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ORIGINAL PAPER

Perissodactyla from the late Middle Miocene Gratkorn locality (Austria)

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Abstract Although quite rare in comparison to other large mammal groups, the Perissodactyla from Gratkorn show a diverse assemblage. Besides the three rhinocerotid species, *Aceratherium* sp., *Brachypotherium brachypus* (Lartet, 1837), and *Lartetotherium sansaniense* (Lartet, in Laurillard 1848), the families Chalicotheriidae and Equidae are represented by *Chalicotherium goldfussi* Kaup, 1833 and *Anchitherium* sp., respectively. The perissodactyl assemblage fits well in a late Middle Miocene (Sarmatian) riparian woodland with diverse habitats from active rivers to drier more open environments, as were present at the Gratkorn locality.

Keywords *Chalicotherium* · *Aceratherium* · *Brachypotherium* · *Lartetotherium* · *Anchitherium* · late Middle Miocene · Sarmatian · Central Europe

Introduction

The Gratkorn locality (clay pit St. Stefan) is located 10 km NNW of Graz (Styria, Austria). The fossil-bearing palaeosol of late Middle Miocene age (late Sarmatian sensu stricto; 12.2–12.0 Ma; Gross et al. 2011) comprises abundant small and large vertebrate fossils and is one of very few qualitatively and quantitatively rich vertebrate localities of this time period of the Paratethys realm. While artiodactyls are abundant within the large mammals from Gratkorn, perissodactyl remains are rare and comprise only some isolated teeth and some fragmented bones. Taxonomic determination is therefore limited for the material and cannot supply much information on general taxonomic and phylogenetic questions. For palaeoenvironmental considerations on the Gratkorn locality, the perissodactyls are essential elements. In contrast to many other, though richer, localities, they can furthermore provide confidently dated material for stratigraphic range estimations.

Materials and methods

Rhinocerotidae vel Chalicotheriidae: UMJGP 204701 (distal fragment of humerus sin.?), UMJGP 204719 (petrosum)
Rhinocerotidae indet: UMJGP 203705 (distal fragment of tibia dex.?), GPIT/MA/2400 (costa sin.?; proximal fragment)
Chalicotherium goldfussi: UMJGP 204676 (M3 dex.)
Aceratherium sp.: UMJGP 203711 (fragment of D2 sin.)
Brachypotherium brachypus: UMJGP 203434 (lateral half of astragalus sin.), UMJGP 204720 (Mt II sin.)
Lartetotherium sansaniense: UMJGP 203459 (m1 sin.; fragment of m2 sin.)
Anchitherium sp.: UMJGP 204694 (distal articulation of humerus sin.), UMJGP 203422 (distal articulation of radius dex.)

Terminology for dental material of Chalicotheriidae follows Fahlke et al. (2013; except for the term ectoloph, which is understood sensu Zapfe 1979; postfossette is understood sensu Butler 1965; and labial is used instead of buccal). For Rhinocerotidae, it is modified after Heissig (1969, 1972), and Heissig and Fejfar (2007). For postcranial

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This article is a contribution to the special issue "The Sarmatian vertebrate locality Gratkorn, Styrian Basin."

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elements, current anatomical terms are used. Measurements are taken with a digital calliper (where possible with a precision of 0.1 mm) in the way indicated on Figs. 2 and 3. The way of measurement follows modified Heissig (1969), Zapfe (1979), Hünermann (1989) and Antoine (2002).

Institutional abbreviations

BMNH	British Museum of Natural History, London, Great Britain
GPIT	Paläontologische Sammlung der Universität Tübingen, Tübingen, Germany
SNSB-BSPG	Staatliche Naturwissenschaftliche Sammlungen Bayerns - Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany
NHMW	Naturhistorisches Museum Wien, Wien, Austria
NMA	Naturmuseum Augsburg, Augsburg, Germany
UMJGP	Universalmuseum Joanneum, Graz, Austria

Anatomical abbreviations

L	Anteroposterior length of tooth
l max	Maximum anteroposterior length of tooth
l basally	Basal length of tooth at the base of the tooth crown (sensu Heissig 1969)
l ling	Lingual anteroposterior length of tooth
w ant	Anterior linguolabial width of tooth
w post	Posterior linguolabial width of tooth

Systematic palaeontology

Order Perissodactyla Owen, 1848
Rhinocerotidae vel Chalicotheriidae

Description and comparison

In size and morphology, specimen UMJGP 204701 fits well to the distal articulation of a left humerus from a large perissodactyl. It resembles *Anisodon grande* (see, e.g. Zapfe 1979, fig. 69, and Guérin 2012, fig. 1), but differs from it in the stronger distal concavity of the trochlea and the more rounded medial condyle. Furthermore it is slightly larger than *Anisodon grande*, which would fit well to *Chalicotherium goldfussi* (Zapfe 1989). However the morphology also resembles the humeri of Rhinocerotidae [see, e.g. Heissig 2012, figs. 65–67, *Brachypotherium* from Petersbuch (SNSB-BSPG 1969; Germany; Miocene), or Rhinocerotidae indet. from Mering (SNSB-BSPG 1960 I 121; Germany; Middle Miocene)]. In comparison to the Gratkorn specimen, the concavity in the distal trochlea is even stronger in the two rhinocerotid humeri (personal observation). As no humerus of *Chalicotherium goldfussi* was available for comparison and as the fragment resembles both large perissodactyl families recorded from Gratkorn but slightly differs from both and cannot be assigned with certainty, it is assigned only to Rhinocerotidae vel Chalicotheriidae.

The size of an isolated petrosal fragment (UMJGP 204719) also corresponds with a rather large mammal. It is smaller than a proboscidean and larger than *Anchitherium* and all occurring Artiodactyla from Gratkorn. Whether it represents a chalicothere or a large rhinocerotid cannot be determined. It is therefore also assigned to Rhinocerotidae vel Chalicotheriidae.

Family Chalicotheriidae Gill, 1872
Subfamily Chalicotheriinae Gill, 1872
Genus *Chalicotherium* Kaup, 1833
Type species: *Chalicotherium goldfussi* Kaup, 1833

Chalicotherium goldfussi Kaup, 1833

Lectotype: M3 dex. (Kaup 1833, tab. VII, fig. 3)
Type locality: Eppelsheim, Rheinhessen, Germany

Description and comparison

The M3 dex. (UMJGP 204676; l: 41.5 mm, w ant: 44.2 mm, w post: ~37 mm; Figs. 1, 2a–e) is well preserved. It is low crowned and possesses a trapezoid shape decreasing in width posteriorly. Paracone, protocone, metacone, and hypocone are well developed. The paracone is the dominant cusp with a strongly inclined labial wall. The protocone is large and as strong as the hypocone. It is located slightly more posterior than the paracone. Para- and mesostyle are distinct, the metastyle is little developed and nearly fused with the metacone. The ectoloph is triconcave with a small depression anterior to the parastyle; its largest depression is at the labial wall of the paracone. A protoloph and paraconule are present and are connected to the paracone but only by a faint basal ridge to the protocone. The protoloph is short and the paraconule is lower than the protocone. The anterior valley is shallow, while the central valley is strongly developed, lingually open, and deeply incised into the lingual wall of the mesostyle. The posterior part of the ectoloph, comprising the metacone and metastyle, is directed posterolingually. The short metastyle is bent to the rear becoming almost longitudinal at its end. The posterior crest of the hypocone turns labially. Basally, it is connected to the metastyle forming a short posterior cingulum enclosing with the metacone a basally narrow and occlusally more open postfossette. A strong anterior and a weak lingual cingulum are present, while labially no cingulum is developed. At the protocone, the lingual cingulum rises and is less distinct, but is clearly still present.

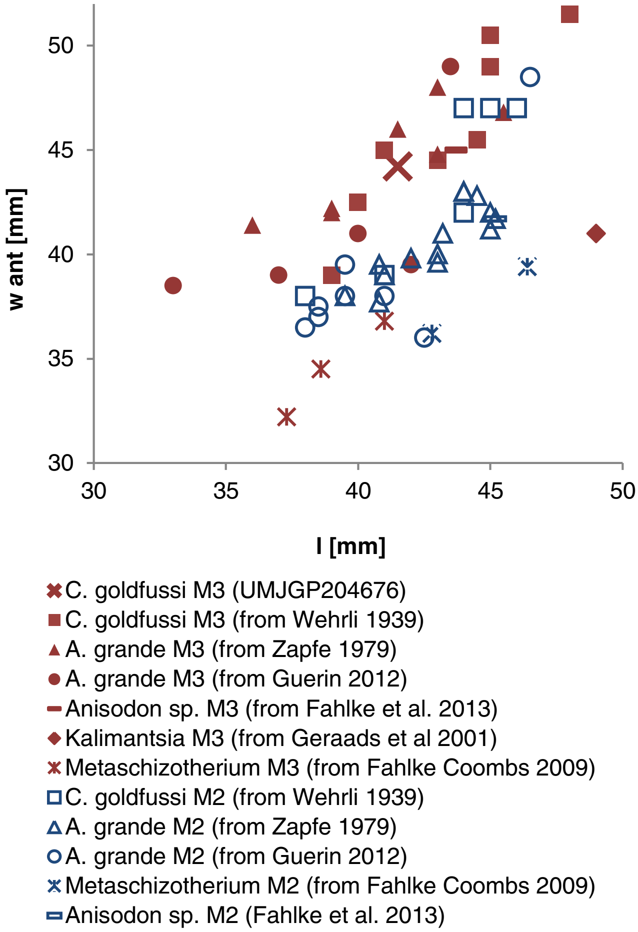


Fig. 1 Bivariate plot of length (*l [mm]*) versus anterior width (*w ant [mm]*) of M3 of *Chalicotherium goldfussi* from Gratkorn (UMJGP 204676) in comparison to M2 and M3 of other Chalicotheriidae (references given in *parentheses*)

Following Anquetin et al. (2007), the upper M3 of Gratkorn must be assigned to the subfamily Chalicotheriinae because of the nonfusion of protoloph and protocone. A weak ridge connecting the paraconule and protocone very basally, which is observed in the specimen from Gratkorn, is not considered a fusion sensu Anquetin et al. (2007), as it can also be observed in the type specimen of *Chalicotherium goldfussi* (Schaefer and Zapfe 1971; Zapfe 1979). As in most Chalicotheriinae (Fahlke et al. 2013), the protocone is posterior to the paracone. Furthermore, Schizotheriinae possess an anteroposteriorly elongated rectangular shape in the upper molars in contrast to the square shape in Chalicotheriinae (Zapfe 1979; Coombs 1989), as observed in UMJGP 204676. In size, the Gratkorn specimen is well within the dimensions of both *Chalicotherium goldfussi* and *Anisodon grande* (de Blainville, 1849) (overlap of dimensions also recorded by Zapfe 1979; Coombs 1989) and is clearly wider than representatives of the Schizotheriinae (Fig. 1). In general shape, it fits best to *Chalicotherium goldfussi*. With this species, the specimen shares the presence of a cingulum at the lingual wall of the protocone (Schaefer and Zapfe 1971), a wide and lingually open central valley (Schaefer and Zapfe 1971; Zapfe 1979), and the course of the labial wall of metacone–metastyle and hypocone (fig. 30 in Schaefer and Zapfe 1971; Anquetin et al. 2007). In *A. grande*, the metacone and metastyle are differently shaped and aligned to the anteroposterior axis of the tooth (see, e.g. fig. 31 in Schaefer and Zapfe 1971; Anquetin et al. 2007) and the central valley is narrower and lingually closed (Schaefer and Zapfe 1971; Zapfe 1979). In the M3 of *Anisodon* sp. from Dorn-Dürkheim 1 (Germany; Late Miocene; MN 11), which possesses a wider central valley than observed in *A. grande* (Fahlke et al. 2013), the central valley is still narrower than in the specimen from Gratkorn. From the M3 of *Kalimantsia* Geraads et al., 2001, the specimen differs by a more subsquare shape and the pattern and morphology of meta-, hypocone, and metastyle (Geraads et al. 2001).

Family Rhinocerotidae Gray, 1821

Rhinocerotidae indet.

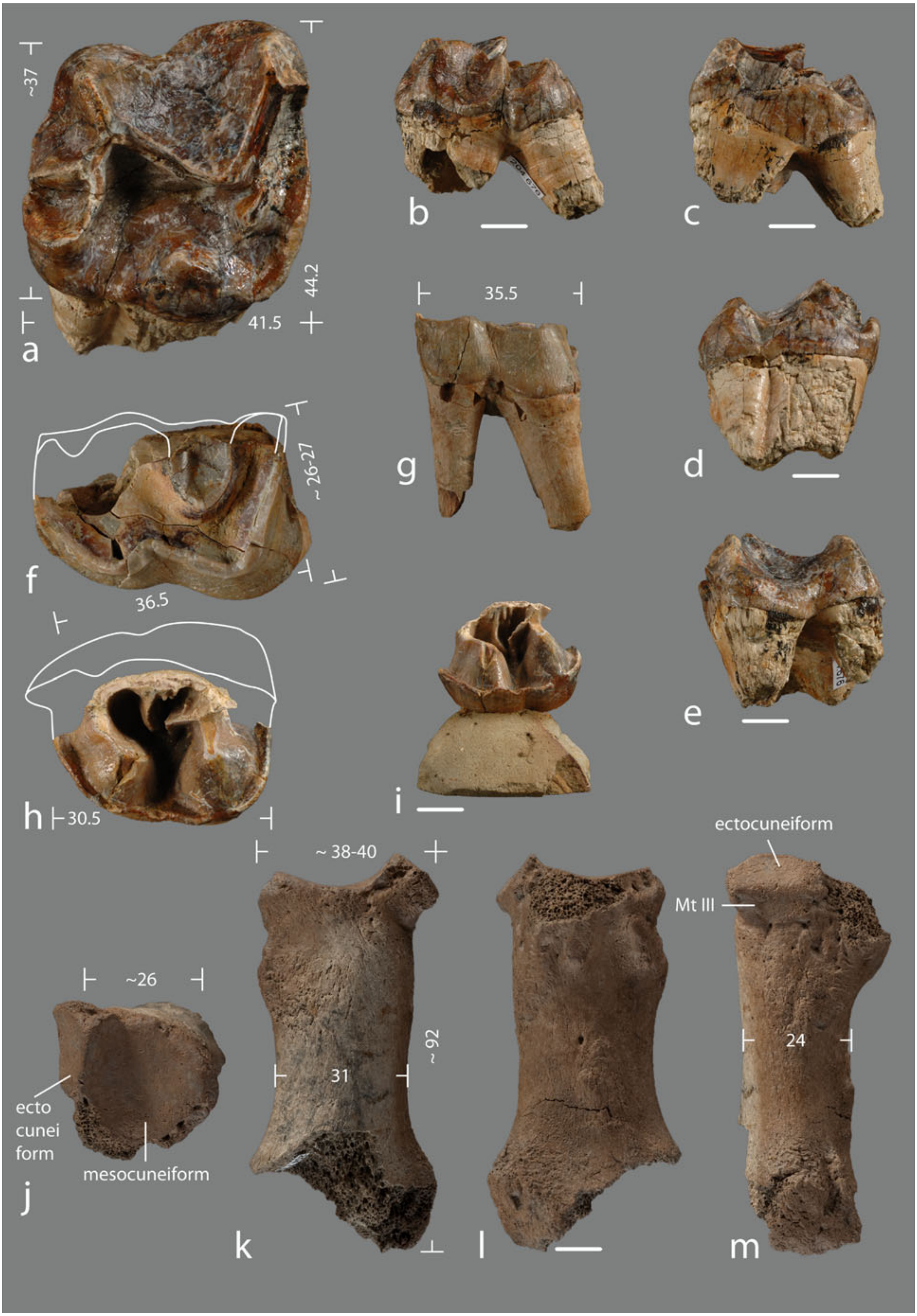
Description and comparison

The dorsal half of a broad distal articular facet of a tibia dex. (UMJGP 203705) shows two grooves, a wider and deeper lateral one and a shallower and narrower medial one. A rather low ridge separating the grooves is oblique to the mediolateral axis. The articulation is very small in comparison to *Anisodon grande* (see, e.g. Zapfe 1979) and may, therefore, represent a large rhinocerotid.

The proximal part of a left rib (GPIT/MA/2400; Fig. 3e) has a large caput costae and a smaller tuberculum costae. In cross-section, the sulcus costae is not clearly set off, the cross-section of the corpus costae is drop-shaped, pointed anteriorly. This bone is far too small to represent a chalicothere and is therefore taken to be a rhinocerotid.

Subfamily Aceratheriinae Dollo, 1885
Tribe Aceratheriini Dollo, 1885
Genus *Aceratherium* Kaup, 1832

Type species: *Aceratherium incisivum* Kaup, 1832
Lectotype: Skull fragment, HLMD DIN 1927
Type locality: Eppelsheim, Rheinhessen, Germany
Remarks: So far, no general consensus has been reached concerning the taxonomic status of the diverse *Aceratherium*-like Rhinocerotidae in the Early and Middle Miocene of Europe. Geraads and Saraç (2003) even stated that most of the Middle Miocene *Aceratherium*-like "'genera' correspond to poorly defined evolutionary grades rather than to clades" (Geraads and Saraç 2003, p. 218). Heissig (2009) observed only a few differences between *Alicornops* and *Aceratherium* in dentition and stated that they may not exceed


~37
a
44.2
41.5
b
c
35.5
g
d
~26-27
f
36.5
e
i
h
30.5
~38-40
ectocuneiform
Mt III
~26
31
~92
24
ecto
cunei
form
mesocuneiform
j
k
l
m

◀ **Fig. 2** **a**–**e** M3 dex. of *Chalicotherium goldfussi* from Gratkorn (UMJGP 204676; **a** occlusal view, **b** posterior view, **c** anterior view, **d** lingual view, **e** labial view); **f**, **g** m1 sin. of *Lartetotherium sansaniense* from Gratkorn (UMJGP 203459; **f** occlusal view, **g** labial view); **h**, **i** D2 sin. of *Aceratherium* sp. from Gratkorn (UMJGP 203711; **h** occlusal view, **i** lingual view); **j**–**m** Mt II sin. of *Brachypotherium brachypus* from Gratkorn (UMJGP 204720; **j** proximal view, **k** dorsal view, **l** plantar view; **m** lateral view; articulation facets labelled); *scale bar* 10 mm

subgeneric or even specific rank. He included *Alicornops* as a subgenus in the genus *Aceratherium*. Antoine et al. (2010) and Becker et al. (2013) provided cranial, dental, and postcranial characters and observed many differences between *Aceratherium incisivum* and *Alicornops simorrense*, thus enabling now a better discrimination between the different Aceratherium-like Rhinocerotidae. Unfortunately, the only characteristic feature observable on the D2 cannot be observed on the specimen from Gratkorn described below due to fragmentation. Therefore, we can only use the genus attribution *Aceratherium* here sensu lato.

Aceratherium sp.

Description and comparison

The lingual fragment of a D2 sin. (UMJGP 203711; l ling: 30.5 mm; Fig. 2h, i) could be assigned to *Aceratherium* sp.. It is little worn, low crowned, and possesses a subrounded lingual wall. The protoloph and metaloph are well developed, and oriented obliquely, respectively perpendicular to the anteroposterior axis of the tooth. The crista is fused with the ectoloph. The crochet arises anteriorly from the metaloph near its connection to the ectoloph. On the lingual wall of the ectoloph anteriorly and posteriorly to the crista, one and two additional small folds, respectively, are developed. The crista is oriented perpendicular to the length axis of the tooth, the crochet subparallel. They are not fused and the medifossette is not closed. The tooth possesses a weak anterior protocone groove and a strong postfossette. Due to breakage, the shape of the prefossette cannot be reconstructed. A strong basal cingulum reaches lingually from anterior to posterior interrupted briefly only at the hypocone.

In dimensions and morphology, the tooth strongly resembles D2 of *Aceratherium incisivum* described by Kaya and Heissig (2001) from Yulafli (Turkey; Late Miocene; Vallesian) and of *Aceratherium* sp. from Çandir (Turkey; Middle Miocene; MN 6; Geraads and Saraç 2003), differing only in the lingually open medifossette and the lack of a sharp incision of the lingual cingulum at the medisinus. *Aceratherium* sp. from Çandir possesses furthermore an additional fossette anterior to the medifossette, absent in the specimen from Yulafli as well as in the specimen from Gratkorn. From the similar-sized *Hoploaceratherium tetradactylum* (Lartet, 1836), the tooth from Gratkorn differs in the straight unbending protoloph, the lingually open medifossette, a less pronounced lingual cingulum and in a shorter lingual length (Heissig 2012). The D2 of *Lartetotherium sansaniense* (Lartet in Laurillard, 1848) differs from the Gratkorn specimen in a smaller size, the reduced crista and a smaller postfossette (Heissig 2012). Dimensions of D1 of *Brachypotherium brachypus* (Lartet, 1837) (Heissig 2012) indicated a larger size for the D2 in this species than in the specimen from Gratkorn. At the moment, three genera (*Aceratherium*, *Alicornops*, *Hoploaceratherium*) are considered valid for the aceratheres from the Middle and Late Miocene of Western Europe (MN6 –MN13; Giaourtsakis 2003). Heissig (2009) explained that the only dental difference between *Alicornops* and *Aceratherium* is the size of the big incisors. Generally, teeth are very similar within the tribe (Heissig 2004) and differentiation based on teeth is difficult even between genera such as *Hoploaceratherium* and *Aceratherium*, due to the similarity in "cheek tooth characters" (Heissig 2004, p. 228). Giaourtsakis (2003) also stated that an assignment of isolated teeth to one of these genera is difficult and that the type locality of *Aceratherium incisivum* might contain more than one species as also indicated by Heissig (1972, 1996). The tooth from Gratkorn described here shows most similarities in dimensions and morphology with the genus *Aceratherium* s. l., but cannot be assigned to a species and is therefore left in open nomenclature as *Aceratherium* sp.

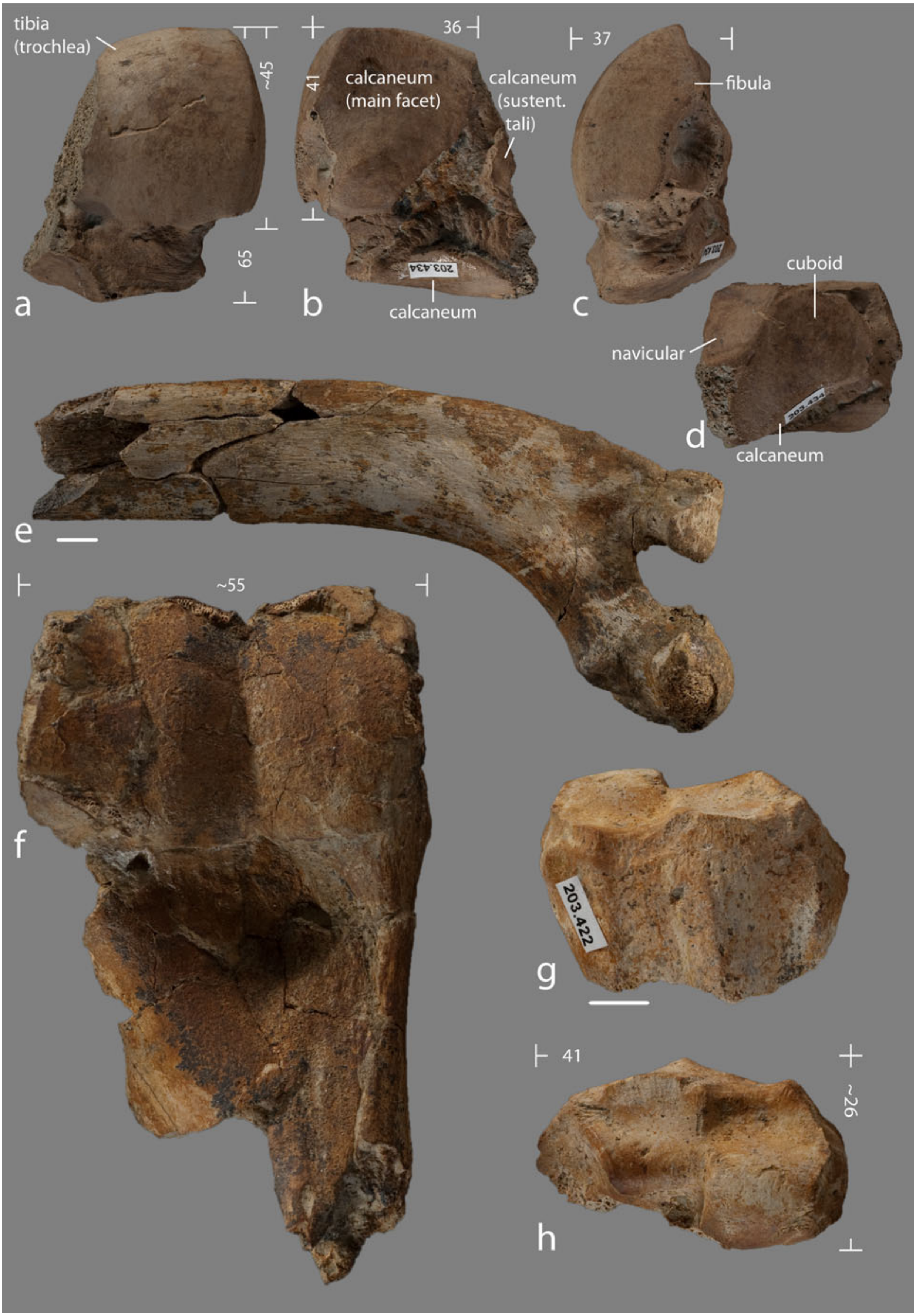
Tribe Teleoceratini Hay, 1902
Genus *Brachypotherium* Roger, 1904
Type species: *Brachypotherium brachypus* (Lartet, 1837)

Remarks: At the moment, two European *Brachypotherium* species are considered valid, *B. brachypus* and *B. goldfussi* (Kaup, 1834), though synonymy of the two taxa is possible (Heissig 2012).

Brachypotherium brachypus
Type: not designated (see also Heissig 2012)
Type locality: Simorre, Gers, France

Description and comparison

Of an astragalus sin. the lateral half is preserved (UMJGP 203434; lateral proximodistal length: about 65 mm; lateral dorsoplantar width of trochlea: 37 mm; lateral proximodistal length of trochlea: ~45 mm; proximodistal length of main (=ectal) facet for calcaneum: 41 mm; mediolateral width of main facet for calcaneum: 36 mm; Fig. 3a–d). The astragalus is proximodistally shorter than it is in Equidae (see, e.g. Alberdi et al. 2004), but longer than in Chalicotheriidae (see, e.g. Zapfe 1979) as it is typical in Rhinocerotidae (Heissig 2012). On the dorsal side, it still shows the convex lateral part of the trochlea with a shallow trochlear notch indicated medially. In lateral view, the narrow radius of the trochlea can be observed. The trochlea proximally meets the large


tibia (trochlea)
~45
65
a
41
calcaneum (main facet)
36
calcaneum (sustent. tali)
203.434
b
calcaneum
37
fibula
c
cuboid
navicular
203.434
d
calcaneum
e
~55
f
203.422
g
41
~26
h

◀**Fig. 3** **a**–**d** Astragalus sin. of *Brachypotherium brachypus* from Gratkorn (UMJGP 203434; **a** dorsal view, **b** plantar view, **c** lateral view; **d** distal view; articulation facets labelled); **e** left rib of Rhinocerotidae indet. (GPIT/MA/2400) from Gratkorn; **f** humerus sin. of *Anchitherium* sp. from Gratkorn (UMJGP 204694); **g**, **h** radius dex. of *Anchitherium* sp. from Gratkorn (UMJGP 203422; **g** dorsal view, **h** distal view); *scale bar* 10 mm

lateroproximal main facet for the articulation with the calcaneum at an acute angle. The latter possesses the typical "saddle-structure" of rhinoceroses, but is only slightly concave proximally and increasingly convex distally. It meets the facet for the articulation to the fibula to form an obtuse angle. The fibula facet is broad and convex. The narrow distal articular facet with the calcaneum is transversely elongated and meets the facet for articulation with the cuboid at an obtuse angle, while only a small part of the sustentaculum tali facet is preserved. The three calcaneum facets are separated by wide grooves. The cuboid facet is large, oval to subtriangular, and slightly convex along its short axis (dorsomedial to lateroplantar). Along its length axis, it changes from convex laterally to faintly concave medioplantarily. Of the facet for the articulation with the navicular, only the lateral-most part is preserved which is concave in both directions. It meets the cuboid facet at a rectangular to obtuse angle and is inclined laterally. The collum tali separating the articular facets for navicular and cuboid from the trochlea by a shallow depression is about 16 mm high laterally.

The astragalus from Gratkorn is most similar to that of *Brachypotherium brachypus*. As is typical for the Teleoceratini, it is broad and possesses only a shallow trochlear notch (Heissig 2012). With *Brachypotherium brachypus*, the specimen shares, besides the general shape, the distal prolongation of the main facet for the articulation with the calcaneum (Heissig 1976; Ginsburg and Bulot 1984; Cerdeño 1993; Geraads and Saraç 2003). While this is a constant feature in the species, dimensions seem to vary over time (Geraads and Saraç 2003). *Brachypotherium brachypus* from Bézian à La Romieu (Gers, France; Early Miocene; MN 4; Ginsburg and Bulot 1984), from Middle Miocene localities from France (Cerdeño 1993), and from Çandir (Turkey; Heissig 1976) are generally larger. A few smaller specimens are recorded from Çandir and Sofca (Turkey; late Middle Miocene; MN 7/8; Geraads and Saraç 2003; Heissig 1976). The astragalus from Gratkorn differs from those of representatives of the Rhinocerotinae by the separation of all the three calcaneum facets, whereas the distolateral one is fused to the sustentacular facet in this subfamily (Heissig 2009). In dimensions, the astragalus from Gratkorn would also fit well with *Aceratherium incisivum* from Höwenegg (Germany; Late Miocene; MN 9; Hünermann 1989), Rudabánya (Hungary; Late Miocene; MN 9; Heissig 2004) and Atzelsdorf (Austria; Late Miocene; MN 9; Heissig 2009), but differs in general morphology. In *Aceratherium*, the main facet for the articulation with the calcaneum is more strongly concave and distally not prolonged (Hünermann 1989; Heissig 2009; Antoine et al. 2010), the collum tali is shorter (Hünermann 1989), the trochlea is less bent in lateral view (Heissig 2009), the trochlear notch is deeper (see figs. in Hünermann 1989 and Heissig 2004), and in dorsal view, the distal rim of the trochlea rises more strongly proximally in the medial direction (see figs. in Heissig 2009). The latter two features and the non-elongated main calcaneum facet also distinguish the astragalus of *Hoploaceratherium tetradactylum* from the Gratkorn specimen (see figs. in Heissig 2004, 2012). In *A.* (*Alicornops*) *simorrense*, the main calcaneum articulation is also more strongly convex (Antoine et al. 2010). Based on size and morphology, UMJGP 203434 can be assigned to *Brachypotherium brachypus*.

A partial metatarsal II sin. (UMJGP 204720; Fig. 2j-m), missing the distal part, is preserved (preserved length: 92 mm; preserved proximal mediolateral width: ~38–40 mm; mediolateral width of facet for mesocuneiform: ~26 mm; smallest mediolateral width of diaphysis: 31 mm; smallest dorsoplantar width of diaphysis: 24 mm). The distal articulation and the lateroplantar part of the articulations for the ectocuneiform and metatarsal III are broken. In proximal view, the plantar half of the medial rim possesses at least three large foramina. The subtriangular articular surface for the mesocuneiform is large and mediolaterally moderately concave. Laterally, it borders the articular surface for the ectocuneiform. The latter is inclined to the proximal surface and abuts the articular surface for metatarsal III. These two dorsolateral facets meet at an angle of about 130–140°. Only the dorsolateral facets are preserved. The further presence of plantolateral facets is not proved but probable. In the space between the preserved dorsal and the missing plantar facets, there is a foramen near the margin of the proximal facet.

The Gratkorn second metatarsal is shorter and more massive than that of all rhinoceroses of the Middle Miocene except *Brachypotherium*. Further, the proximal facet for the mesocuneiform is broader and less concave than in *Aceratherium* (Hünermann 1989) and *Lartetotherium* (Heissig 2012). The inclination of the articular facet for the ectocuneiform is a typical sign of shortened metapodials and also occurs in other rhinocerotids with short metapodials. As for the astragalus, the metatarsal II differs from most specimens of *Brachypotherium brachypus* in its smaller size. Great size variability, as, e.g. observed above for the astragalus, can also be observed for the distal elements of the hind limb. A high variability has also been noticed for carpal elements of Late Miocene *Teleoceras* from Florida (Harrison and Manning 1983). A *Brachypotherium* metatarsal III from Sofca (Heissig 1976) fits well to the Gratkorn metatarsal II described here. UMJGP 204720 can therefore be readily assigned to *Brachypotherium brachypus*.

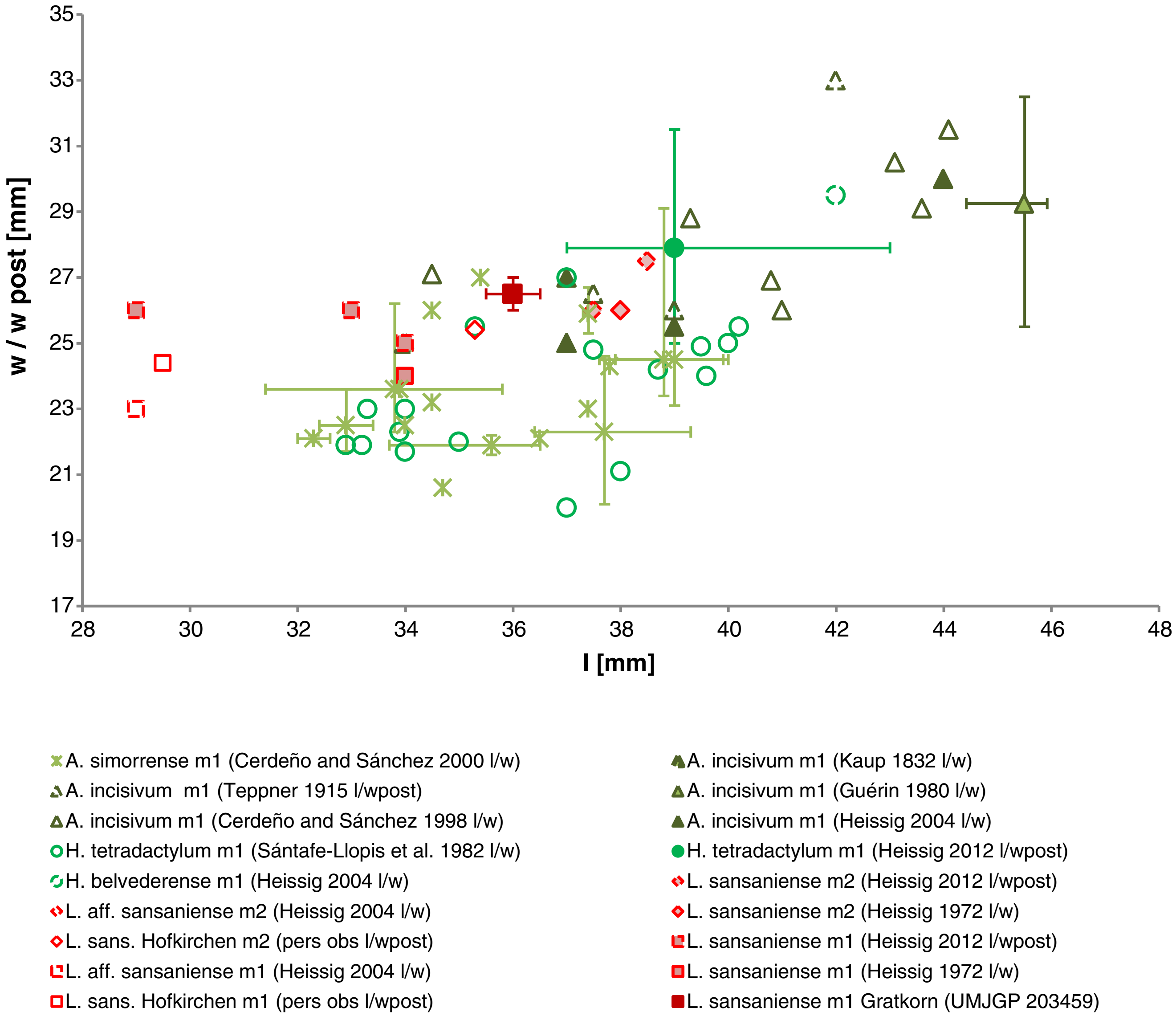


Fig. 4 Bivariate plot of length (*l [mm]*) versus width of m1 of *Lartetotherium sansaniense* from Gratkorn (UMJGP 203459) in comparison to m1 and m2 of other Rhinocerotidae of similar dimensions (if given posterior width was used, *[mm]*; for the Gratkorn specimen, the mean and the range from l basally to l max is given). References for measurements are given in *parentheses* (*L. sansaniense* from Hofkirchen (SNSB-BSPG 1958 I 170; Germany; Early/Middle Miocene)

Subfamily Rhinocerotinae Dollo, 1885
Tribe Rhinocerotini Dollo, 1885
Genus *Lartetotherium* Ginsburg, 1974
Type and only species: *Lartetotherium sansaniense* (Lartet in Laurillard, 1848)

Lartetotherium sansaniense (Lartet in Laurillard, 1848)

Holotype: Skull with mandible MNHN Sa 6478 (monotype)
Type locality: Sansan, France
Remarks: For a long time, there have been doubts whether this genus was single- or double-horned. After the determination that there was no trace of a second horn (Heissig 2012), the separation of *Lartetotherium* from the double-horned *Dicerorhinus* was fully justified. This is also well in accordance with Antoine et al. (2010), who reconstructed a phylogenetic position for *Lartetotherium* remote from *Dicerorhinus sumatrensis* (Fischer, 1814), and observed a sister group relationship with the one-horned *Gaindatherium*.

Description and comparison

A lower m1 sin. and a small fragment of a m2 sin. (UMJGP 203459; l max m1: 36.5 mm, l basally m1: 35.5, w post m1: ~26–27 mm; Fig. 2f, g) are preserved with some jaw fragments. The m2 fragment exhibits no usable characters. The m1 is fragmented lacking most of the trigonid, of which only the labial wall is preserved. The length of the paralophid and the width of the trigonid cannot be estimated therefore. The lingual wall of the talonid is also missing. The tooth is strongly worn (maximal preserved height at hypoconid: 15 mm). It possesses a short anterior and posterior, but lacks a labial cingulid. The labial wall is steep and forms an angle of about 120° with the occlusal surface at the hypoconid. The metalophid and hypolophid are united by wear. The trigonid and talonid are angular. The ectoflexid is distinct but not deep. It is inclined posteriorly. The incision of the talonid groove is not deep. The enamel is weakly wrinkled.

Tooth dimensions are quite variable between and among rhinocerotid species (compare, e.g. dimensions in Kaup 1832; Teppner 1915; Heissig 1972; Guérin 1980; Sántafe-Llopis et al. 1982; Cerdeño 1993; Cerdeño and Sánchez 1998, 2000; Heissig 2004, 2012; Fig. 4). Even if p4 and m1 cannot be distinguished by size (Heissig 2012), the rather open angulation of the hypolophid excludes the determination as a premolar. Many characters, such as a basally inclined labial wall and a moderately deep ectoflexid, are common to a lot of rhinoceros species. Because the most striking character for the separation of Rhinocerotini and Aceratheriini, the length of the paralophid, is not preserved, the only valuable character is the configuration of the cingulids. There is absolutely no labial cingulid and the anterior and the posterior cingulid are short and do not proceed onto the labial side. This configuration excludes the Aceratheriinae, which have longer terminal cingulids, mainly on the posterior side, and often short cingular ridges or cuspules below the ectoflexid. "*Dicerorhinus*" *steinheimensis* Jäger, 1839, which also has strongly reduced cingulids, differs from the Gratkorn specimen by a clearly smaller size. The strongly reduced cingulids are very characteristic for *Lartetotherium sansaniense* (Heissig 2012). So the tooth proves the presence of this third species, which is widespread in Middle Miocene faunas.

Family Equidae Gray, 1821
Subfamily Anchitheriinae Leidy, 1869
Genus *Anchitherium* Meyer, 1844
Type species: *Anchitherium aurelianense* (Cuvier, 1825)

Lectotype: Left upper jaw with P2-M3 (Sa 5154; Abusch-Siewert 1983; pl. 16, fig. 1)
Type locality: Sansan, France

Anchitherium sp.

Description and comparison

The distal fragment of the humerus sin. (UMJGP 204694; Fig. 3f) is compressed, but the biconcave equine condylus humeri can still be recognised. It comprises a stronger medial and a shallower lateral depression. In size (distal lateromedial width of articulation: ~55 mm) it fits well in the variability of *A. aurelianense* from Baigneaux (France; Early Miocene; MN 4; Alberdi et al. 2004), Sansan (France; Middle Miocene; MN 6; Alberdi and Rodríguez 2012) and Sandelzhausen (Germany; Middle Miocene; MN 5; personal observation).

Although the distal articulation of a right radius (UMJGP 203422; Fig. 3g, h) is fragmented, lacks most of the processus styloideus radii, and shows intense small mammal gnawing, its typical equine morphology can still be observed. The trochlea radii is bipartite, the medial condyle being larger than the lateral and shifted more in the palmar direction along the sagittal plane. Anterior to the two condyles of the trochlea radii is a depression, which is only slightly biconcave. Distally the radius is not fused with the ulna, as is typical for *Anchitherium* (see, e.g. *A. aurelianense*, Alberdi et al. 2004, and *A. corcolense*, Iñigo 1997) in contrast to *Hipparion* (Alberdi and Rodríguez 1999), where the ulna and radius are fused distally. The distal part of the concavity for the articulation to the ulna is preserved.

The distal fragment from Gratkorn fits well in shape and dimensions (distal lateromedial width of articulation: 41 mm; distal dorsopalmar width of articulation: ~26 mm) to *A. aurelianense* from Baigneaux (Alberdi et al. 2004), Sansan (Alberdi and Rodríguez 2012), and Sandelzhausen (personsal observation, material SNSB-BSPG), as well as to *A. corcolense* Iñigo, 1997 from Córcoles (Spain; Early Miocene; MN 4; Iñigo 1997), but is smaller than in the larger genus *Sinohippus* Zhai, 1962 (Salesa et al. 2004). As the taxonomic status of late Middle Miocene to Late Miocene *Anchitherium* species is still unresolved (Abusch-Siewert 1983), and the two fragments from Gratkorn do not show any species diagnostic features, they are left in open nomenclature as *Anchitherium* sp..

Stratigraphic and ecological considerations

The perissodactyl fauna from Gratkorn fits well as a Middle Miocene mammal assemblage. Although *C. goldfussi* was defined by Kaup (1833) on material from the Dinotheriensande from Eppelsheim, so far considered to be of Late Miocene age, its occurrence was not restricted to Upper Miocene sediments, but it is also known from late Middle Miocene localities, such as Saint-Gaudens and La Grive (both France; MN 7/8; Anquetin et al. 2007). Böhme et al. (2012) showed, furthermore, that the Dinotheriensande (Eppelsheim Fm) are not restricted to the Upper Miocene but also include faunal elements of strictly Middle Miocene age. *Brachypotherium*, *Aceratherium* and *Lartetotherium* are part of phylogenetic lineages ranging from Early to Late Miocene (Heissig 2009, 2012). Though Late Miocene occurrences of *Anchitherium* are recorded in some European localities (see, e.g. Villalta and Crusafont 1945; Thenius 1950; Alberdi 1974;

Sondaar 1971; Abusch-Siewert 1983; Hernández Fernández et al. 2003; Daxner-Höck and Bernor 2009), the species is common mainly in the Early and Middle Miocene (Abusch-Siewert 1983). In association with the other large mammal remains, it fits well in a late Middle Miocene assemblage. A general size increase in the Eurasian Anchitheriinae was observed during the Miocene by Mayet (1908), Wehrli (1938), Abusch-Siewert (1983) and Alberdi and Rodríguez (2012), while Salesa et al. (2004) noted co-occurrence of different size classes in some localities. A late Middle Miocene age could not be verified by the increased size of *Anchitherium* remains from Gratkorn, however, because of the scarcity of the material and especially due to the total absence of dental material, in which a size increase can be much better observed than in postcranial elements (Alberdi and Rodríguez 2012).

The fossil assemblage from Gratkorn is preserved in a palaeosol and shows no signs of reworking (Gross et al. 2011; Havlik et al. 2014, this issue). The composition of the fossil assemblage was most likely strongly controlled by ecological factors. Secondary accumulation of very large mammals, due to a higher preservation potential of their robust hard tissues, as, e.g. observed in fluvial sediments, was thus not the case at the locality (for further discussion, see Havlik et al. 2014, this issue). The wider landscape around Gratkorn supplied a great range of habitats, such as active and abandoned channels, riparian woodland, floodplain soils, and ephemeral ponds as well as nearby drier, open areas (Gross et al. 2011; Böhme and Vasilyan 2014, this issue). For the locality itself and the nearer surroundings, it can be assumed that only a limited amount of biomass was available. Perissodactyls with larger body sizes and thus a higher amount of daily food intake, such as Rhinocerotidae and Chalicotheriidae, were therefore most likely rarer in Gratkorn than the artiodactyls with their smaller body sizes (for further discussion, see Aiglstorfer et al. 2014a, this issue). The few records of the equid *Anchitherium* sp. might be explained by ecological adaptation to more open environments than, e.g. in ruminants, which are the most common large mammals in Gratkorn (for further discussion, see Aiglstorfer et al. 2014b, this issue). Generally considered to be non-selective browsers, *B. brachypus* and *A. incisivum* (Heissig 2009) would fit well in this ecosystem with a wide range of habitats. Stable isotope ($\delta^{18}O_{CO3}$, $\delta^{13}C$) analyses on the enamel of *Lartetotherium sansaniense* from Gratkorn even indicate a certain amount of feeding in a more open environment (see Aiglstorfer et al. 2014a, this issue). Because of the lack of lingual cingula on the upper premolars, this species has often been interpreted as a selective browser (Heissig 2012), but this feature does not exclude a considerable amount of low abrasive grasses. Kaiser (2009) recorded a mixed feeding strategy for *A. aurelianense* from Sandelzhausen, terming it a “dirty” browser. Hernández Fernández et al. (2003) considered *Anchitherium* to be generally a browser. Semprebon et al. (2011) assigned *C. goldfussi* to the browsing guild by microwear analysis, but, because of the higher enamel abrasion, reconstructed a certain amount of hard fruits, seeds or nuts in their diet. Referring to observations by Zapfe (1979) on the fissure fillings from Devínska Nová Ves (Slovakia; Middle Miocene; MN 6), Semprebon et al. 2011) have suggested that *Celtis* fruits, as a possible diet source, could produce microwear patterns, such as those observed for European Chalicotheriinae in their study. Microwear studies have so far not been accomplished for Gratkorn, but could help to verify the hypothesis of Semprebon et al. (2011) with *Celtis* being a common element of the flora in Gratkorn and therefore a potential food source for *C. goldfussi*. However, the higher potential for preservation of this fruit in comparison to other flora has of course to be taken into consideration. As is common in Central and Western Europe during that time, grazing as a dominant feeding strategy is not indicated in the perissodactyl large mammals from Gratkorn.

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