to *Miotragocerus monacensis* is given in the following to support the assessment of the herein described horn cores GPIT/MA/09981, 16736, 17024.

In comparison to *M. pannoniae*, the horn cores of *M. monacensis* are in general more gracile. They have lower DAP_0 than *M. pannoniae* differing maximally by 20 mm ([Stromer von Reichenbach 1928](#); [Thenius 1948](#); [Fuss et al. 2015](#)). Those metrical differences also depend on ontogeny ([Fuss et al. 2015](#)). Furthermore, the horn cores of *M. monacensis* are strongly inclined backwards and gently curved upwards in their distal half. The angles between the horn core and the fronto-parietal surface range from 35–44°, whereas *M. pannoniae* exhibits a much steeper angle of about 70° ([Stromer von Reichenbach 1928](#); [Thenius 1948](#); [Fuss et al. 2015](#)). Additionally, the horn cores of *M. pannoniae* are laterally

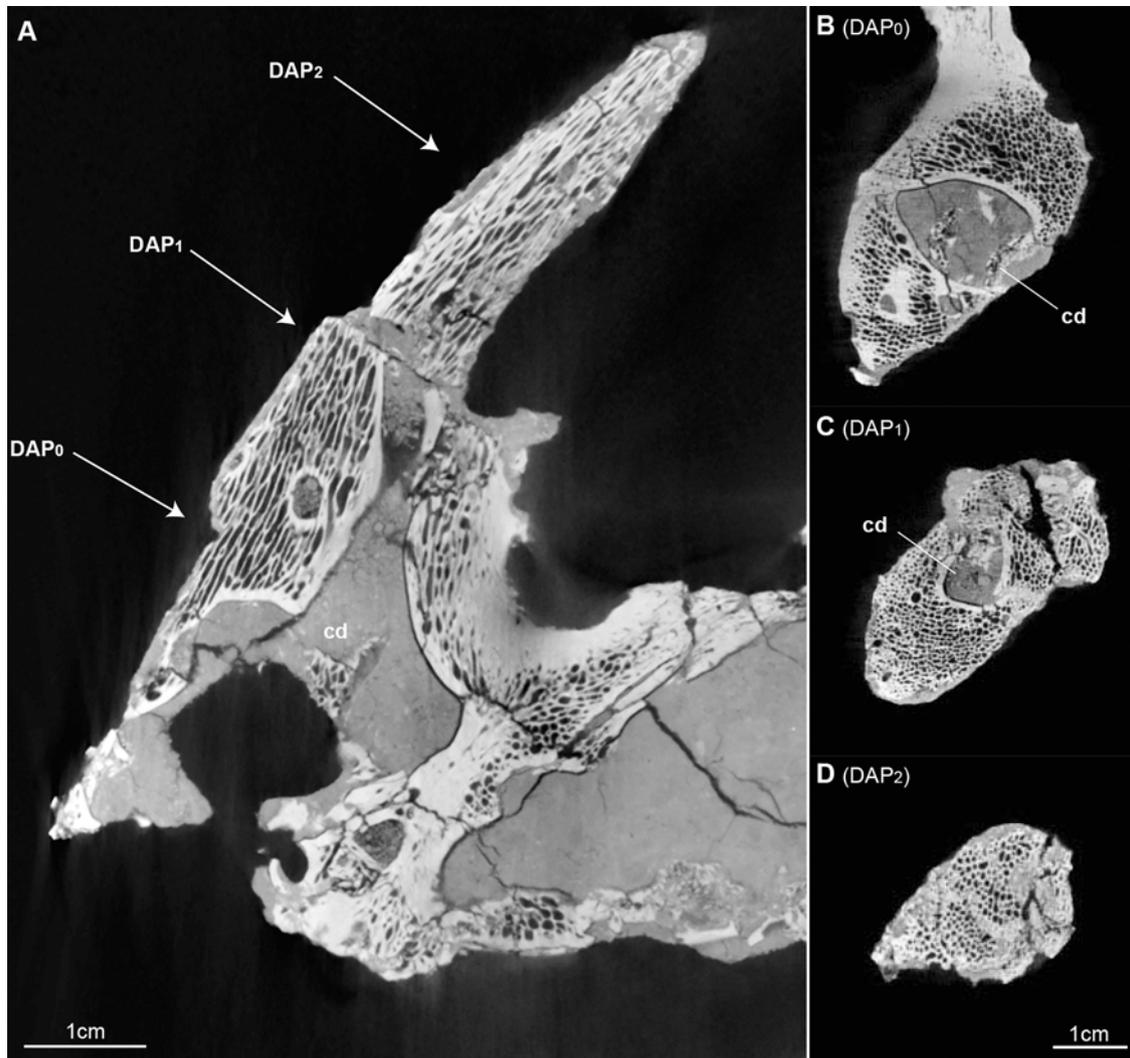


Fig. 4. μ CT analysis of the frontal sinus of GPIT/MA/13480 showing a deep penetration depth of the cornual diverticulum. **A** – Cross-section of the longitudinal axis. **B** – Proximal horizontal cross-section through the left horn core. **C** – Medial horizontal cross-section through the left horn core. **D** – Distal horizontal cross-section through the left horn core. cd: cornual diverticulum, DAP: anterior-posterior diameter (length).

compressed at the base (KRETZOI 1941; ROMAGGI 1987) and less symmetric. The anterior keel is well-developed in both taxa, whereas *M. pannoniae* often has several steps. This feature changes during ontogeny (THENIUS 1948) and is not recorded in *M. monacensis*, where only one step is present. In *M. monacensis* the diameter along the anterior keel decreases progressively above the step, changing to a circular cross-section. *M. pannoniae* sometimes shows an oval distal cross-section, which can be laterally compressed. The horn cores of *Protragocerus chantrei* show an anterior and a posterior keel. They are running from the base to the top without any step. The base cross-section is oval to subtriangular (DEPERÉT 1887; THENIUS 1948; FUSS et al. 2015). *Austroportax latifrons* differs from *M. monacensis* by possessing a keel without a step, but with considerable torsion. The basal

cross-section is elongated and triangular in shape, whereas the horn cores of *M. monacensis* have a nearly straight keel with a single step and a transversely compressed basal cross-section. The distal cross section of *A. latifrons* is compressed in comparison to the circular cross-section in *M. monacensis* (FUSS et al. 2015).

5. Discussion

So far, GPIT/MA/13480 represents the most complete skull of *M. monacensis*. The basicranium is unique

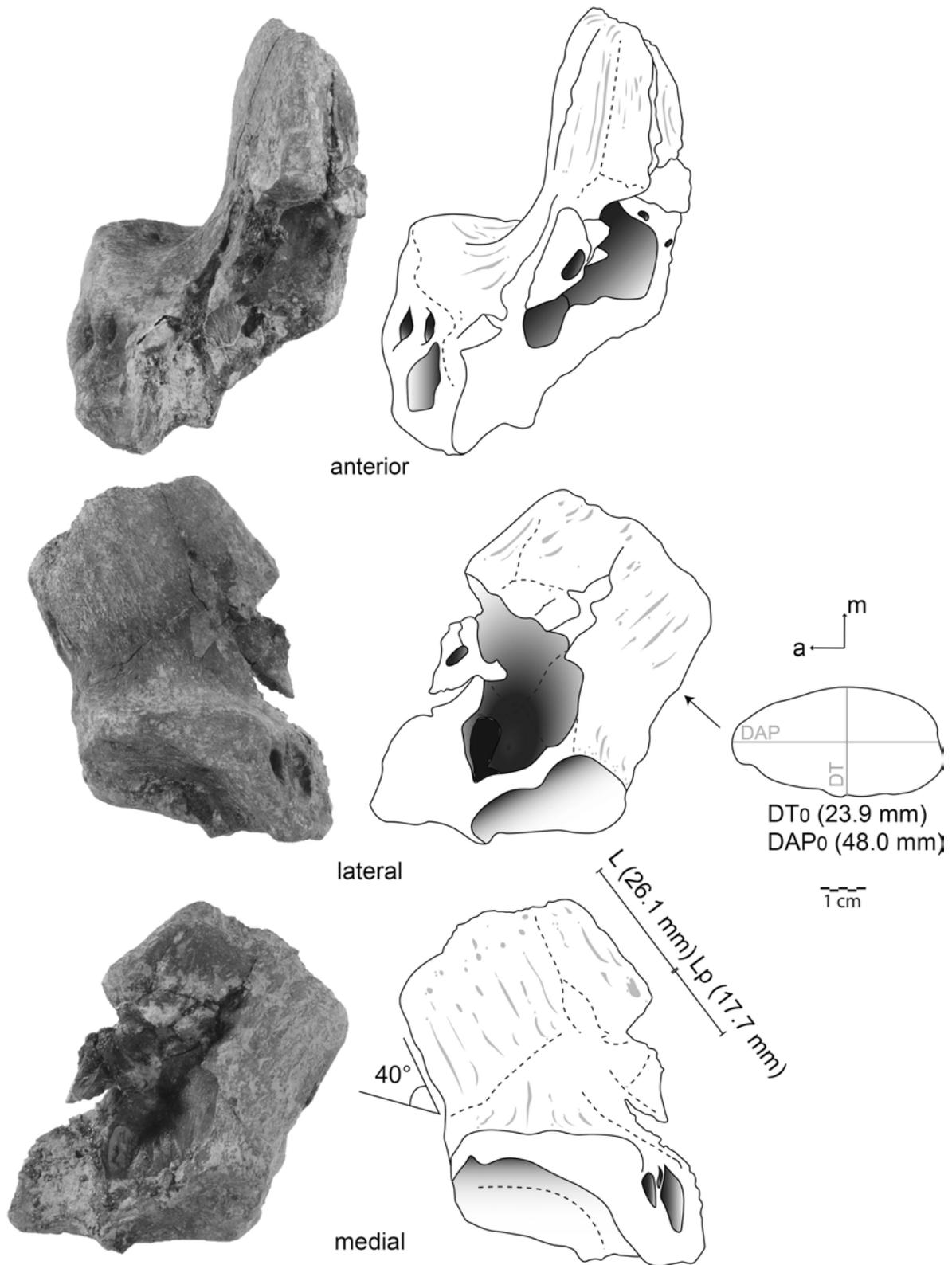


Fig. 5. GPIT/MA/09981 (HAM 5). Base of sinistral horn core of *Miotragocerus monacensis* attached to pedicle with piece of frontal bone. a: anterior, DAP: anterior-posterior diameter (length), DT: transverse diameter (width), L: length (Lk and Lc), Lp: length of pedicle, m: medial.

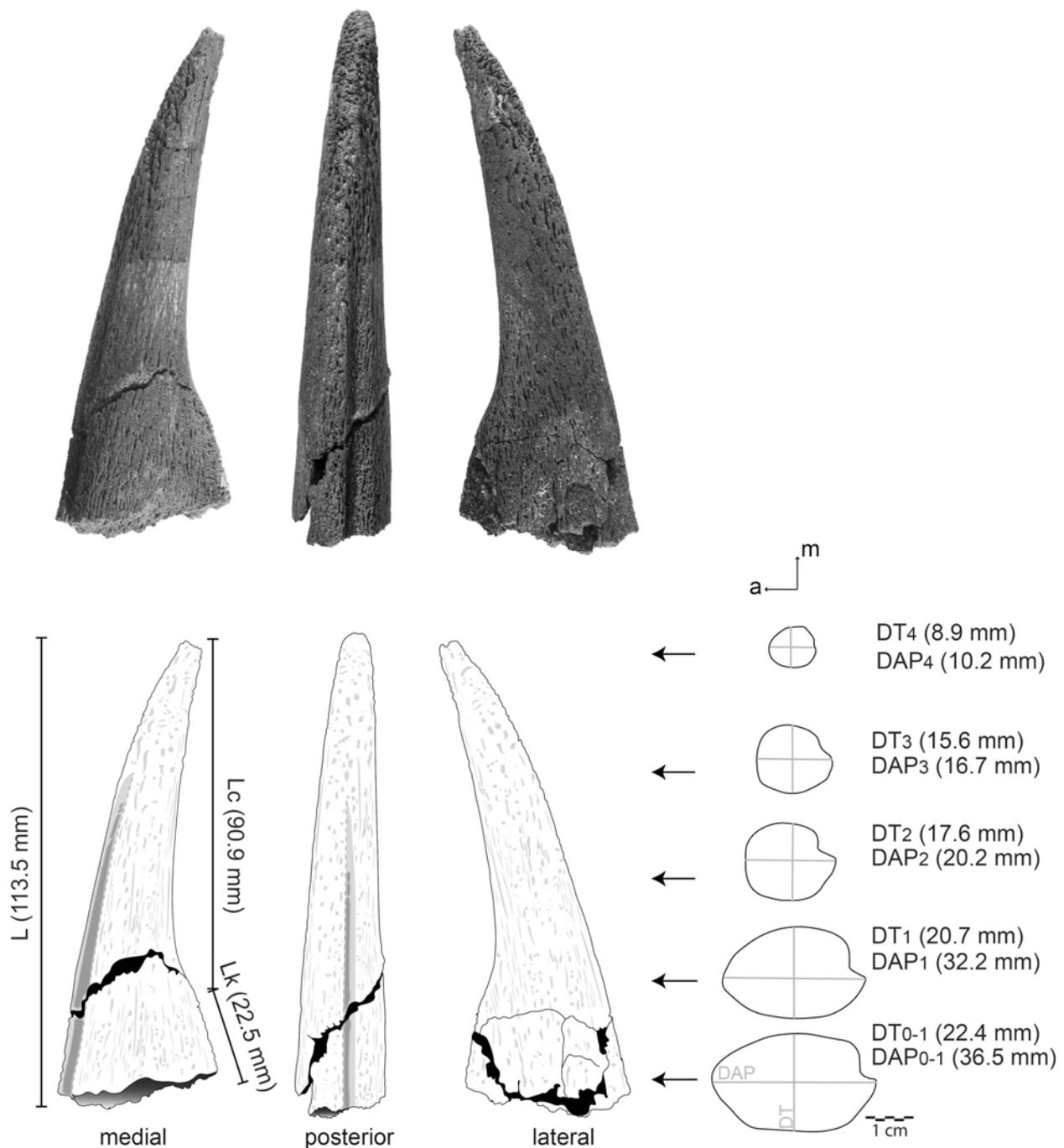


Fig. 6. GPIT/MA/16736 (HAM 4). Sinistral horn core of *Miotragocerus? monacensis*. a: anterior, DAP: anterior-posterior diameter (length), DT: transverse diameter (width), L: length (Lk and Lc), Lc: length of convex part above the step, Lk: length of keel, m: medial.

in morphology and shows significant differences to *M. valenciennesi*, *T. rugosifrons*, and *M. pannoniae* (pers. obs.). Hence, basicranial morphology could provide additional autapomorphies for a revision of

the systematics of taxa variously grouped within *Miotragocerus* and fossil Boselaphini. However, skulls of early late Miocene Boselaphini, that are almost contemporaneous to *M. monacensis*, are rare and an over-

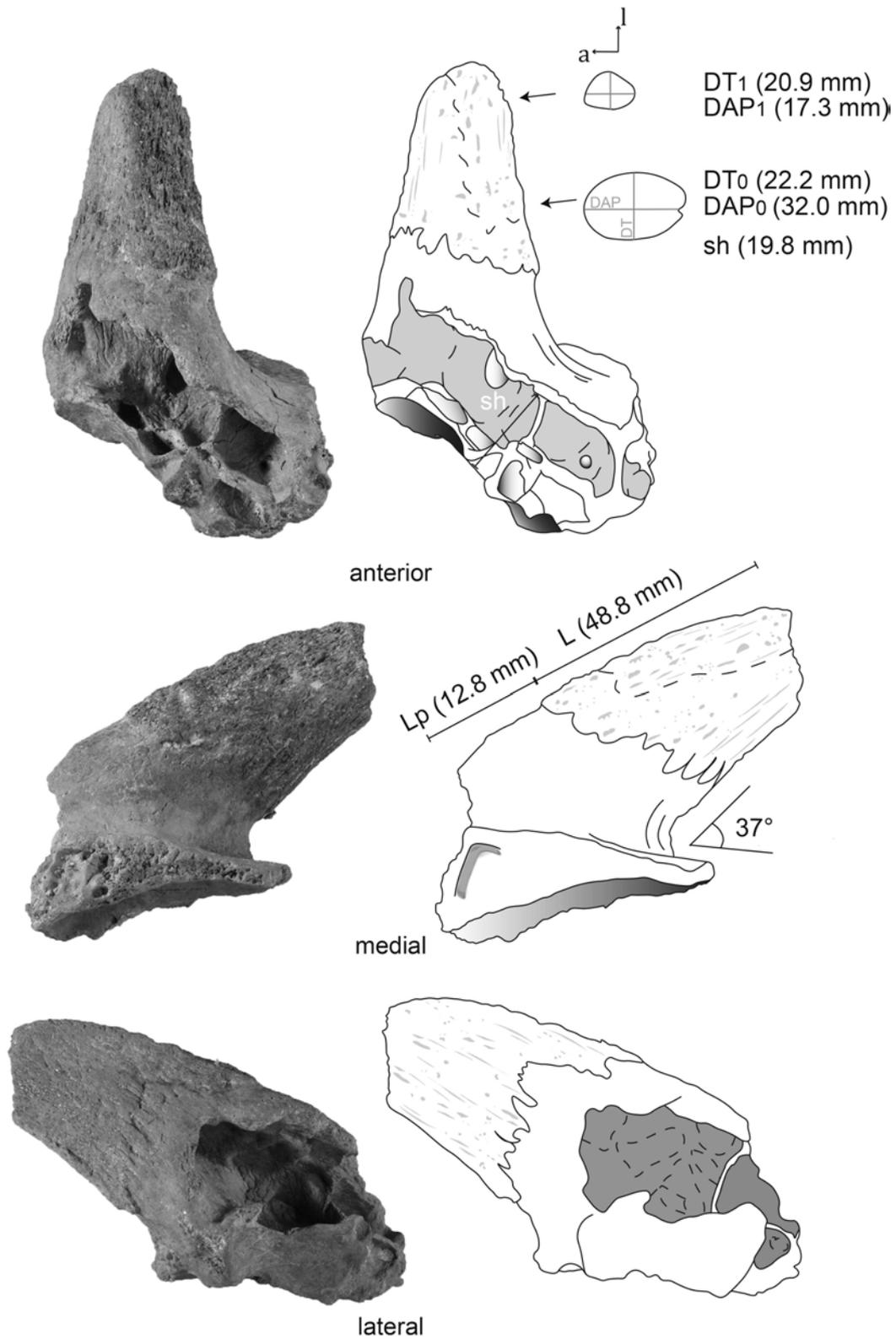


Fig. 7. GPIT/MA/17024 (HAM 4). Dextral horn core of *Miotragocerus monacensis* attached to pedicle with piece of frontal bone. a: anterior, DAP: anterior-posterior diameter (length), DT: transverse diameter (width), l: lateral, L: length (Lk and Lc), Lp: length of pedicle, sh: sinus height.

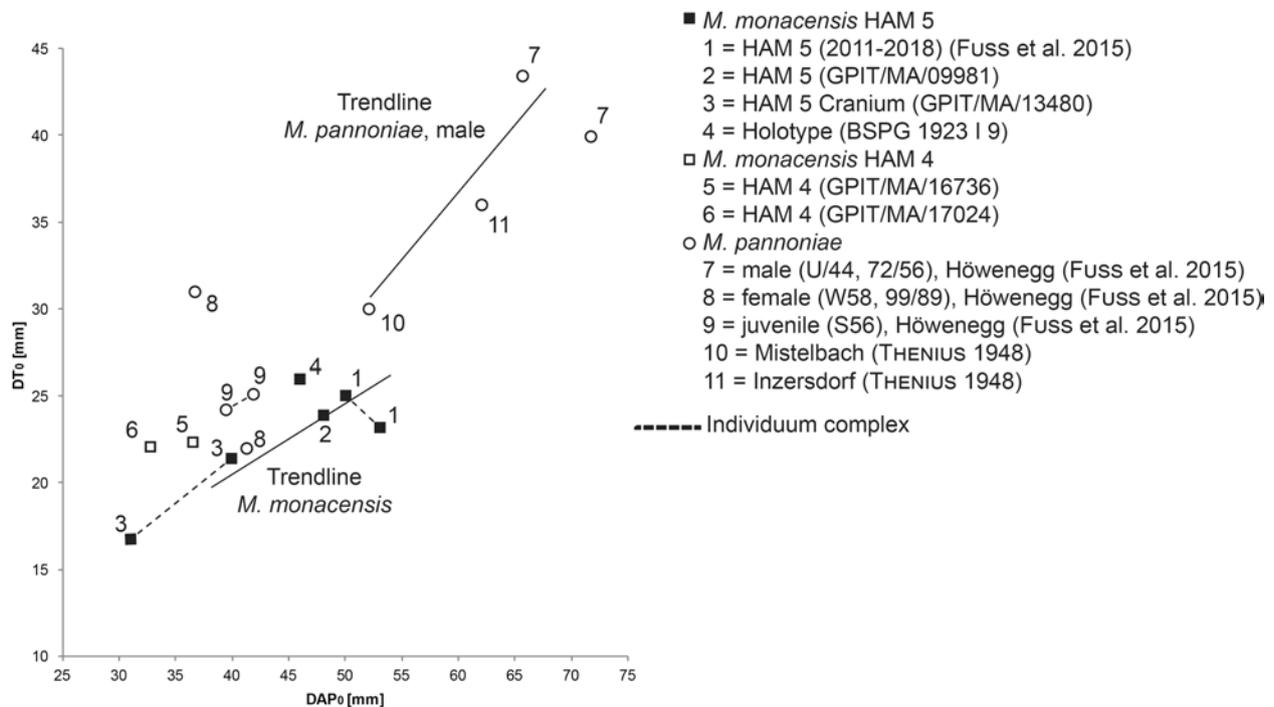


Fig. 8. Horn core metrics comprising horn cores of *Miotragocerus monacensis* (HAM 5 and HAM 4) and *Miotragocerus pannoniae* (Höwenegg, Mistelbach and Inzersdorf).

all revision of fossil Boselaphini needs to await more material.

Besides taxonomic information, the cranium of *M. monacensis* could additionally provide insights into a potential sexual dimorphism in this species if more skulls were available for quantitative analyses of sinus penetration depth within the next years. FARKE (2007) reported of higher penetration depths of the cornual diverticulum in the horns of females of *Alcelaphus buse-laphus lichtensteinii*, because the load of male horns is larger than the load of the more gracile female horns. This is not reported from other taxa so far, but should be investigated further in *M. pannoniae* as complete skulls are available and a sexual dimorphism of the horns is present (ROMAGGI 1987).

Cranial sinuses, air-filled chambers, are one of the most enigmatic structures within the bovid skull. They result from removal of trabecular bone and can extend far into the horn cores. They show a great variability within different vertebrate groups and have been mainly studied in primates, among mammals. Some studies even compare cranial sinuses of bovids with ornithischian or ceratopsian dinosaurs (FARKE 2010b; O'BRIEN et al. 2016). Sinus size, penetration of the

horn core and complexity are probably correlated to ontogeny (FARKE 2010a; FUSS et al. 2015). Regarding bovids, the “opportunistic pneumatization hypothesis” suggests primarily functionless paranasal sinuses, resulting from the removal of structurally unnecessary bone (FARKE 2010a). In general, frontal sinus size correlates with size of the frontal bone and not necessarily with overall cranial size or horn size and the relative sinus volume and sinus complexity do not strongly support its role as shock absorber during head butting (FARKE 2007; FARKE 2008; FARKE 2010a; FARKE 2010b). However, the morphology of paranasal sinuses can be used for phylogenetic implications, in which possessing a frontal sinus is a plesiomorphic condition. A small frontal sinus is already present in *Eotragus sansaniensis* (FARKE 2010a). As a consequence, it is not surprising that *M. monacensis*, a basal bovid, shows a deep penetration depth of the cornual diverticulum in this specimen described here, which is the only one scanned by μ CT so far.

For clear diagnosis of bovid species, the morphology of horn cores still remains the most common method, though only the bony core and not the sheath itself is preserved in fossils. However, horn cores are

strongly influenced by ontogeny, sexual dimorphism and also intraspecific variability. Ontogenetic variation in *M. monacensis* was already observed by FUSSE *et al.* (2015), where especially the frontal sinus became enlarged during ontogeny. But also, the morphology of the bovid horn core itself changed through ontogeny (CASTELLÓ 2016).

Ontogenetic growth series are known for *M. monacensis* (FUSSE *et al.* 2015) and male specimens of *M. pannoniae* (THENIUS 1948). So far, the Hammerschmiede yielded only subadult or adult specimens. Certainly, GPIT/MA/16736 (Fig. 6) shows similarities to a juvenile specimen of *M. pannoniae* (THENIUS 1948) by possessing a characteristic proximal step with an anterior keel and a posterior groove. The specimen does not show a cornual diverticulum. However, in contrast to *M. pannoniae*, the distal part of the horn core is relatively long and its shape rather suggests, that the horn core was strongly inclined backwards (pers. comm. KOSTOPOULOS 2020). Furthermore, the size of GPIT/MA/16736 matches the dimensions of GPIT/MA/03483 (FUSSE *et al.* 2015, HAM 5) and the holotype of *M. monacensis*. GPIT/MA/16736 furthermore shows adult features such as a strong developed, single stepped keel and a well-developed anterior inclination of the tip, which can be interpreted as adult characters of a distal horn core of *M. monacensis* (KOSTOPOULOS, pers. comm. 2020).

Prominent posterior grooves are a feature of *M. pannoniae* (THENIUS 1948, figs. 1–3) and are not known from *M. monacensis* so far (pers. obs.; see also SPASSOV & GERAADS 2004: table 5 and for adult horn cores FUSSE *et al.* 2015) and, therefore, we refer to the specimen GPIT/MA/16736 as *Miotragocerus ? monacensis* until more material will be available. However, in *M. pannoniae* these grooves are symmetric and occur numerously on the horn cores. THENIUS (1948) hypothesized that these grooves functioned as a pathway for blood supply. Single asymmetric grooves are unreported from early late Miocene bovids so far, although they were influenced by intraspecific variations and, thus, can change in number and shape (pers. obs.; see also THENIUS 1948). Further material is needed to investigate a potential earliest occurrence of *M. pannoniae* in Europe (Sopron, KRETZOI 1941, Pannonian B in KIRSCHER *et al.* 2016). It is noticeable though, that GPIT/MA/17024 (Fig. 7) was also found in the HAM 4 horizon and does not bear a posterior groove. This might be due to its fragmentary preservation, but can also imply a coexistence of *M. pannoniae* and *M. monacensis*.

6. Conclusions

The central European middle-to-late Miocene transition comprises at least three different bovid genera (FUSSE *et al.* 2015): *Protragocerus*, *Miotragocerus* and *Austroportax*, which are mainly distinguishable by features of their horn cores. The species *M. monacensis* was previously known from five localities with its last occurrence at 11.6 Ma (FUSSE *et al.* 2015; KIRSCHER *et al.* 2016): Atzgersdorf/Mauer, Nexing, Ober-Holla-brunn, Oberföhring/Unterföhring and Hammerschmiede (HAM 5). The new finds from HAM 4 (11.44 Ma, KIRSCHER *et al.* 2016) represent the stratigraphic youngest record of this taxon.

Furthermore, for the first time, we described the most complete skull of *M. monacensis* including its basicranium. We showed, that the basicranium contains potential autapomorphies as *M. monacensis* differs significantly in basicranial morphology from the three closely related and more similar boselaphin taxa *Tragoptax rugosifrons*, *M. valenciennesi*, and *M. pannoniae*. Accordingly, the basicranium of *M. monacensis* possesses unique characters such as (i) a striated keel limited to the basioccipital, (ii) weakly-developed posterior tuberosities, (iii) the absence of anterior tuberosities, and (iv) a central depression at the basisphenoid. These new features of *M. monacensis* might aid in a future revision of ingroup taxonomy of the genus *Miotragocerus* and also within other closely related fossil Boselaphini. However, if these unique characters are of taxonomic and phylogenetic importance has to await future investigations.

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