Herbivorous large mammals from the late Middle Miocene Gratkorn locality (Styria, Austria)

Taxonomy and Isotopic Tracking of Palaeoecology ($\delta^{18}O_{CO3}$, $\delta^{13}C$, $^{87}Sr/^{86}Sr$)

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Manuela Aiglstorfer

aus Nördlingen

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Dekan: Prof. Dr. Wolfgang Rosenstiel

1. Berichterstatter: Prof. Dr. Madelaine Böhme

2. Berichterstatter: Prof. Dr. Hervé Bocherens

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Abstract

During transition from Middle to Late Miocene strong geographic, climatic, and biotic changes had a strong impact on aquatic and terrestrial ecosystems in Central Europe. Large-scale erosion in the Central Paratethys realm caused a lack of terrestrial sediments from this time period and thus resulted in a remarkable palaeobiological "blackout" for the record on land in this region from late Sarmatian to early Pannonian.

The here presented Gratkorn locality, well dated to an age of 12.2/12.0 Ma (early late Sarmatian) provides a rich vertebrate assemblage (species diversity as well as total number of specimens) with 65 recorded species up to date. It represents a unique window to the terrestrial record of this time period and helps to understand the evolution of vertebrate faunas during the Middle-Late Miocene transition. Remains of herbivorous large mammals were morphologically described and assigned to the following taxa (Suidae not part of this thesis): *Deinotherium levius* vel *giganteum*, *Aceratherium* sp., *Brachypotherium brachypus*, *Lartetotherium sansaniense*, *Chalicotherium goldfussi*, *Anchitherium* sp., *Listriodon splendens, Parachleuastochoerus steinheimensis*, *Dorcatherium naui*, *Micromeryx flourensianus*, ?*Hispanomeryx* sp., *Euprox furcatus*, Palaeomerycidae gen. et sp. indet., and *Tethytragus* sp..

Except of *Dorcatherium naui*, presence and evolutionary stage of the large mammals are well in accordance with a late Middle Miocene assemblage. The records of *Euprox furcatus* and *Micromeryx flourensianus* comprise the first for the Styrian Basin and *Hispanomeryx* has not been recorded for Central Europe so far besides the locality Steinheim a. A.. *Dorcatherium naui* is considered a typical faunal element of the Late Miocene and has been described only recently from Middle Miocene localities. With the rich material from Gratkorn assignation of this species to a more selenodont phylogenetic lineage together with *Dorcatherium guntianum* and well distinct from *Dorcatherium crassum* can be verified and the descent of the species from the latter thus shown to be unlikely.

The fossil assemblage from Gratkorn is considered an autochthonous taphocoenosis without any significant time averaging or faunal mixing. Most likely the accumulation did not last longer than a few years or decades and local accumulation of large mammal bones was the result of scavenging.

Based on the taxonomic record, morphology of skeletal and dental elements, and especially isotope analyses ($\delta^{18}O_{CO3}$, $\delta^{13}C$, $^{87}Sr/^{86}Sr$), dominance of C3 vegetation, semi-arid and subtropical climate with distinct seasonality, and too little precipitation for closed canopy woodlands can be reconstructed for the wider area around the locality. The landscape provided diversity in plant resources to allow occupation of different niches by herbivorous large mammals: subcanopy browsing, rooting, top canopy browsing, facultative frugivory, and mixed feeding. Comparison with data from other Miocene localities from different areas and time slices showed rather stable niche partitioning for the herbivorous large mammal species. Thus these seem to be affected only to a minor degree by climatic conditions but rather represent a typical partitioning for a Middle Miocene ecosystem.

Zusammenfassung

Starke geographische, klimatologische und biotische Veränderungen während des Übergangs vom Mittleren zum Späten Miozän hatten einschneidende Auswirkungen auf aquatische als auch terrestrische Ökosysteme Zentraleuropas. Durch stark erosive Ereignisse wurden terrestrische Ablagerungen aus diesem Zeitbereich in der zentralen Paratethys abgetragen und führten dort zu einem paläobiologischen "Blackout" im festländischen Raum für spätes Sarmatium bis frühes Pannonium.

Von der hier vorgestellten Lokalität Gratkorn, gut datiert auf 12.2/12.0 Ma (frühes Spätsarmatium), ist eine reiche Wirbeltierfauna (Arten- und Individuenreichtum) mit bisher 65 dokumentierten Arten überliefert. Die Fundstelle stellt ein einzigartiges Fenster in die terrestrischen Ablagerungen dieses Zeitabschnittes dar und ist essentiell für das Verständnis der Faunenentwicklung während des Übergangs vom Mittleren zum Späten Miozän. Reste von herbivoren Großsäugern wurden morphologisch beschrieben und folgenden Taxa zugeordnet (Suidae nicht Teil dieser Arbeit): *Deinotherium levius* vel *giganteum*, *Aceratherium* sp., *Brachypotherium brachypus*, *Lartetotherium sansaniense*, *Chalicotherium goldfussi*, *Anchitherium* sp., *Listriodon splendens*, *Parachleuastochoerus steinheimensis*, *Dorcatherium naui*, *Micromeryx flourensianus*, ?*Hispanomeryx* sp., *Euprox furcatus*, Palaeomerycidae gen. et sp. indet. und *Tethytragus* sp..

Bis auf *Dorcatherium naui* passen alle Großsäuger-Taxa und die jeweilige evolutive Stufe gut in eine spätmittelmiozäne Vergesellschaftung. *Euprox furcatus* und *Micromeryx flourensianus* werden zum ersten Mal aus dem Steirischen Becken beschrieben und für *Hispanomeryx* ist es nach der Fundstelle Steinheim a. A. erst der zweite Nachweis aus Zentraleuropa. *Dorcatherium naui* ist typisch für obermiozäne Faunenvergesellschaftungen und wurde erst vor kurzem aus mittelmiozänen Fundstellen beschrieben. Mit dem reichen Material von Gratkorn konnte die Zuordnung dieser Art zusammen mit *Dorcatherium guntianum* zu einer selenodonteren, deutlich von *Dorcatherium crassum* getrennten phylogenetischen Linie verifiziert werden. Eine Abstammung der Art *Dorcatherium naui* von *Dorcatherium crassum* kann daher nun als unwahrscheinlich eingestuft werden.

Die Fossilvergesellschaftung wird als schnell abgelagerte, autochthone Taphocoenose interpretiert, die vermutlich in nur wenigen Jahren bis Jahrzehnten akkumuliert wurde. Die lokale Anreicherung geht wahrscheinlich zu einem großen Teil auf Aasfresser zurück. Anhand der Faunenvergesellschaftung, morphologischen Untersuchungen und vor allem Isotopenanalysen ($\delta^{18}O_{CO3}$, $\delta^{13}C$, $^{87}Sr/^{86}Sr$) kann für die Gegend um die Fundstelle eine von C3 Pflanzen dominierte Vegetation in einem semi-ariden, subtropischen Klima mit ausgeprägter Saisonalität und zu geringer Niederschlagsmenge für eine geschlossene Waldfläche rekonstruiert werden. Der Lebensraum bot verschiedene ökologische Nischen für herbivore Großsäuger: „subcanopy browsing", Rhizophagie, „top canopy browsing", fakultative Frugivorie und „mixed feeding". Der Vergleich mit Daten von Miozänen Fundstellen anderer Ablagerungsräume und Zeitabschnitte zeigt eine gewisse Konstanz in der Einnischung der Großsäuger. Die in Gratkorn beobachtete jeweilige ökologische Nische scheint daher für ein mittelmiozänes Ökosystem typisch zu sein und weniger stark von klimatischen Rahmenbedingungen abzuhängen.

1. Introduction

For the understanding of climatologic and geodynamic changes and their impact on ecosystems through time and space, a comprehensive data set, including data from marine as well as terrestrial deposits, is indispensible. The Miocene (23.03–5.33 Ma; Cohen et al. 2013) has proven an essential time slice for the decoding of our continent's cenozoic history. Many geodynamic changes (e.g. the uplift of the Alpine mountain chain) took place during this epoch, which strongly influenced and finally led to the modern shape of our continents and landscapes. Furthermore, it is marked as a time of strong climatic turnovers and characterized by the diversification of many mammal groups, as for example Ruminantia, Rhinocerotidae, and Primates (e.g. Rössner 1995; Heissig 1999; Bibi and Güleç 2008; Casanovas-Vilar et al. 2011).

While there is more and often far better information available for aquatic sedimentary sections, investigations on terrestrial deposits lack the necessary frame data in many cases, as for example well-founded stratigraphic dating and especially estimation of the stratigraphic coverage. Furthermore, the more patchy occurrence of localities and the regular lack of any information for certain time slices very often enhance the incorporation of terrestrial data in the "big picture".

The here presented Gratkorn locality can be assigned to such a time slice poor in data so far. It provides besides a rich vertebrate fauna also the necessary frame data to integrate the locality in the stratigraphic, palaeoenvironmental, and palaeoclimatological context of the Central European Miocene sedimentary succession.

1.1. Miocene sedimentary succession of the Central Paratethys realm

During Miocene, Central Europe was influenced by the North Sea in the north, the Mediterranean Sea in the south and to a great extent by the Paratethys Sea (Early to Middle Miocene)/Lake Pannon (Late Miocene to Pliocene) in between (Rasser et al. 2008). The Paratethys realm can be subdivided in Western (Rhone Basin, Alpine Foreland Basins from Switzerland to Austria), Central (Vienna Basin to Carpathian Foreland) and Eastern Paratethys (Fig.1; Steininger and Wessely 2000; Rasser et al. 2008). Its sedimentary succession was controlled by tectonics, sea level fluctuations, and climatic changes, leading to permanently changing and complex seaways and land bridges between the above mentioned marine systems as well as the western Indo-Pacific and causing an alternating sequence of marine and terrestrial deposits (Steininger and Wessely 2000; Harzhauser et al. 2007; ter Borgh et al. 2013). This led to a strong biogeographic differentiation and consequently resulted in the establishment of different chronostratigraphic and lithostratigraphic concepts (Steininger and Wessely 2000; Rasser et al. 2008). The regional stage concept of the Central Paratethys realm (Fig. 2; housing the late Middle Miocene locality Gratkorn), is well established by the combination of litho-, bio-, cyclo-, and magneto-stratigraphy as well as astrochronology and the correlation with eustatic sea level fluctuations (Rögl 1998; Gross et al. 2007a; Gross et al. 2007b; Schreilechner and Sachsenhofer 2007; Gross 2008; Harzhauser et al. 2008; Lirer et al. 2009; Vasiliev et al. 2010; Flügel et al. 2011; Gross et al. 2011; ter Borgh et al. 2013; Gross et al. 2014).
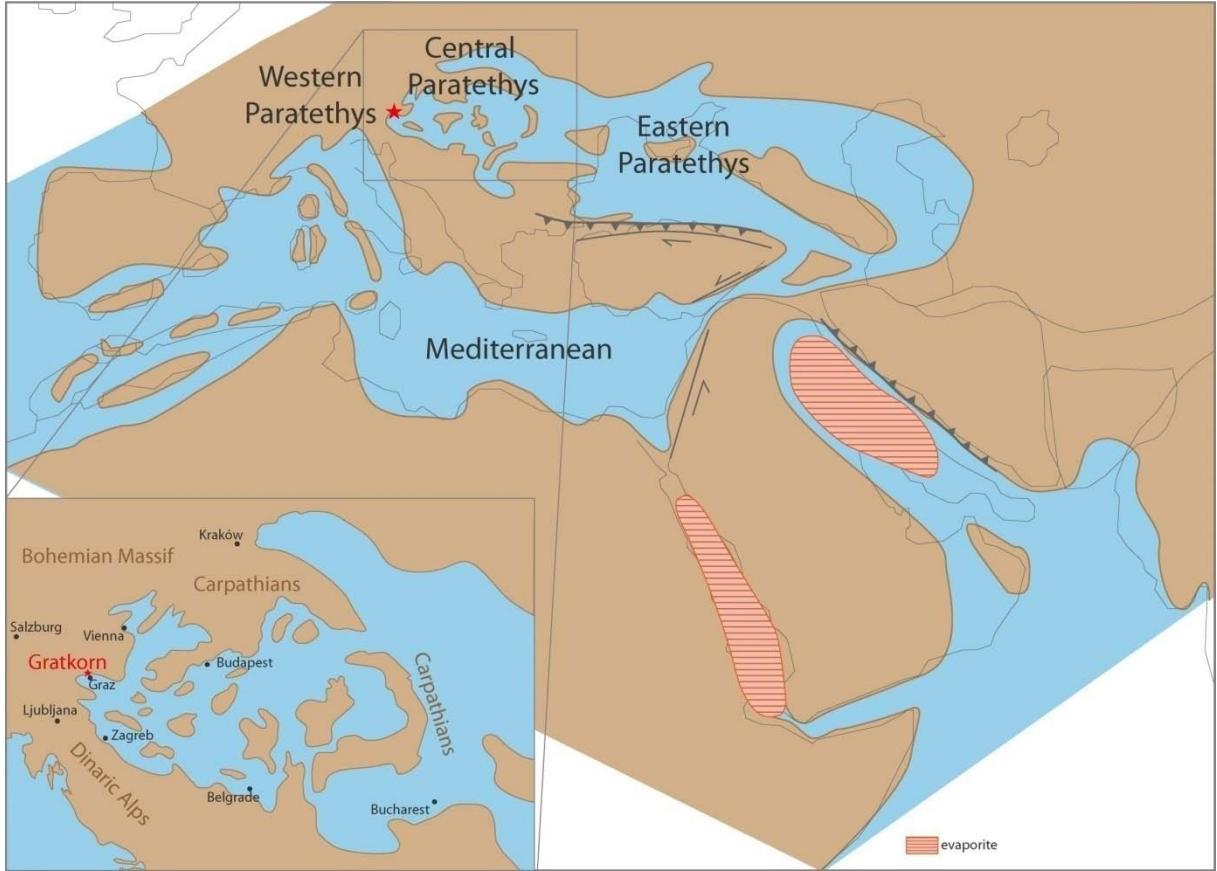
Fig. 1: Palaeogeographic situation in Central Europe at the time of the early Sarmatian with focus on Central Paratethys realm (modified after Rögl 1998; Lukeneder et al. 2011).

1.2. Miocene mammal record of Central Europe

In the earlier Middle Miocene many localities can be found rich in vertebrates and reasonably well dated with methods independent of biochronology and thus enabling a comparison of faunal assemblages and the reconstruction of climatic frame conditions (Abdul Aziz et al. 2008; Gross and Martin 2008; Kälin and Kempf 2009; Abdul Aziz et al. 2010; Sachsenhofer et al. 2010; Reichenbacher et al. 2013). During late Middle and early Late Miocene substantial turnovers strongly affected aquatic as well as terrestrial life in Central Europe [see e.g. decline in species diversity in Tragulidae and Cervidae in Central Europe on Fig. 2 (only localities with well determined material and reliable dating are taken into consideration; influences of sampling biases, as e.g. faunal mixing cannot be completely ruled out but are considered in evaluation of data), or the Sarmatian-Pannonian-extinction-event (Harzhauser and Piller 2007)]. After the warm and humid Miocene climatic optimum (Böhme 2003), the Middle Miocene climatic cooling (14–12 Ma; Shevenell et al. 2004; Anthonissen 2012) and geodynamic changes led to a decrease in the mean annual temperature (MAT), an increase in seasonality as well as generally more pronounced aridity during the late Middle Miocene and early Late Miocene in Central Europe (Böhme et al. 2008; Böhme et al. 2011b). The successive enlargement of the East Antarctica ice shield during the Serravallian can be well observed in the marine record (Zachos et al. 2001; Abels et al. 2005). A cooling of more than 7 °C in MAT is indicated

for the terrestrial record of Central Europe by the disappearance of reptiles adapted to warmer temperatures, like e.g. crocodiles and giant tortoises (Böhme 2003), but also short phase intensifications of the hydrologic cycle (more humid and warm; "washhouse-climate phases" *sensu* Böhme et al. 2008) are recorded (Böhme 2003; Böhme et al. 2008).

The isolation of the Pannonian basin at 11.6 Ma triggered maybe by an eustatic sea level drop was sustained by the uplift of the Carpathian Mountains (ter Borgh et al. 2013) and led to large-scale erosion of Upper Sarmatian/Lower Pannonian deposits is in the Central Paratethys (Schreilechner and Sachsenhofer 2007; Kováč et al. 2008; Fig. 2). Consequently, terrestrial sediments of this time period are only rarely preserved in the Styrian Basin, which led to a remarkable palaeobiological "blackout" at about the Late Sarmatian to Early Pannonian (~12.5–11.5 Ma; Gross et al. 2011).

For the North Alpine Foreland Basin (NAFB) late Middle Miocene localities delivering a noteworthy large mammal assemblage are rare as well and often comprise only fluvial accumulations providing mainly big sized large mammal remains, such as proboscideans (Eronen and Rössner 2007). This can either be explained by the deficiency of fieldwork (which is rather unlikely considering the strong record of scientific publications dealing with the Neogene sedimentary succession of the NAFB), strong tectonic/orogenic changes (Frisch et al. 1998; Kuhlemann 2007; Ziegler and Dèzes 2007), or climatic changes like the aforementioned global cooling and the formation of open landscapes in temperate zones (Böhme et al. 2008). However, biostratigraphic and lithostratigraphic investigations indicate a continuous sedimentation from 14 to 11 Ma for Western Bavaria in contrast to the deposits from Styria (M. Böhme pers. comm. March 21st 2014).

Other terrestrial records for the terminal Middle Miocene in Central and Western Europe either comprise fissure fillings [e.g. Przeworno (Poland; Glazek et al. 1971) and La Grive (France; Mein and Ginsburg 2002)], for which estimations on stratigraphic age/range and accumulation processes are often limited, or present accumulations most likely biased by a considerable degree of redeposition (overrepresentation of mammals with large body sizes, such as proboscideans and rhinocerotids; see e.g. data from Fortelius (2014)). Recently, the existence of a short time faunal turnover in Spain at about 9.75 Ma (Early/Late Vallesian; "Mid Vallesian Crisis") has been questioned (at least for small mammals; Casanovas-Vilar et al. 2014). They consider a scenario with a series of extinctions over a longer time span more realistic for the early Late Miocene in this region.

In any case, late Middle Miocene/early Late Miocene localities providing a rich sympatric vertebrate fauna are still rare and thus the detailed chronologic context and response of large mammal communities in Europe to the climatic change during the Middle Miocene Cooling and the late Middle Miocene climax in aridity followed by the "washhouse" phases during the Tortonian (Böhme et al. 2008) remain open questions so far. An interesting point concerning this topic is also the evolution of hominoids. While the first record of hominoids in Europe dates back to about 17 Ma (Böhme et al. 2011a), the quite rich record of late Middle to early Late Miocene hominoid findings points to a diverse and geographically wide spread fauna in Europe (e.g. Abocador de Can Mata (Valles Penedes; Spain), St. Gaudens and La Grive (France), and St. Stephan (Austria); Casanovas-Vilar et al. 2011).

Cervidae

Lucentia aff. pierensis
Procapreolus loczyi
Amphiprox anocerus
Cervavitus variabilis
Euprox dicranocerus
Euprox furcatus
Euprox minimus
Paradicrocerus elegantulus
Dicrocerus elegans
Heteroprox eggeri
Heteroprox larteti
Procervulus dichotomus
Procervulus praelucidus

sp.

Tragulidae

Dorcatherium peneckei
Dorcatherium vindebonense
Dorcatherium crassum
D. naui
Dorcatherium guntianum

record for species
cf. or tentative record for species
possible stratigraphic range for locality

MAP_t/MAP_0 [%]

250
200
150
100
50
0

Washhouse Climate
Mi 7?
Washhouse Climate
Mi 6
Mi 5
Mi 4
Middle Miocene Cooling
Mi 3 b
Mi 3 a
Miocene Climatic Optimum

Central Paratethys stage

Pannonian
Sarmatian
Late Badenian
Middle Badenian
Early Badenian
Karpatian
Ottnangian

international stage

Tortonian
11.62 Ma
Serravallian
13.82 Ma
Langhian
15.97 Ma
Burdigalian

ELMMZ

Turolian
Vallesian
Astaracian
Orleanian

series

Late Miocene
Middle Miocene
Early Miocene

polarity chron

C4
C4A
C5
C5A
C5AA
C5AB
C5AC
C5AD
C5B
C5C
C5D
C5E

Ma
8
9
10
11
12
13
14
15
16
17
18

4

◄   Fig. 2: Stratigraphic chart (including international and regional stratigraphy as well as European Land Mammal Zones (ELMMZ)) with recorded species diversity of Tragulidae and Cervidae (focus on Central Europe) correlated to the mean annual precipitation (MAP) of the Paratethys area (Central and Eastern Europe) and to major climatic events (green = more humid and warm; blue = cooling; Mi 3a–7? = deep sea Miocene isotope events referred to glaciation) and geodynamic events recorded in the Central Paratethys realm (dark grey lines = erosional surfaces and light grey = general increase of erosion) [stratigraphic stages after Gross et al. (2014); absolute ages follow Cohen et al. (2013); climatic events after Böhme (2003), Abels et al. (2005), Böhme et al. (2008), Mourik et al. (2011); erosional surfaces after Schreilechner and Sachsenhofer (2007) and Kováč et al. (2008); MAP (means and ± 1σ confidence intervals (grey shaded area) of the MAP in relation to the modern local value: MAPt/MAP0 (×100%); age uncertainties not included) modified (following M. Böhme pers. comm. March 17th 2014) after Böhme et al. (2011b); tragulid record after Aiglstorfer et al. (2014d) and cervid record modified after Böhme et al. (2012)].

The here presented terrestrial vertebrate locality Gratkorn closes one of these big gaps in the record of terrestrial environments in Central Europe and provides besides a rich fauna also the necessary frame data. It is stratigraphically well defined and due to lithological and taphonomical analysis can be termed a sympatric large mammal assemblage (Gross et al. 2011; Gross et al. 2014; Havlik et al. 2014). Its faunal content shows strong affinities to other localities of this time slice, like the fissure fillings from La Grive and especially the alluvial deposits of Abocador de Can Mata (Spain), famous for their high diversity in hominoids.

1.3. Research history, geographical and geological setting and stratigraphy of the Gratkorn locality

The term "Gratkorn locality" stands for a late Middle Miocene (Sarmatian *sensu stricto*; 12.2/12.0 Ma) fossil site rich in terrestrial vertebrates (Gross et al. 2011). It is located in the clay pit St. Stefan (15°20'56"E/47°08'14"N) 700 m E of the town Gratkorn (about 10 km NNW of Graz; Fig. 1; Gross et al. 2014). Besides lacustrine sediments yielding mostly plant and invertebrate remains (Meller and Gross 2006; Gross et al. 2007a; Gross et al. 2007b; Klaus and Gross 2007; Gross 2008; Klaus and Gross 2010) the site comprises a fossiliferous layer housing nearly all vertebrate findings from this locality (Gross et al. 2011; Gross et al. 2014). While the first fossil findings from the area around St. Stefan were described more than 160 years ago (Unger 1850, 1852; Gross 1999), the vertebrate comprising palaeosol was detected not until 2005, when the first bones were discovered during geological mapping of the region. So far this has led to 18 scientific publications (Gross et al. 2007b; Harzhauser et al. 2008; Daxner-Höck 2010; Prieto et al. 2010a; Prieto et al. 2010b; Gross et al. 2011; Aiglstorfer et al. 2014a; Aiglstorfer et al. 2014b; Aiglstorfer et al. 2014c; Aiglstorfer et al. 2014d; Angelone et al. 2014; Böhme and Vasilyan 2014; Göhlich and Gross 2014; Gross et al. 2014; Havlik et al. 2014; Prieto et al. 2014a; Prieto et al. 2014b; Made et al. in press; not listed: contributions to scientific congresses).

To avoid confusion, especially with the locality "St. Stefan im Lavanttal" (Carinthia, Austria), famous for its *Dryopithecus*-findings (Mottl 1957), and as "St. Stefan"/"St. Stephan" is quite a common name in Austria, it was decided to name the locality "Gratkorn" instead of "St. Stefan" (Gross et al. 2014).
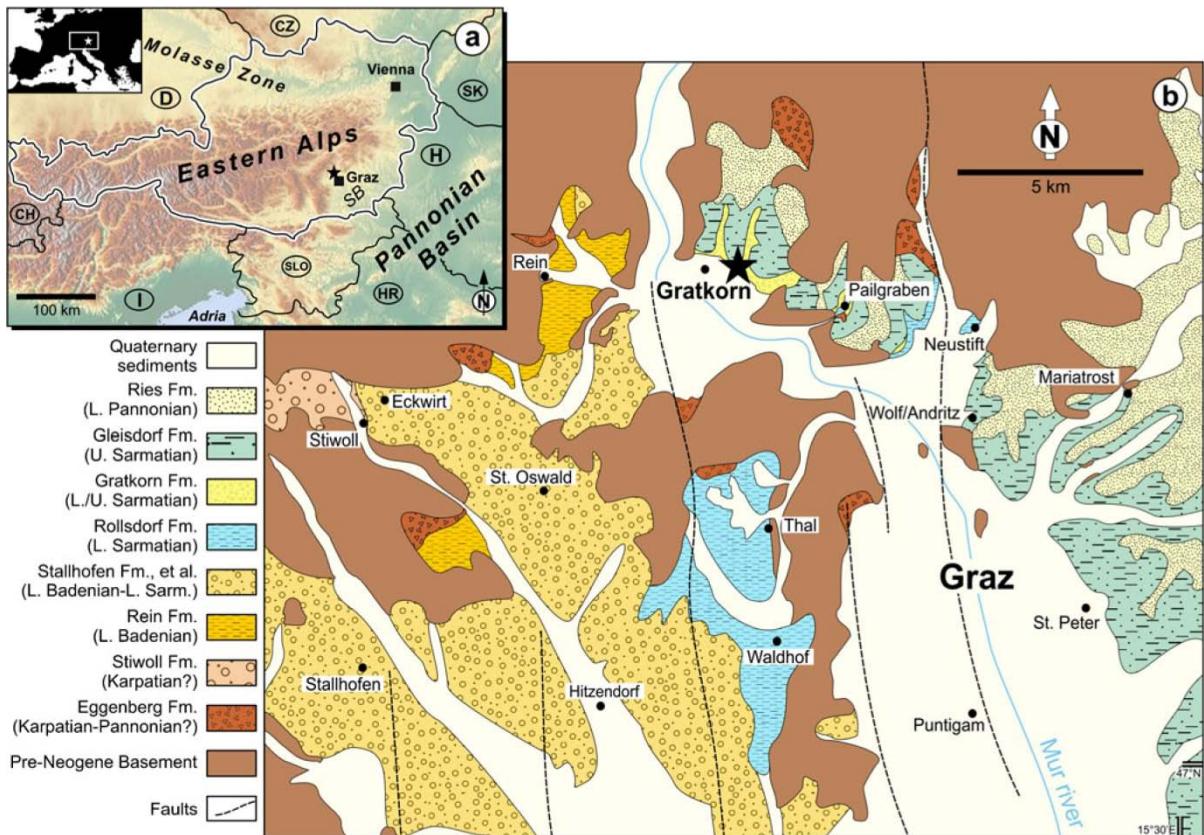
Fig. 3: Geographical and Geological setting of the Gratkorn locality (from Gross et al. 2014).

The locality is situated in the Gratkorn Basin, a satellite basin at the northern margin of the Styrian Basin (Fig. 3). To the North this basin is bordered by Palaeozoic basement (Flügel and Hubmann 2000; Flügel et al. 2011) and to the South most of the Sarmatian strata are covered by Pannonian and younger sediments (Fig. 3). The Styrian Basin as part of the Pannonian Basin System is a N-S striking extensional structure formed in connection with the extrusion of the Eastern Alps (Sachsenhofer 2000; Steininger and Wessely 2000; Gross et al. 2007a). The sedimentary filling of the Basin was initiated in the Early Miocene (syn-rift phase; Gross et al. 2007a). The oldest Neogene sediments can be roughly assigned to the Ottnangian, the youngest Miocene sediments are dated as Late Pannonian (Gross et al. 2007a).

The most basal sediments in the eastern Gratkorn basin are interpreted as braided river system with influences of alluvial fans (polymict gravels/conglomerats in alternating sequence with more sand dominated deposits; Gross et al. 2014; Fig. 4). They are assigned to the Gratkorn Formation (Fm) and house the here discussed vertebrate yielding palaeosol (on top of the so called Gratkorn Gravel) (Flügel et al. 2011; Gross et al. 2014). On top of the Gratkorn Fm the up to 25 m thick limnic pelites of the Peterstal Member (Mb; Gleisdorf Formation) comprise the clay, which is mined in Gratkorn. Up section follow the upper part of the Gleisdorf Formation (Lustbühel Mb); alternating sequences of gravel, sand, and pelite) and the fluviatile Ries Formation (Gross et al. 2014).
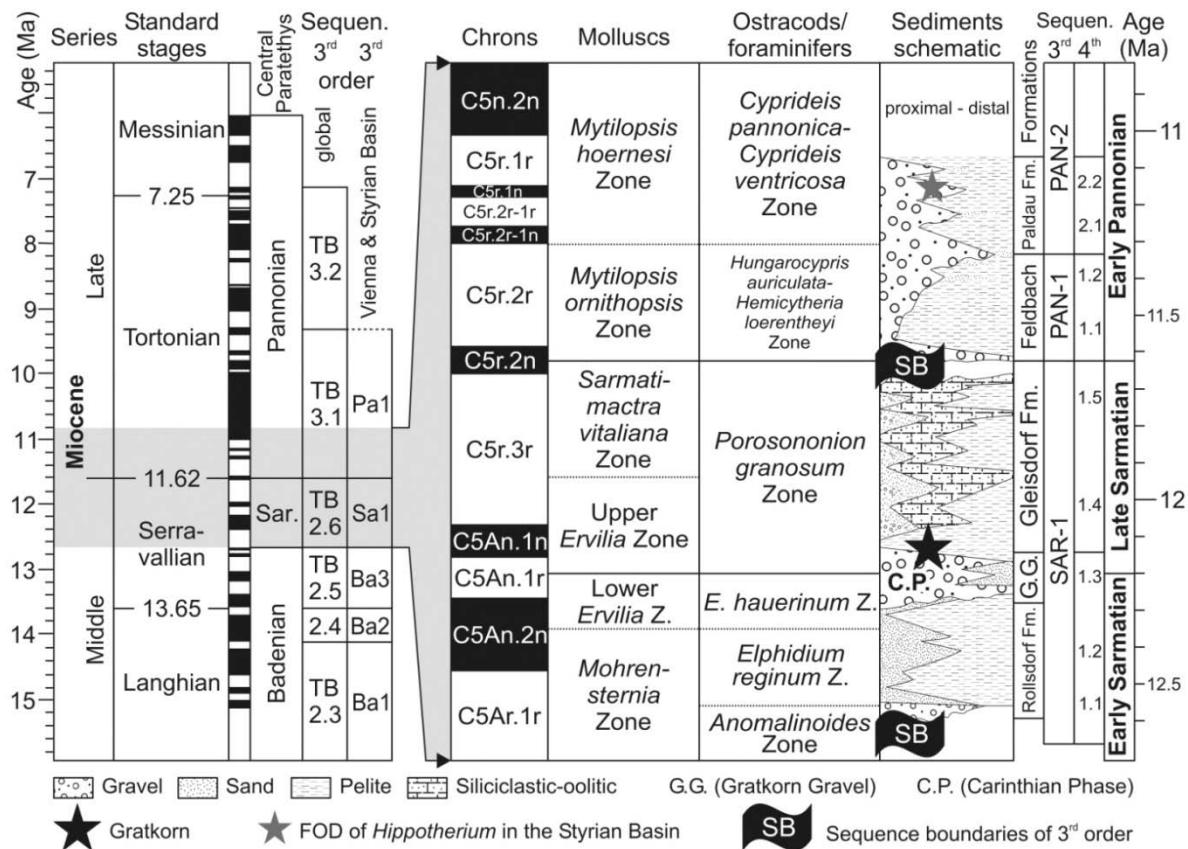
Fig. 4: Stratigraphic position of the Gratkorn locality (from Gross et al. 2011).

The latter is already early Late Miocene (Pannonian) of age (Flügel et al. 2011; for more detailed discussions on lithostratigraphy and lithofacies see Gross et al. (2014) and references therein). The Gratkorn Fm can be traced at least as far as to the northern part of the Styrian Basin, where it is underlain by marine sediments of lower Sarmatian age (Rollsdorf Fm; Flügel et al. 2011; Gross et al. 2014). The overlying Peterstal Mb is likely older than Late Miocene due to the abundance of *Podocarpium podocarpum* and the Lustbühel Mb was biostratigraphically dated in the area around Graz as late Sarmatian (Gross et al. 2014 and references therein). Due to its litostratigraphic position the Gratkorn Fm can be correlated to the so called "Carinthian Phase", at the end of the early Sarmatian and thus can be well integrated in the sequence stratigraphical concept of the Styrian Basin (Gross et al. 2014 and references therein). An age of 12.2 Ma has been proposed for the early/late Sarmatian boundary (Lirer et al. 2009). Normal magnetic polarity of the Peterstal Mb at Gratkorn locality imply correlation to Chron C5An.1n (12.174–12.049 Ma; Gross et al. 2014 and references therein).

1.4. Lithology of the vertebrate bearing palaeosol and frame conditions during soil formation

The here described fossil bearing palaeosol is located in the top of a coarse-grained braided-river sequence of the Gratkorn Fm and overlain by marly to pellitic lacustrine sediments of the Peterstal Mb (Fig. 5; Gross et al. 2011; Gross et al. 2014; Havlik et al. 2014). The lithology of the vertebrate bearing palaeosol itself evolves from non-laminated silty fine sand/fine sandy silt (lower part) to weakly
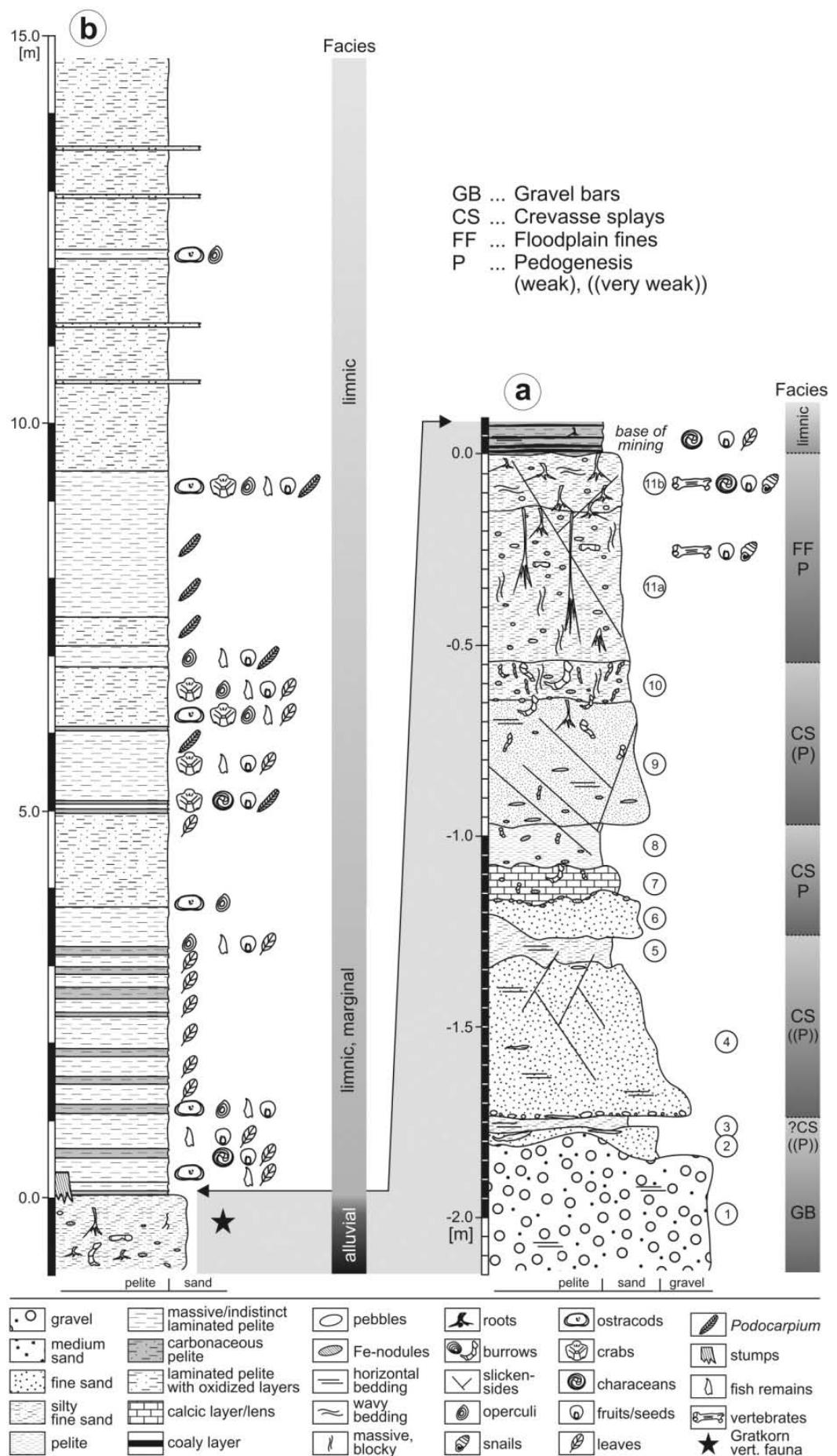
Fig. 5: Lithologic section of the Gratkorn locality (from Gross et al. 2011).

laminated, strongly mottled fine sandy (sometimes more clayey) silt (upper part; Gross et al. 2011; Gross et al. 2014; Havlik et al. 2014). The lower part bears larger oxidized root traces, ferruginous nodules, hackberry fruits (*Celtis*; usually clustered in dozens of specimens), and more rarely septaria like glaebules, as well as very seldom phosphoric coprolites. Oxidized root traces, *Celtis*-clusters, gastropod remains, as well as sand-filled burrows of different sizes are quite common in the upper part, which houses as well carbonate nodules, interpreted as microbialites (Gross et al. 2011; Gross et al. 2014; Havlik et al. 2014). The layer is interpreted as a pedogenically altered overbank deposit, occasionally influenced by a braided river system (Gross et al. 2014). The lack of distinct soil horizons, the partly articulated or at least associated vertebrate remains, the preservation of bird of prey pellets, and rare coprolite findings indicate a short time span for the soil formation, assumably only a few years or decades (Gross et al. 2011; Aiglstorfer et al. 2014b; Gross et al. 2014; Havlik et al. 2014; Prieto et al. 2014a). Especially the pellets in the upper part of the palaeosol point to rapid burial (less than one year?; Gross et al. 2011; Gross et al. 2014; Prieto et al. 2014a). Sedimentology and faunal content indicate transient water-logging during soil formation and consequently alternating wet and dry periods (Gross et al. 2014). Furthermore, more pronounced hydromorphic conditions and a weaker effect of pedogenic processes can be assumed for the upper part in comparison to the lower part of the palaeosol (Gross et al. 2014). The observed ferric staining and iron oxide/-hydroxide incrustation of the vertebrate remains and early diagenetic iron hydroxide rhizoconcretions are typical features in hydromorphic and weakly to moderately developed soils in warm and seasonal climates (Gross et al. 2014; Havlik et al. 2014; and references therein). However, most likely water-logging varied significantly laterally due to the local topography and variable colours of the fossil content in the palaeosol point to changing moisture conditions (Gross et al. 2014) and/or influences of diagenetic fluids. The common occurrence of root traces indicates plant cover of the palaeosol, although some of the roots might belong to vegetation growing at the time of the following lake formation (Gross et al. 2014; Havlik et al. 2014). Only the mentioned *Celtis* fruits (primarily mineralized and thus offering higher potential for preservation; Aiglstorfer et al. 2014c; Gross et al. 2014) can be clearly assigned to the time of the soil formation and prove that medium-sized hackberry trees have been growing in the area (Gross et al. 2014; Havlik et al. 2014). At least in the upper part of the palaeosol vital infauna is recorded with subterranean gastropods (Harzhauser et al. 2008) and ichnofossils tentatively assigned to insects (Gross et al. 2014; Havlik et al. 2014).

Lithology and ectothermic vertebrates point to semiarid/subhumid climate with clear seasonality (Gross et al. 2011; Böhme and Vasilyan 2014; Gross et al. 2014). Based on the herpetofauna a mean annual precipitation (MAP) of 486 ± 252 mm and a MAT of less than 15 °C can be estimated for the time of the soil formation (Böhme and Vasilyan 2014).

2. Methods and abbreviations

Chapter three to five summarize the content of the publications included in this thesis. To avoid unnecessary iteration the publication(s), which is/are summarized are given at the beginning of the respective chapter and not repeatedly cited in the text.

Morphologic descriptions and measurements were accomplished according to standard procedures and specific terminologies follow the references given in Aiglstorfer et al. (2014b), Aiglstorfer et al. (2014c), and Aiglstorfer et al. (2014d). Linear measures on dental and bone material were taken with a digital calliper (where possible with a precision of 0.1mm) in the way indicated in the respective publication. Methods for taphonomical analyses comprise besides standard procedures like determination of minimum number of individuals (MNI), weathering stages, age classes, body size distribution, and Voorhies analysis also analyses of mineralogy and content and distribution of rare earth elements (REE) (for detailed information see Havlik et al. 2014). $\delta^{18}O_{CO3}$ and $\delta^{13}C$ values (quoted in reference to Vienna Pee Dee Belemnite (V-PDB)) as well as strontium isotope composition ($^{87}Sr/^{86}Sr$ ratio) were analyzed in order to gain information about diet, drinking behaviour, as well as provenance and migration of animals (for detailed information see Aiglstorfer et al. 2014a). Taphonomical and isotope analyses follow the protocols given in Havlik et al. (2014) and Aiglstorfer et al. (2014a).

Institutional abbreviations

GPIT	Paläontologische Sammlung der Universität Tübingen, Tübingen, Germany
HLMD	Hessisches Landesmuseum Darmstadt, Darmstadt, Germany
BMNH	British Museum of Natural History, London, UK
MNHN	Muséum National d'Histoire Naturelle, Paris, France
NHMW	Naturhistorisches Museum Wien, Wien, Austria
SMNS	Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany
SNSB-BSPG	Staatliche Naturwissenschaftliche Sammlungen Bayerns-Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany
UMJGP	Universalmuseum Joanneum, Graz, Austria

Anatomical abbreviations

sin.	sinistral/left
dex.	dextral/right
C	upper canine
P2, -3, -4	second, third, fourth upper premolar
M1, -2, -3	first, second, third upper molar
i1, -2, -3	first, second, third lower incisor
p1, -2, -3, -4	first, second, third, fourth lower premolar
m1, -2, -3	first, second, third lower molar

3. Taxonomic assignation of herbivorous large mammals

Up to date 65 vertebrate species have been described from the Gratkorn locality comprising all major vertebrate groups [fishes (2 taxa), amphibians (8 species), reptiles (17 species), birds (4 species), and mammals (34 taxa; excluding carnivores, of which scientific description is still in progress); Gross et al. 2014; Tab. 1]. The locality thus holds the most diverse sympatric vertebrate fauna from stratigraphically well defined sediments in the late Middle Miocene of Europe (Gross et al. 2014).

Class	Order	Family	Taxon		Reference
Teleostei	Cypriniformes	Cyprinidae	Leuciscinae	indet.	Böhme and Vasilyan 2014
	Perciformes	Gobiidae	Gobiidae	indet.	Böhme and Vasilyan 2014
Amphibia	Urodela	Salamandridae	*Triturus*	aff. *vulgaris*	Böhme and Vasilyan 2014
			Chelotriton	aff. *paradoxus*	Böhme and Vasilyan 2014
			Salamandra	*sansaniensis*	Böhme and Vasilyan 2014
	Anura	Discoglossidae	*Latonia*	sp.	Böhme and Vasilyan 2014
		Bufonidae	*Bufotes*	cf. *viridis*	Böhme and Vasilyan 2014
		Pelobatidae	*Pelobates*	*sanchizi*	Böhme and Vasilyan 2014
		Ranidae	*Pelophylax*	sp.	Böhme and Vasilyan 2014
			Rana	sp.	Böhme and Vasilyan 2014
Reptilia	Testudines	Emydidae	*Clemmydopsis*	*turnauensis*	Böhme and Vasilyan 2014
		Chelydridae	*Chelydropsis*	*murchisonae*	Böhme and Vasilyan 2014
		Testudinidae	*Testudo*	cf. *steinheimensis*	Böhme and Vasilyan 2014
			Testudo	cf. *steinheimensis*	Böhme and Vasilyan 2014
	Iguania	Gekkonidae	Gekkonidae	indet.	Böhme and Vasilyan 2014
	Scincomorpha	Lacertidae	*Lacerta*	s.l. sp. 1	Böhme and Vasilyan 2014
			Lacerta	s.l. sp. 2	Böhme and Vasilyan 2014
			Lacerta	s.l. sp. 3	Böhme and Vasilyan 2014
			Miolacerta	*tenuis*	Böhme and Vasilyan 2014
			Edlartetia	sp.	Böhme and Vasilyan 2014
		Scincidae	*Scincidae*	gen. et sp. indet.	Böhme and Vasilyan 2014
	Anguimorpha	Anguidae	*Ophisaurus*	*spinari*	Böhme and Vasilyan 2014
		Varanidae	*Varanus*	sp.	Böhme and Vasilyan 2014
	Serpentes	Colubridae	Colubrinae	sp. 1	Böhme and Vasilyan 2014
			Colubrinae	sp. 2	Böhme and Vasilyan 2014
			Natricinae	sp. indet.	Böhme and Vasilyan 2014
		Elapidae	*Naja*	sp.	Böhme and Vasilyan 2014
Aves	Galliformes	Phasianidae	*Miogallus*	*altus*	Göhlich and Gross 2014
			cf. *Palaeocryptonyx*	*edwardsi*	Göhlich and Gross 2014
			cf. *Palaeocryptonyx*	sp.	Göhlich and Gross 2014
	Coliiformes	Coliidae	*Necrornis*	cf. *palustris*	Göhlich and Gross 2014
Mammalia	Eulipotyphla	Erinaceidae	*Schizogalerix*	*voesendorfensis*	Prieto et al. 2010b, 2014a
			Galericinae	gen. et sp. indet.	Prieto et al. 2010b, 2014a
		Talpidae	*Desmanodon*	*fluegeli*	Prieto et al. 2010b, 2014a
		Soricidae	*Dinosorex*	sp.	Prieto et al. 2010b, 2014a
	Chiroptera	Vespertilionidae	cf. *Myotis*	sp.	Prieto et al. 2010b, 2014a
	Rodentia	Cricetidae	"*Cricetodon*"	*fandli*	Prieto et al. 2010a, 2014a
			Democricetodon	n.sp.	Prieto et al. 2010a, 2014a
			Megacricetodon	*minutus*	Prieto et al. 2010a, 2014a
			Eumyarion	sp.	Prieto et al. 2010a, 2014a
		Gliridae	*Muscardinus*	aff. *sansaniensis*	Daxner-Höck 2010; Prieto et al. 2014a
			Miodyromys	sp.	Daxner-Höck 2010; Prieto et al. 2014a
		Eomyidae	*Keramidomys*	sp.	Daxner-Höck 2010; Prieto et al. 2014a
		Sciuridae	*Albanensia*	*albanensis*	Daxner-Höck 2010; Prieto et al. 2014a
			Forsythia	*gaudryi*	Daxner-Höck 2010; Prieto et al. 2014a
			Blackia	sp.	Daxner-Höck 2010; Prieto et al. 2014a
			Spermophilinus	*bredai*	Daxner-Höck 2010; Prieto et al. 2014a
		Castoridae	*Euroxenomys*	*minutus minutus*	Prieto et al. 2014 a,b
	Lagomorpha	Ochotonidae	*Prolagus*	*oeningensis*	Angelone et al. 2014; Prieto et al. 2012, 2014a
			cf. *Eurolagus*	*fontannesi*	Angelone et al. 2014; Prieto et al. 2012, 2014a
			Ochotonidae	gen. et sp. indet.	Angelone et al. 2014; Prieto et al. 2014a
	Perissodactyla	Chalicotheriidae	*Chalicotherium*	*goldfussi*	Aiglstorfer et al. 2014c
		<mark>Rhinocerotidae</mark>	<mark>*Aceratherium*</mark>	<mark>sp.</mark>	<mark>Aiglstorfer et al. 2014c</mark>
			<mark>*Brachypotherium*</mark>	<mark>*brachypus*</mark>	<mark>Aiglstorfer et al. 2014c</mark>
			<mark>*Lartetotherium*</mark>	<mark>*sansaniense*</mark>	<mark>Aiglstorfer et al. 2014c</mark>
		Equidae	*Anchitherium*	sp.	Aiglstorfer et al. 2014c
	Artiodactyla	Suidae	*Listriodon*	*splendens*	Made et al. in press
			Parachleuastochoerus	*steinheimensis*	Made et al. in press
		Tragulidae	*Dorcatherium*	*naui*	Aiglstorfer et al. 2014d
		Moschidae	*Micromeryx*	*flourensianus*	Aiglstorfer et al. 2014d
			?*Hispanomeryx*	sp.	Aiglstorfer et al. 2014d
		Cervidae	*Euprox*	*furcatus*	Aiglstorfer et al. 2014d
		Palaeomerycidae	Palaeomerycidae	gen. et sp. indet.	Aiglstorfer et al. 2014d
		Bovidae	*Tethytragus*	sp.	Aiglstorfer et al. 2014d
	Proboscidea	Deinotheriidae	*Deinotherium*	*levius* vel *giganteum*	Aiglstorfer et al. 2014b

Tab. 1: Fossil vertebrates from the Gratkorn locality (except of Carnivora) with reference to scientific description (after Gross et al. 2014).

The herbivorous large mammals from the Gratkorn locality, excavated so far, are assigned to the following taxa (except of Suidae part of this thesis):

Proboscidea:	*Deinotherium levius* vel *giganteum*
Perissodactyla:	==*Aceratherium* sp., *Brachypotherium brachypus*, *Lartetotherium sansaniense*== *Chalicotherium goldfussi*, *Anchitherium* sp.
Artiodactyla - Suidae:	*Listriodon splendens, Parachleuastochoerus steinheimensis*
Artiodactyla - Ruminantia:	*Dorcatherium naui*, *Micromeryx flourensianus*, ?*Hispanomeryx* sp., *Euprox furcatus*, Palaeomerycidae gen. et sp. indet., *Tethytragus* sp.

3.1. Proboscidea - *Deinotherium levius* vel *giganteum*

[Aiglstorfer M, Göhlich UB, Böhme M, Gross M. (2014): A partial skeleton of *Deinotherium* (Proboscidea, Mammalia) from the late Middle Miocene Gratkorn locality (Austria). Palaeobiodiversity and Palaeoenvironments 94, 49-70. Publication #1]

Deinothere remains are frequent findings in the Miocene of Europe and a useful tool for biochronological and biostratigraphical considerations (see, e.g. Dehm 1960; Huttunen 2002a, 2002b; Böhme et al. 2012; Pickford and Pourabrishami 2013). Taxonomy of deinotheres has been in discussion for long (e.g. Gräf 1957; Bergounioux and Crouzel 1962; Harris 1973; Gasparik 1993; Antoine 1994; Huttunen 2000; Gasparik 2001; Ginsburg and Chevrier 2001; Duranthon et al. 2007; Markov 2008b, a; Vergiev and Markov 2010; Böhme et al. 2012; Pickford and Pourabrishami 2013). Besides different opinions on valid genera, the number of species is still in discussion. Some authors accept five valid morpho- (Böhme et al. 2012) or chronospecies (Pickford and Pourabrishami 2013), others only four (Gasparik 1993, 2001; Markov 2008a; Vergiev and Markov 2010) or even only two species (Huttunen 2002a). In this thesis two genera, *Prodeinotherium* Éhik, 1930 and *Deinotherium* Kaup, 1829, and five species, *Prodeinotherium cuvieri* (Kaup, 1832) and *P. bavaricum* (von Meyer, 1831), *Deinotherium levius* Jourdan, 1861*, D. giganteum* Kaup, 1829 and *D. proavum* Eichwald, 1835, are considered valid.

While the genus *Prodeinotherium* is indicative for the Early to middle Middle Miocene, *Deinotherium* first occurs in Europe during the Middle Miocene (Mottl 1969; Svistun 1974) and is recorded up to the terminal Late Miocene (Markov 2008b). Although deinothere remains are quite common in the fossil record, they often comprise only isolated teeth or bones accumulated in fluvial sediments, like for example in the famous *Dinotheriensande* (Eppelsheim Formation). Skeletons are less common but recorded for the smaller genus *Prodeinotherium* (e.g. Heizmann 1984; Musil 1997; Huttunen and Göhlich 2002; Huttunen 2004) and for the largest species *Deinotherium proavum* (Stefanescu 1894; Tarabukin 1968; Bajgusheva and Titov 2006; Kovachev and Nikolov 2006). Up to now the only well described skeleton of a medium sized deinothere is the partial *Deinotherium levius* skeleton from Gusyatin (Middle Miocene; Svistun 1974). The assignation of deinothere remains from Opatov to *Deinotherium levius* (Middle Miocene; Zázvorka 1940; Musil 1997; most likely representing at least two skeletons) could not be fully verified so far. Dental measurements given by Zázvorka (1940) would fit with a medium-sized deinothere, however (Fig. 7).
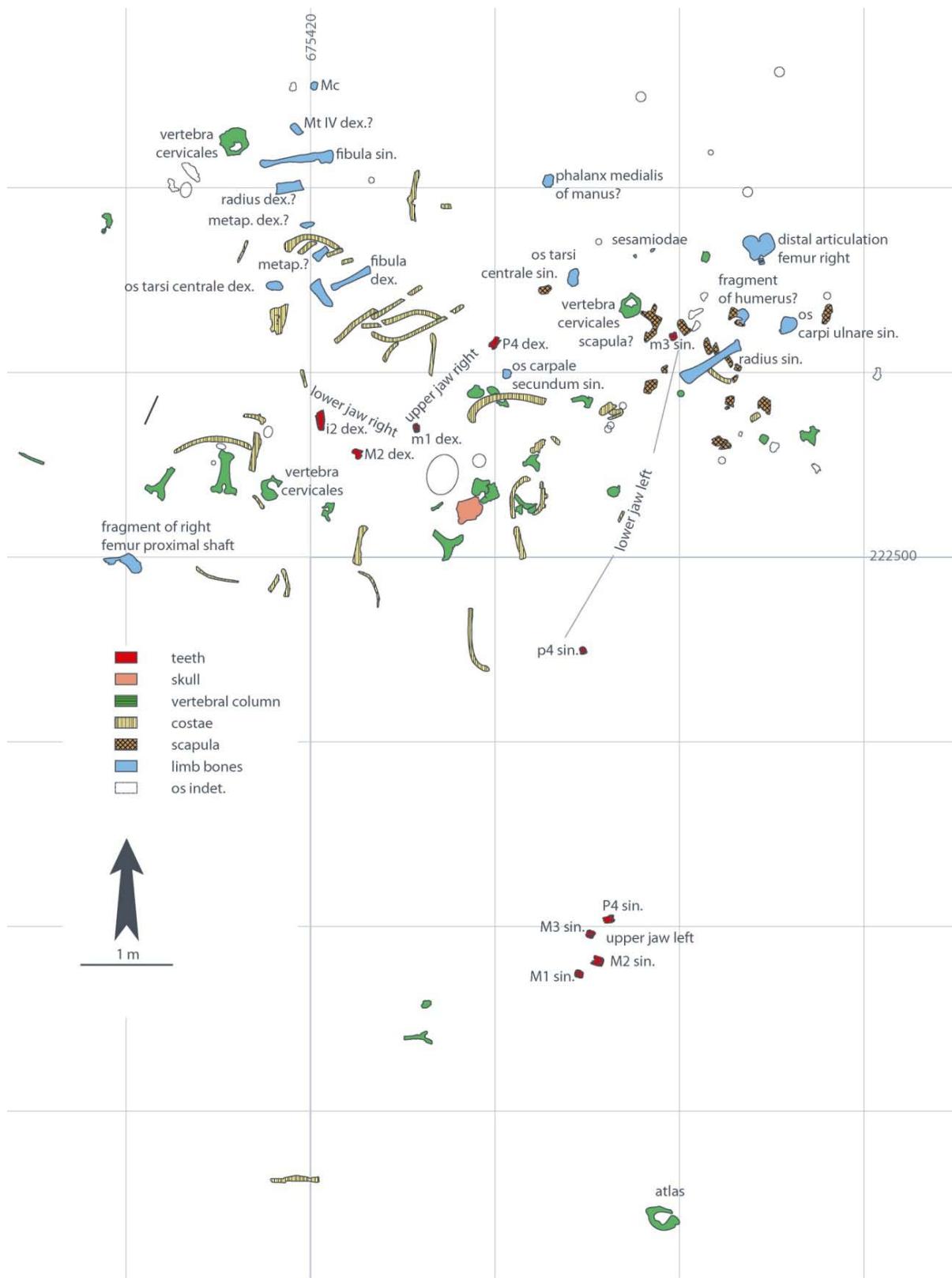
Fig. 6: Excavation plan of the partial *Deinotherium levius* vel *giganteum* skeleton from Gratkorn with identification of skeletal elements (modified after excavation plan by M. Gross (excavations 2005–2008); coordinates are in Austrian Grid (BMN M34 – GK); from Aiglstorfer et al. 2014b

3.2. Perissodactyla

[Aiglstorfer M, Heissig K, Böhme M. (2014): Perissodactyla from the late Middle Miocene Gratkorn locality (Austria). Palaeobiodiversity and Palaeoenvironments 94, 71-82. Publication #2]

Although few in findings the Perissodactyla from Gratkorn represent a quite diverse assemblage, with at least 5 different taxa: the chalicotheriid *Chalicotherium goldfussi* Kaup, 1833, three rhinocerotid species (*Aceratherium* sp., *Brachypotherium brachypus* (Lartet, 1837), and *Lartetotherium sansaniense* (Lartet, in Laurillard 1848)), and the equid *Anchitherium* sp..

Order Perissodactyla Owen, 1848
Family Chalicotheriidae Gill, 1872
Subfamily Chalicotheriinae Gill, 1872
Genus *Chalicotherium* Kaup, 1833
Type species: *Chalicotherium goldfussi* Kaup, 1833

Chalicotherium goldfussi

Lectotype: M3 dex. (Kaup 1832-1839, pl. VII, fig. 3; HLMD BIN 3167)
Type locality: Eppelsheim, Rheinhessen, Germany

Following Anquetin et al. (2007) an M3 dex. of a chalicotheriid from Gratkorn (Fig. 8 a-e) must be assigned to the subfamily Chalicotheriinae because of the non-fusion of protoloph and protocone. As in most Chalicotheriinae (Fahlke et al. 2013), the protocone is posterior to the paracone. Schizotheriinae possess an anteroposteriorly elongated rectangular shape in the upper molars in contrast to the square shape in Chalicotheriinae (Zapfe 1979; Coombs 1989). A square shape can be observed in the specimen from Gratkorn. In size, it is well within the dimensions of both *Chalicotherium goldfussi* and *Anisodon grande* (de Blainville, 1849) (overlap of dimensions also recorded by Zapfe (1979) and Coombs (1989)) and is clearly wider than representatives of the Schizotheriinae. In general shape, it fits best to *Chalicotherium goldfussi*. With this species, the Gratkorn 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).

Family Rhinocerotidae Gray, 1821
Subfamily Aceratheriinae Dollo, 1885
Tribe Aceratheriini Dollo, 1885
Genus *Aceratherium* Kaup, 1832
Type species: *Aceratherium incisivum* Kaup, 1832

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Aceratherium sp.

The taxonomic status of the diverse *Aceratherium*-like Rhinocerotidae in the Early and Middle Miocene of Europe is still in discussion. Geraads and Saraç (2003) 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 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 differences between *Aceratherium incisivum* and *Alicornops simorrense*, thus enabling now a better discrimination between the different *Aceratherium*-like Rhinocerotidae.

A lingual fragment of a D2 sin. (Fig. 8 h, i) from Gratkorn shows most similarities in dimensions and morphology with an *Aceratherium*-like Rhinocerotidae. Unfortunately, the only characteristic feature described by Antoine et al. (2010) and Becker et al. (2013) observable on a D2 cannot be observed on the specimen from Gratkorn due to fragmentation.

Therefore, the genus attribution *Aceratherium* was used *sensu lato* and the specimen left in open nomenclature as *Aceratherium* sp.

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

Brachypotherium brachypus

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

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

The lateral half of an astragalus sin. (Fig. 9 a-d) from Gratkorn and a partial metatarsal II sin. (Fig. 8 j-m) are assigned to the rhinocerotid *Brachypotherium brachypus*. The astragalus is broad and possesses only a shallow trochlear notch as typical for Teleoceratini (Heissig 2012). With *Brachypotherium brachypus* it shares the general shape, a main facet for the articulation with the calcaneum distally more prolonged and less concave than in *Aceratherium*, a longer collum tali than in *Aceratherium*, the separation of all three calcaneum facets in contrast to Rhinocerotinae (distolateral and sustentacular ones are fused in these) (Heissig 1976; Ginsburg and Bulot 1984; Hünermann 1989; Cerdeño 1993; Geraads and Saraç 2003; Heissig 2009; Antoine et al. 2010). The specimen from Gratkorn is smaller than most representatives of the species, but overlaps well with a few specimens from Çandir and Sofca (Turkey; late Middle Miocene; MN 7/8; Heissig 1976; Geraads and Saraç 2003).

Fig. 8: 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, I plantar view; m lateral view; articulation facets labelled); scale bar 10 mm; from Aiglstorfer et al. 2014c

The metarsal II sin. is shorter and more massive than that of all rhinoceroses of the Middle Miocene except of *Brachypotherium*. Furthermore, the proximal facet for the mesocuneiform is broader and less concave than in *Aceratherium* (Hünermann 1989) and *Lartetotherium* (Heissig 2012). Like the astragalus it is smaller in dimensions than what is usually observed for the species, but fits well to a metatarsal III of *Brachypotherium brachypus* from Sofca (Heissig 1976).

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

A m1 sin. (Fig. 8 f, g) and a small fragment of a m2 sin. from the same individual (together with some jaw fragments) are assigned to *Lartetotherium sansaniense*. Tooth dimensions seem to be rather variable inter- but also intraspecific among rhinocerotid species. Thus the use of size as discriminative feature can only give indications for species assignation and is less valuable than in other groups. In any case the m1 from Gratkorn is smaller than teeth assigned to the genus *Brachypotherium* and larger than teeth assigned to "*Dicerorhinus*" *steinheimensis* Jäger, 1839. As the most useful character for the separation of Rhinocerotini and Aceratheriini, the length of the paralophid, is not preserved in the m1, the configuration of the cingulids is used for species determination. Due to the lack of any labial cingulid and the rather short anterior and the posterior cingulids, which do not proceed onto the labial side the assignation to Aceratheriinae can be excluded. The strongly reduced cingulids are very characteristic for *Lartetotherium sansaniense* (Heissig 2012).

Labels visible in figure:
- a — ~37, 44.2, 41.5
- b
- c
- g — 35.5
- d
- f — ~26-27, 36.5
- h — 30.5
- e
- i
- j — ~26, ectocuneiform, mesocuneiform
- k — ~38-40, 31, ~92
- l
- m — ectocuneiform, Mt III, 24
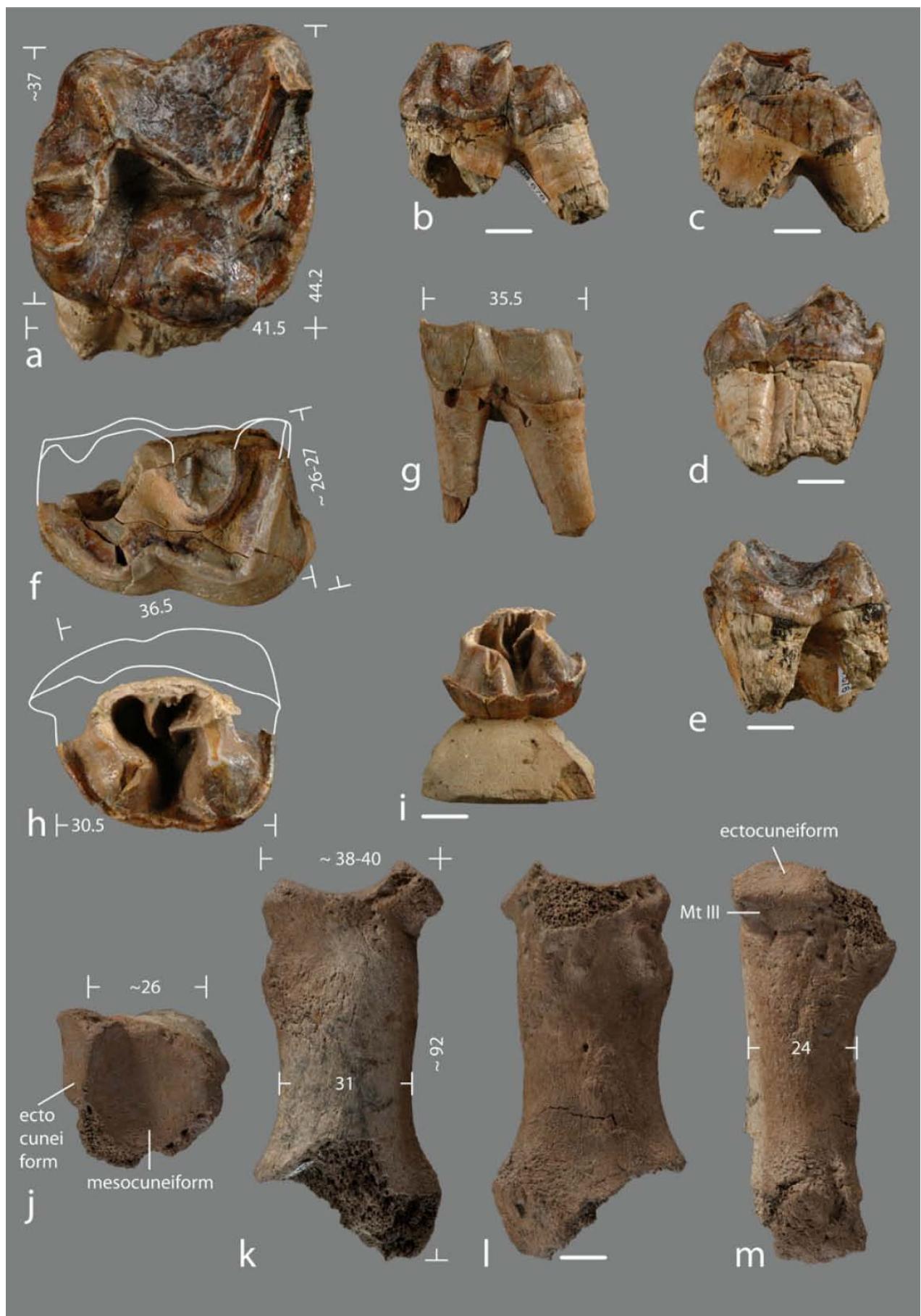
Family Equidae Gray, 1821

Subfamily Anchitheriinae Leidy, 1869

Genus *Anchitherium* Meyer, 1844

Type species: *Anchitherium aurelianense* (Cuvier, 1825)

Anchitherium sp.

The distal fragments of a humerus sin. (Fig. 9 f) and a radius dex. (Fig. 9 g, h) from Gratkorn can be assigned to the equid *Anchitherium*. In morphology and dimensions the humerus is well in the variability of *A. aurelianense* from several Middle Miocene localities. Due to the fragmentary nature of the specimen no species diagnostic features can be observed, however.

The radius fragment does not indicate any distal fusion of radius and ulna as typical for *Anchitherium* and distinguishing it from *Hipparion* (Iñigo 1997; Alberdi and Rodríguez 1999; Alberdi et al. 2004). In shape and dimensions it fits well to *A. aurelianense* from Baigneaux (Alberdi et al. 2004), Sansan (Alberdi and Rodríguez 2012), and Sandelzhausen (personal observation), as well as to *A. corcolense* Iñigo, 1997 from Córcoles (Spain; Early Miocene; MN 4; Iñigo 1997), but is smaller than *Sinohippus* Zhai, 1962 (Salesa et al. 2004).

As a clear species assignation is not possible at the moment the two fragments from Gratkorn are left in open nomenclature as *Anchitherium* sp..

Fig. 9: 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; from Aiglstorfer et al. 2014c
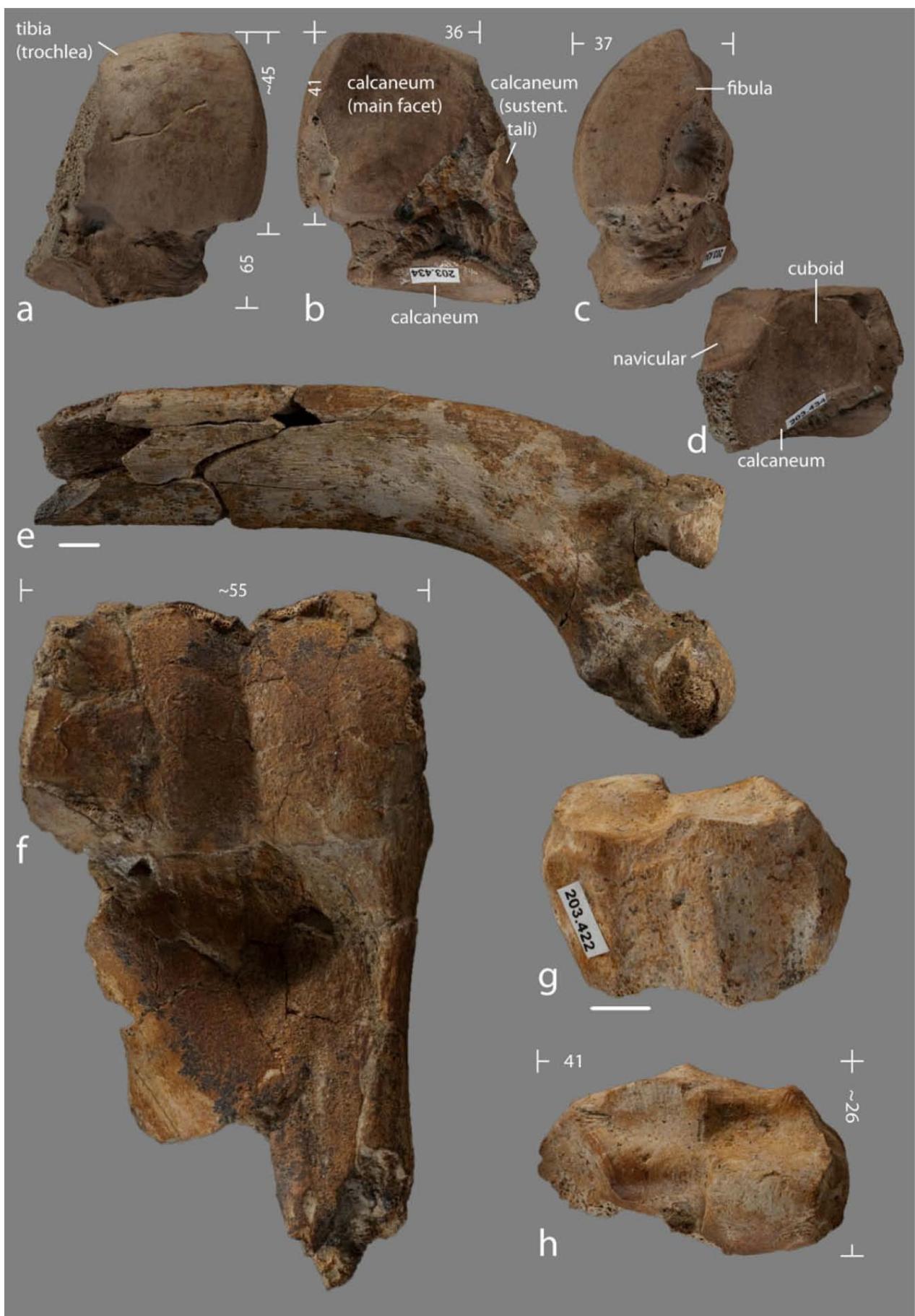
4. Taphonomical considerations with focus on large mammal taphonomy

[Havlik P, Aiglstorfer M, Beckman A, Gross M, Böhme M. (2014): Taphonomical and ichnological considerations on the late Middle Miocene Gratkorn locality (Styria, Austria) with focus on large mammal taphonomy. Palaeobiodiversity and Palaeoenvironments 94, 171-188. Publication #4]

[Aiglstorfer M, Göhlich UB, Böhme M, Gross M. (2014) A partial skeleton of *Deinotherium* (Proboscidea, Mammalia) from the late Middle Miocene Gratkorn locality (Austria). Palaeobiodiversity and Palaeoenvironments 94, 49-70. Publication #1]

Analysis of the taphonomy of a fossil assemblage is the base for the evaluation of ecological and diagenetical influences on composition and preservation of the accumulation. First of all depositional mechanisms and time coverage of the deposition have to be considered: analysis of sedimentology, stratigraphic distribution of faunal elements horizontally and vertically and, accumulation mechanisms [analysis of disarticulation, decomposition, disruption and weathering, bioerosion, taxonomic-, body size-, and age-distribution, frequency of different anatomical elements (e.g. Voorhies analysis)]. Furthermore, estimations on diagenetic overprint and recrystallization (like e.g. analysis of mineralogy and content/distribution of REE) are indispensible e.g. for evaluating the informative value of the isotopic composition of mammalian hard tissues in context of ecosystem reconstruction.

Nearly all vertebrate remains described from the locality originate from a single palaeosol layer except of the rare fish remains, which come from the hanging lacustrine pelites (Gross et al. 2011; Gross et al. 2014; Havlik et al. 2014). Field observations showed that locally accumulated pellets (assumably from owls; Gross et al. 2011), as well as articulated/associated fossorial smaller vertebrates (small mammals and ectothermic vertebrates) are restricted to the upper part of the palaeosol and cervid remains are more common here than in the lower part, while suids and heavier large mammals are more common in the lower part. Detailed assignment of the findings to different levels of the palaeosol is enhanced due to gradual change in lithology and strong neotectonic activities. Furthermore, fragments from the same bone were excavated in different horizons of the palaeosol. All large mammal findings should be considered as more or less deposited in a short time span, maximally several decades. Bones and teeth are ferruginous stained, display iron oxide and iron hydroxide coatings, as well as root traces and were gnawed by small and large mammals. Colour ranges from whitish to black (Gross et al. 2011; Gross et al. 2014; Havlik et al. 2014). Fragmentation of bones and teeth can be observed regularly. Diagenetic alteration is low in the fossil assemblage. Gastropod shells are preserved in primary (aragonitic) mineralization.
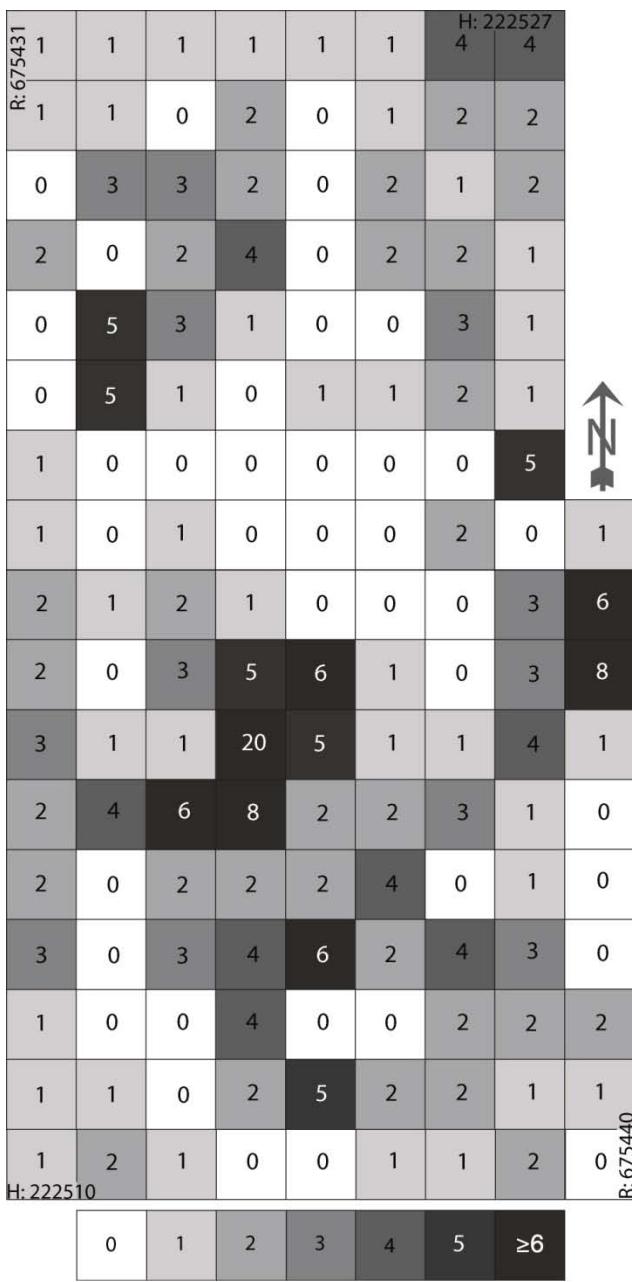
Fig. 13: Excavation map of campaigns 2011 and 2012 with additional data from 2013 showing the heterogeneous concentration of large mammal specimen per square meter. Numbers indicate the number of objects excavated; coordinates are in Austrian Grid (BMN M34–GK); modified after Havlik et al. 2014

Bone, dentine, and especially enamel of large mammals show a relatively low total REE content, indicating low diagenetic alteration. Shapes of REE distribution patterns have been used to evaluate degree and time of diagenetic alteration (Badiola et al. 2009). Although uptake of REE has proven more complex than assumed so far (Kocsis et al. 2010; Herwartz et al. 2013; Trueman 2013), the flat pattern (no considerable enrichment in medium-sized rare earth elements) in the specimens from Gratkorn still indicate a minor degree of recrystallization (Kowal-Linka et al. 2014). Similar values and patterns for tissues from the upper and the lower part are well in accordance with the assumption of a "uniform" diagenetical history and shale-normalised ratios of La/Sm (0.337 to 1.6198) and of La/Yb (0.1302 and 0.9903) are well in the variability for "terrestrial samples" (Trueman et al. 2006; Herwartz et al. 2013).

The large mammal remains are not randomly distributed in the palaeosol but locally concentrated (Fig. 13), in general disarticulated but still roughly associated. No indication for fluviatile transportation, as e.g. abrasion, current alignment or size sorting, can be detected on the large mammal remains. Although an expanded Voorhies analysis based on a NISP (number of identified specimens) of 363 from all excavation campaigns up to 2012 shows a clear dominance of Voorhies Group III (elements resistant to prolonged fluviatile transportation, such as teeth, jaw fragments, and astragali), a remarkable amount can also be attributed to Voorhies Group I (elements non-resistant to transportation, e.g. vertebra and ribs; Fig. 14 b). The results of the Voorhies analysis object a prolonged fluvial transportation (Badiola et al. 2009), but could be explained by carnivore behavior. Gnawing and scavenging by carnivores is furthermore evidenced by biting and gnawing traces. Taken into consideration the typical consumption sequence (Lyman 1994) strong influence of the assemblage by carnivore behavior furthermore explains the over-representation of teeth (Fig. 14 a).

Carnivores are most likely also responsible for the high percentage of breakage in skeletal elements from Gratkorn. The presence of epiphyses of long bones with biting marks (diaphyses are often missing) indicates extensive marrow consumption. The ratio of vertebrae and ribs versus girdle and limb bones rather points to an accumulation by scavengers than by predators (Palmqvist and Arribas 2001). Trampling and neotectonics must be considered important fracturing mechanisms for large mammal bones and teeth as well and trampling was most likely also an important burial mechanism. The wide distribution of body masses (Fig. 15 a) and high diversity of species is more typical for scavengers than for predators and furthermore makes a fluvial accumulation of the assemblage unlikely (Palmqvist and Arribas 2001).
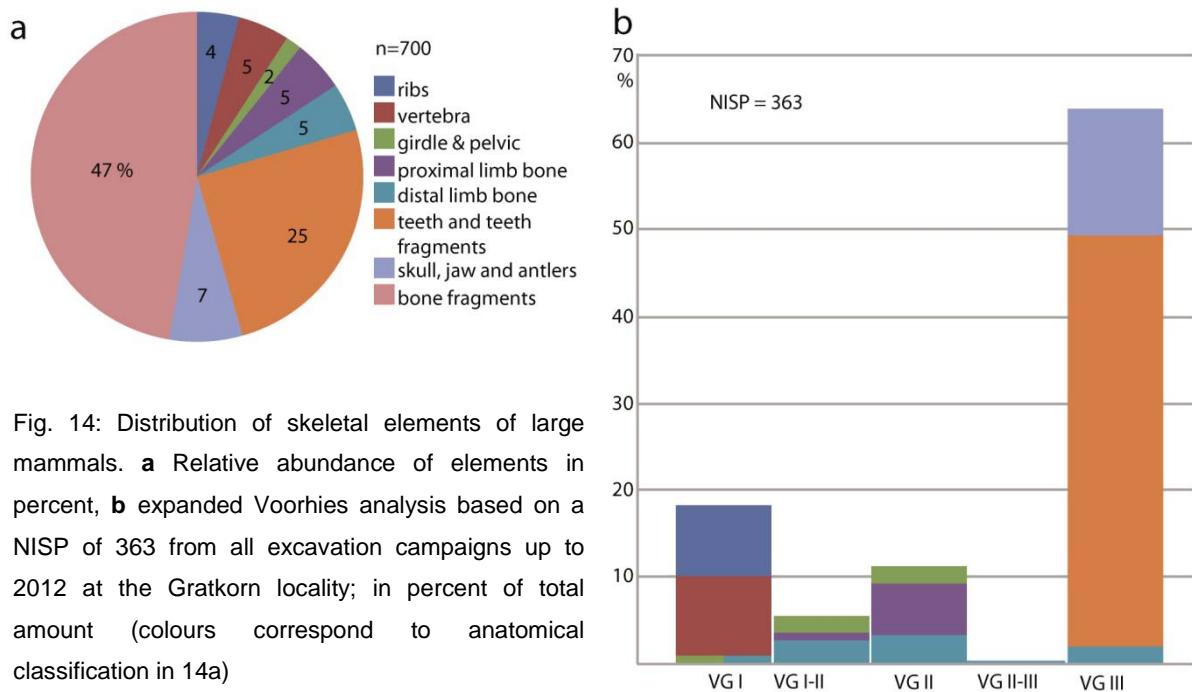
Fig. 14: Distribution of skeletal elements of large mammals. **a** Relative abundance of elements in percent, **b** expanded Voorhies analysis based on a NISP of 363 from all excavation campaigns up to 2012 at the Gratkorn locality; in percent of total amount (colours correspond to anatomical classification in 14a)
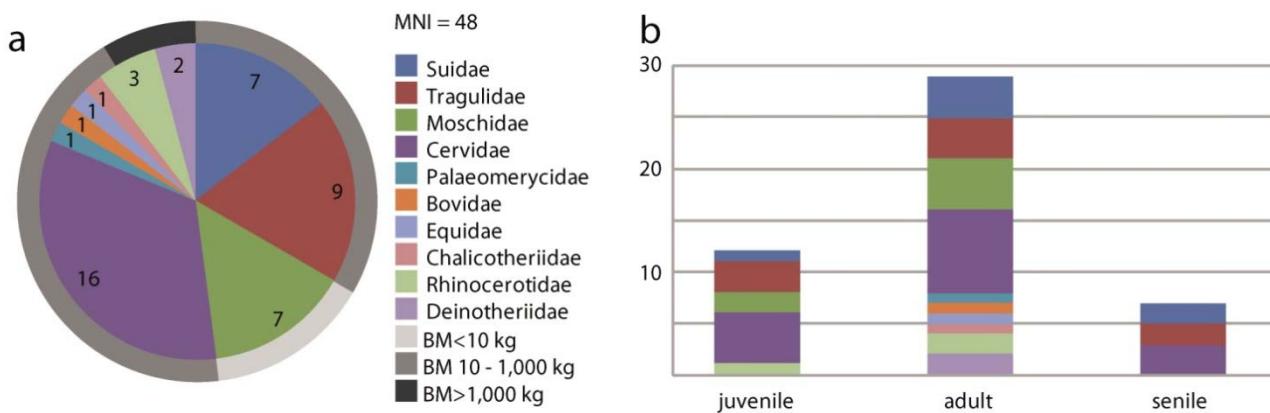
Fig. 15: Faunal composition of the Gratkorn large mammal taphocoenosis: **a** MNI of herbivorous large mammals on family level based on the number of similar anatomical elements and tooth enamel consumption (body mass, BM, follows categories given in Costeur et al. 2013), **b** age model of large mammals based on enamel consumption (juvenile: deciduous dentition; adult: permanent dentition, senile: trigonid of m1 completely worn) and ossification (colours correspond to Fig. 15a)

Although keeping in mind that the data on age profiles from Gratkorn (Fig. 15 b) are not statistically significant, the clear dominance of prime individuals still points to an accumulation either by mass mortality, ambush predators or collection by scavengers (Stiner 1990; Lyman 1994; Palmqvist and Arribas 2001). Due to different weathering stages, anatomical separation and inhomogeneous dispersal of the material, mass mortality can be clearly excluded. Although we cannot exclude the presence of ambush predators like e.g. Felidae, the direct evidence is missing so far and first data on carnivores rather indicates the presence of scavengers (D. Nagel pers. comm. March 2013).

Summing up the large mammal assemblage is considered a more or less autochthonous taphocoenosis. It is contemporaneously deposited (in terms of years or decades), without any significant time averaging (or faunal mixing). It was most likely accumulated to a considerable degree by scavengers.

5. Ecology, provenance and migration

[Aiglstorfer M, Bocherens H, Böhme M. (2014): Large Mammal Ecology in the late Middle Miocene locality Gratkorn (Austria). Palaeobiodiversity and Palaeoenvironments 94, 189-213. Publication #5]

[Aiglstorfer M, Göhlich UB, Böhme M, Gross M. (2014): A partial skeleton of *Deinotherium* (Proboscidea, Mammalia) from the late Middle Miocene Gratkorn locality (Austria). Palaeobiodiversity and Palaeoenvironments 94, 49-70. Publication #1]

[Aiglstorfer M, Heissig K, Böhme M. (2014): Perissodactyla from the late Middle Miocene Gratkorn locality (Austria). Palaeobiodiversity and Palaeoenvironments 94, 71-82. Publication #2]

[Aiglstorfer M, Rössner GE, Böhme M. (2014): *Dorcatherium naui* and pecoran ruminants from the late Middle Miocene Gratkorn locality (Austria). Palaeobiodiversity and Palaeoenvironments 94, 83-123. Publication #3]

$\delta^{18}O_{CO3}$ and $\delta^{13}C$ values of mammalian fossil tooth enamel can help to gain information about diet, drinking water and drinking behaviour of the animals, since differences in isotopic compositions of diet and drinking water are incorporated into body tissues (DeNiro and Epstein 1978; Longinelli 1984; Luz et al. 1984; Bocherens et al. 1996; Kohn 1996; Kohn et al. 1996; Levin et al. 2006; Tütken et al. 2006; Clementz et al. 2008; Tütken and Vennemann 2009; Ecker et al. 2013). In general lower values in $\delta^{18}O_{CO3}$ and $\delta^{13}C$ in herbivores point to feeding in more closed and humid environment, while higher values are indicative for feeding in open and arid environment (Fig. 16). In addition to $\delta^{18}O_{CO3}$ and $\delta^{13}C$ values, the strontium isotopic composition ($^{87}Sr/^{86}Sr$ ratio) of diet and drinking water is incorporated in the skeletal and dental tissues of animals (Hoppe et al. 1999; Maurer et al. 2012). Since this ratio is constant and does not change up the food chain, it reflects the bioavailable $^{87}Sr/^{86}Sr$ in the animal's habitat (Blum et al. 2000; Bentley 2006) and is thus a useful tool for provenance analyses.

14 bulk enamel samples of large mammal teeth (*Parachleuastochoerus steinheimensis, Listriodon splendens, Dorcatherium naui, Euprox furcatus, Micromeryx flourensianus, Tethytragus* sp.), and 21 serial samples of *Deinotherium levius* vel *giganteum* and *Lartetotherium sansaniense* were gained for stable isotope analysis ($\delta^{18}O_{CO3}$, $\delta^{13}C$). Strontium isotopic composition ($^{87}Sr/^{86}Sr$) was measured on

enamel samples of the large mammals *Listriodon splendens, Parachleuastochoerus steinheimensis, Dorcatherium naui, Euprox furcatus, Tethytragus* sp., *Lartetotherium sansaniense,* and *Deinotherium levius* vel *giganteum*. For the taxa *Aceratherium* sp., *Brachypotherium brachypus*, *Chalicotherium goldfussi*, *Anchitherium* sp., *?Hispanomeryx* sp., Palaeomerycidae gen. et sp. indet. material was to scarce or did not comprise any dental material at all. Therefore, ecology of these taxa is not considered specifically in this work.

5.1. Ecology of large mammals

Morphological adaptation and data from stable isotope analyses gained from the large mammalian herbivore record from Gratkorn fit well in a mesic/woodland environment of a pure C3 ecosystem (Fig. 16). None of the taxa derived its diet from closed canopy conditions and different values for $\delta^{18}O_{CO3}$ and $\delta^{13}C$ indicate that the ecosystem provided enough diversity in plant resources to allow occupation of different niches.
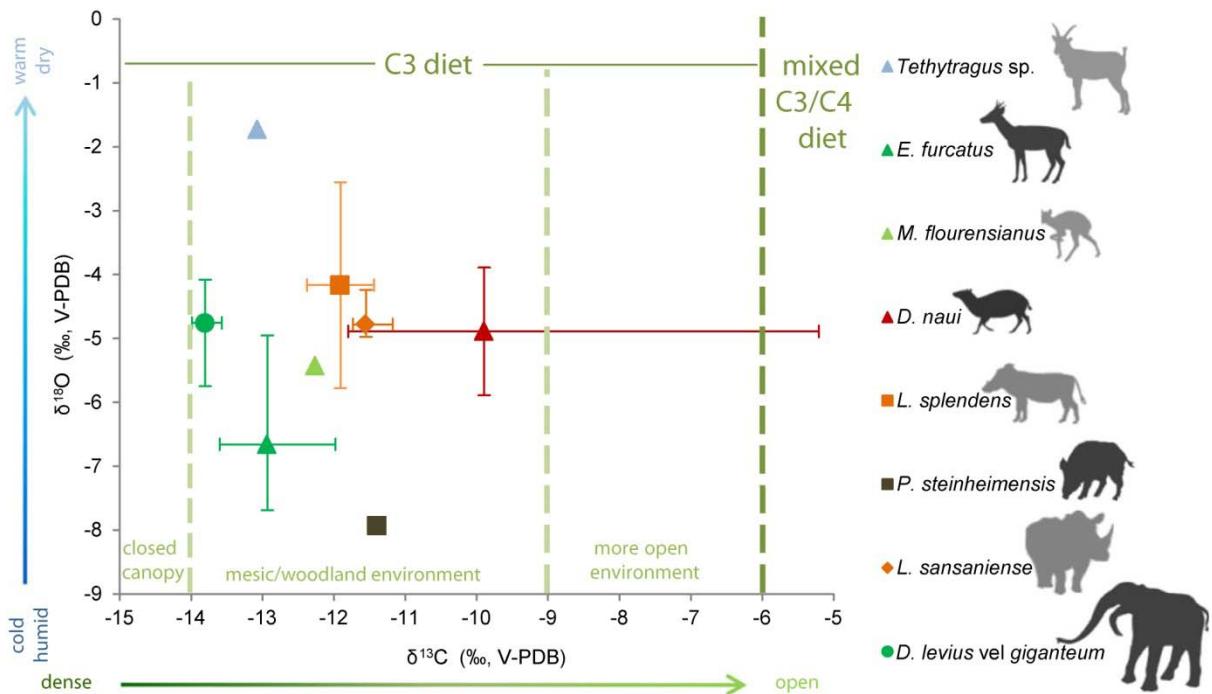
Fig. 16: Mean values with total range of $\delta^{18}O_{CO3}$ (‰V-PDB) versus $\delta^{13}C$ (‰V-PDB) for large mammals (enamel) from the Gratkorn locality with designated niches (after Domingo et al. 2012) in a predominantly C3 vegetation. Trends from dense and cold/humid environment to more open and warm/dry environment are indicated (*E Euprox, M Micromeryx, D Dorcatherium, L Listriodon, P Parachleuastochoerus, L Lartetotherium D Deinotherium*; from Aiglstorfer et al. 2014a

The data fit well with a late Middle Miocene faunal assemblage from this area and are well in accordance with other Middle Miocene large mammal communities from Europe (see e.g. Tütken et al. 2006; Domingo et al. 2009; Tütken and Vennemann 2009; Domingo et al. 2012). They seem to be affected only to a minor degree by climatic conditions but rather represent a typical niche partitioning of large mammals in a Middle Miocene ecosystem.

Deinotherium levius vel *giganteum*

The species represents the largest large mammal taxon recorded at the locality. A body mass of 6t was reconstructed for the not fully grown "young" adult from Gratkorn (representing rather a small value for the taxon). Although body size was most likely smaller for the specimen sampled for stable isotope analyses, it was still by way larger than the other large mammals recorded from the locality.

$\delta^{13}C$ and $\delta^{18}O_{CO3}$ values for *Deinotherium levius* vel *giganteum* fit well with browsing on top canopy leaves (Bocherens and Sen 1998). In comparison to other measurements on Proboscidea from different Miocene localities of different stratigraphic levels, it can be observed that the Gratkorn specimen nests well among the Deinotheriidae (Fig. 17 d). Representatives of this family (with Tapir-like lophodont dentition) in general show values typical for browsing in a C3 dominated mesic/ woodland environment. In contrast, Miocene European Gomphotheres (data from Tütken et al. 2006; Domingo et al. 2009; Tütken and Vennemann 2009; Domingo et al. 2012; more bunodont dentition) usually show higher $\delta^{13}C$ values, indicating a higher degree of mixed feeding and feeding in a more open environment, though still in C3-dominated vegetation.

Serial measurements along the axis of two fragmented teeth from Gratkorn, of assumably one individual, show seasonal variation in $\delta^{18}O_{CO3}$. Each tooth displays one maximum (summer) and one minimum (winter), a 1-year cycle would be recorded by combining the two patterns, under the assumption that both teeth belong to the same individual. Little variation in $\delta^{13}C$ and incoherent with $\delta^{18}O_{CO3}$ imply no seasonal diet change for *Deinotherium levius* vel *giganteum* from Gratkorn but fit to a more generalistic and unselective feeding strategy (Tütken and Vennemann 2009).

Lartetotherium sansaniense

Lartetotherium sansaniense belongs to the second largest mammal group, Rhinocerotidae, in Gratkorn and is the smallest species of rhinocerotids recorded. Its $\delta^{13}C$ values are slightly higher than in the cervid *Euprox furcatus* or the proboscidean *Deinotherium levius* vel *giganteum*, though still nesting well within the range expected for feeding in a mesic/woodland C3-dominated environment (Fig. 16).

Comparing different values for Miocene Rhinocerotidae from literature and own measurements (Fig. 17c), it can be observed that, independent of age and climate, *Lartetotherium sansaniense* usually shows higher values for $\delta^{13}C$ and also frequently for $\delta^{18}O_{CO3}$ than other Rhinocerotidae.

Although more data are needed to reconstruct ecological adaptations for the different rhinocerotid genera and species, the data already indicate different ecological niches with *Brachypotherium* and other teleoceratini feeding in a more closed mesic/woodland environment (also fitting well to the graviportal gait and limb shortening; Heissig 1999), while *Lartetotherium sansaniense* was feeding in more open environment and aceratini occupied niches in between, which is also well in accordance with other considerations on the ecology of the different taxa (Heissig 1999; Bentaleb et al. 2006; Tütken and Vennemann 2009). Due to the morphology of the upper premolars (lack of lingual cingula) *Lartetotherium sansaniense* has often been interpreted as a selective browser (Coombs 1989; Heissig 2012), but this feature does not exclude a considerable amount of low abrasive grasses.
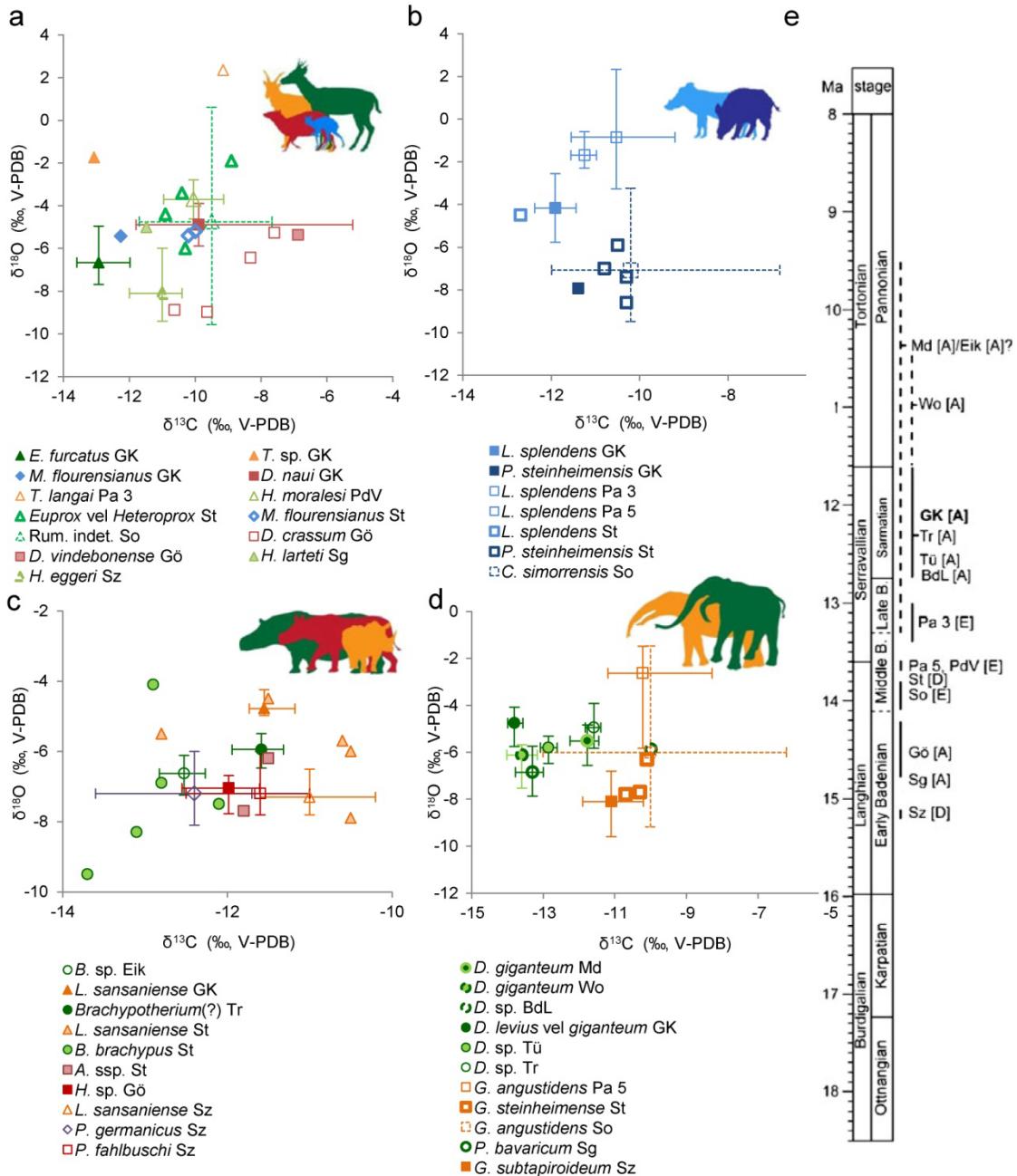
Fig. 17: Mean values with total range of $\delta^{18}O_{CO3}$ (‰V-PDB) versus $\delta^{13}C$ (‰ V-PDB) for large mammals (enamel) from the Gratkorn locality in comparison with data from other Miocene localities [*GK* Gratkorn (own measurements); *Pa 3* Paracuellos 3 (from Domingo et al. 2012); *PDV* Puente de Vallecas (from Domingo et al. 2012); *St* Steinheim a. A. (from Tütken et al. 2006); *So* Somosaguas (from Domingo et al. 2009); *Gö* Göriach (own measurements); *Sg* Seegraben (own measurements); *Sz* Sandelzhausen (from Tütken and Vennemann 2009); *Pa 5* Paracuellos 5 (from Domingo et al. 2012); *Eik* Eichkogel (own measurement); *Tr* Trössing (own measurements); *Md* Mödling (own measurements); *Wo* Wolfau (own measurements); *BdL* Bruck an der Leitha (own measurements)].

a Ruminantia (*E. Euprox*; *T. Tethytragus*; *M. Micromeryx*; *D. Dorcatherium*; *H. Heteroprox*; Rum. Ruminantia); **b** Suidae (*L. Listriodon*; *P. Parachleuastochoerus*; *C. Conohyus*); **c** Rhinocerotidae (*B. Brachypotherium*; *L. Lartetotherium*; *A. Aceratherium*; *ssp.* several species; *H. Hoploaceratherium*; *P. germanicus Prosantorhinus germanicus; P. fahlbuschi Plesiaceratherium fahlbuschi*); **d** Proboscidea (*D. Deinotherium*; *G. Gomphotherium*; *P. Prodeinotherium*); **e** Stratigraphic age of different localities (*A* Austria, *D* Germany, *E* Spain, *B* Badenian); from Aiglstorfer et al. 2014a

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Serial sampling of the Gratkorn rhinocerotid tooth did not show significant variations in δ^{13}C and δ^{18}O$_{CO3}$. As seasonality for the region around Gratkorn is indicated by sedimentology, ectothermic vertebrates (Gross et al. 2011), and the serial measurements on *Deinotherium levius* vel *giganteum*, the height of the rhino tooth fragment might be too short to represent a time interval recording seasonal variation.

Suidae

Listriodon splendens and *Parachleuastochoerus steinheimensis* show similar values for δ^{13}C but are quite distinct in δ^{18}O$_{CO3}$ (Fig. 16). Isotopic measurements of *Listriodon splendens* from Gratkorn fit well within the ecological niche of a specialized folivore and higher values in δ^{18}O$_{CO3}$ indicate a certain amount of mixed feeding or ingestion of maybe upper canopy fruit, fitting well also to traditional interpretations based on morphology (Made 1996; Made et al. in press).

The distinctly lower δ^{18}O$_{CO3}$ values, but similar δ^{13}C values in *Parachleuastochoerus steinheimensis* from Gratkorn, could be explained by digging for roots, as these are depleted in δ^{18}O$_{CO3}$ in comparison to leaves, while δ^{13}C values are similar (Sponheimer and Lee-Thorp 2001). While incisor and general jaw morphology makes consumption of roots for the genus *Listriodon* unlikely (Made 1996; Made et al. in press and references therein), for the subfamily Tetraconodontinae, to which *Parachleuastochoerus* is assigned, a certain amount of root consumption is assumed due to dental morphology (Hünermann 1999; Made et al. in press).

Combining isotopic measurements from Gratkorn with literature data from other Miocene localities (Tütken et al. 2006; Domingo et al. 2009; Domingo et al. 2012; Fig. 17b) different ecological niches for *Listriodon splendens* and for tetraconodontid suids (*Parachleuastochoerus steinheimense* and *Conohyus simorrensis*) are verified and seem to be rather independent of climate and stratigraphic level.

Dorcatherium naui

The tragulid, *Dorcatherium naui*, from Gratkorn had a shoulder height of about 40–50cm and body mass estimates for the Gratkorn specimens are about 28–29kg (min: 26kg, max 30.6kg; n=6), well in accordance with literature data.

Modern Tragulidae inhabit the undergrowth of forested environments (Rössner 2007), and other species of the genus, like *Dorcatherium crassum*, have been considered indicators for wetland conditions. From limb-morphology a low-gear locomotion seems most likely for the species (Leinders 1979; Köhler 1993; Morales et al. 2012) and hind limb morphology indicates an inability of zigzag flight behaviour for the genus (Alba et al. 2011). This led Moyà-Solà (1979) to the assumption that the escaping behaviour in *Dorcatherium* was fleeing straight into the next open water as in the living African tragulid *Hyemoschus* (Dubost 1978) and thus indicating an adaptation to rather more humid environments.

So far, no isotopic measurements have been published on Miocene Tragulidae of Europe. The clearly higher δ^{13}C values (Fig. 16) in *Dorcatherium naui* from Gratkorn in comparison to all other large mammals from the locality were quite unexpected, as one would expect lower values in a taxon adapted to closed and humid undergrowth. δ^{18}O$_{CO3}$ values are instead only slightly higher than in

cervids. These values can be either explained by a certain amount of mixed feeding (leaves and grass) or by ingestion of a considerable amount of fruit. Modern Tragulidae, for example, feed on fallen fruit, seeds, flowers, leaves, shoots, petioles, stems, and mushrooms in the forest undergrowth (Dubost 1984). On the one hand there is no evidence for the existence of a relevant amount of grass in the vegetation of Gratkorn so far. On the other hand an exclusively frugivore diet for the species cannot be assumed, as the climate makes an all-year fruit supply for the area around Gratkorn most unlikely. Today, the fruit supply is not high enough even in evergreen forests for a strictly frugivore feeding of terrestrial frugivores all year long (Smythe 1986). Measurements on other species of the genus, *D. crassum* and *D. vindebonense*, from an intramontane basin (early Middle Miocene locality of Göriach; Austria; ~14.5 Ma ± 0.3 Ma) also showed generally slightly higher $\delta^{13}C$ values than other ruminants (Fig. 17a), which could result as well from an ingestion of a considerable amount of fruits. Based on microwear analyses a frugivore browsing diet was reconstructed for *D. naui* from the Late Miocene locality Atzelsdorf (Austria; 11.1 Ma; Merceron 2009). Furthermore, an ingestion of a certain amount of fruits is also supported by the morphology of the incisor arcade of *D. naui* from Gratkorn. The strongly widened i1 in comparison to i2 and i3 observed in *Dorcatherium naui* and in modern Tragulidae points to a more selective feeding strategy. Although limited in its predictions (Fraser and Theodor 2011), disparity in incisor widths is significantly higher in browsers than in grazers (Janis and Ehrhardt 1988; Clauss et al. 2008). Applying these ecomorphological considerations, a more selective picking of perhaps fruits might explain the higher ratio of i1 width to i2 or i3 width of *Dorcatherium* in comparison to the subcanopy browsing cervid, *Euprox furcatus*, while grazing would not fit with the relative incisor width. On the other hand, a mixed diet was reconstructed for the other more selenodont *Dorcatherium* species, *D. guntianum,* from the NAFB by Kaiser and Rössner (2007). Furthermore, Ungar et al. (2012) observed mixed feeding for Early Miocene Tragulidae from Africa. In addition to different diets, a different digestion system or drinking behaviour in *Dorcatherium* could also explain differences in isotopic ratios in comparison to higher ruminants.

In summary, for the moment, we consider *Dorcatherium naui* from Gratkorn a browser with facultative frugivory, but we cannot completely rule out a certain amount of mixed feeding. In any case, the abundance of *D. naui* at Gratkorn indicates a tolerance to less humid environments for the species than assumed for other species of the genus.

Micromeryx flourensianus

With an estimated body mass of about 4–5kg (min.: 3.8kg, max. 5.0kg; n=6), *M. flourensianus* is the smallest ruminant taxa from Gratkorn and was most likely adapted to a more or less closed environment with sufficient understory, as it can be observed for all modern ruminants of this size class (Köhler 1993; Rössner 2010). A pure C3 browsing diet can be assumed for *M. flourensianus*, possibly with slight enrichment with fruits and seeds, resulting in the slightly higher values for $\delta^{13}C$ and $\delta^{18}O_{CO3}$ in comparison to most of the cervids (Tütken and Vennemann 2009). Although the data from Gratkorn are based on only one individual, the diet reconstruction seems to be quite stable as it fits to isotopic data, and morphologic and microwear analyses of conspecific material from other localities (Köhler 1993; Tütken et al. 2006; Merceron et al. 2007; Merceron 2009; Fig 17a).

Fig. 18: ^{87}Sr/^{86}Sr isotope compositions from Gratkorn versus body mass (mammals only). Gastropods, ▶ the microbialite and small mammals (complete teeth) represent the local ratio for the locality. Most of the large mammals (enamel), especially with larger body mass, show different values from the local ratio due to migration (maybe provoked by limitation of available biomass at the locality). The values are compared to the modern natural mineral water values from Graz (data from Voerkelius et al. 2010), to the range for marine carbonates in general (data from Tütken 2010) and to ratios from measurements on shark teeth and foraminifera from late Karpatian to early Sarmatian sediments from Austria (Bad Vöslau, Leithakalk, Siebenhirten) and Hungary (Danitzpuszta and Himesháza) (data from Hagmaier 2002; Kocsis et al. 2009; VB Vienna Basin; PB Pannonian Basin). Bodymass estimations follow Aiglstorfer et al. (2014d) for ruminants, Costeur et al. (2012) for *Listriodon splendens* and *Prolagus oeningensis*, Aiglstorfer et al. (2014b) and citations therein for *Deinotherium levius* vel *giganteum*, and Fortelius (2013) for *Parachleuastochoerus steinheimensis*; and is oriented for *Schizogalerix voesendorfensis* on the value for *Schizogalerix* sp. given by Merceron et al. (2012); from Aiglstorfer et al. 2014a

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Euprox furcatus

With a body mass of 24–30kg (min: 23.8kg, max: 29.9kg; n=6) and a shoulder height of about 60–70cm, this species was comparable in habitus to the modern red muntjac (*Muntiacus muntjak*; Mattioli 2011). It is assumed that the species possessed the typical sexual dimorphism for cervids with only males displaying cranial appendages (Peters 1871; Heizmann and Reiff 2002) and also indicated by an antlerless articulated *Euprox* vel *Heteroprox* skeleton from Steinheim a. A.. *Euprox furcatus* from Gratkorn generally shows lower values for δ^{13}C and δ^{18}O$_{CO3}$ in comparison to other taxa from Gratkorn (Fig. 16). The lower values in *Euprox furcatus* fit well with an ecological niche comprising mostly subcanopy diet in a more closed, forested C3 environment. The low δ^{18}O$_{CO3}$ values for *Euprox furcatus* in comparison to other large mammals could also indicate an obligate drinking behaviour (Kohn 1996; Kohn et al. 1996).

Combining literature data with the data from Gratkorn (Fig. 17a) it can be observed that *Euprox furcatus* shows lower values, while *Heteroprox* seems to be more enriched in both ^{18}O$_{CO3}$ and ^{13}C. This could be explained by less browsing in subcanopy environment by the latter in comparison to *Euprox furcatus* but a higher degree of mixed feeding. However, occupation of different ecological niches is also dependent on the frame conditions and the number of co-occurring species (DeMiguel et al. 2011) and so far, there is not enough data to define clearly distinct ecological niches for *Euprox furcatus* and *Heteroprox* ssp.. However, the results from Gratkorn and literature data (Tütken et al. 2006; DeMiguel et al. 2011; Domingo et al. 2012) indicate that *Euprox furcatus* rather represents a subcanopy browser and, in the case of co-occurrence with *Heteroprox larteti*, might have displayed a lower degree of mixed feeding than the latter.

Tethytragus sp.

With a body mass of about 27–29kg (min: 27.4kg, max: 29.1kg; n=2), *Tethytragus* sp. from Gratkorn is considered a medium-sized ruminant. It shows the highest value for δ^{18}O$_{CO3}$ observed in the large mammal fauna of the locality (Fig. 16) well in accordance to literature data on the same genus (Domingo et al. 2012; Fig. 17a). This fits well to feeding on top canopy plants exposed to higher evaporation, as was reconstructed, for example, for *Giraffokeryx* (Giraffidae) from Paşalar by
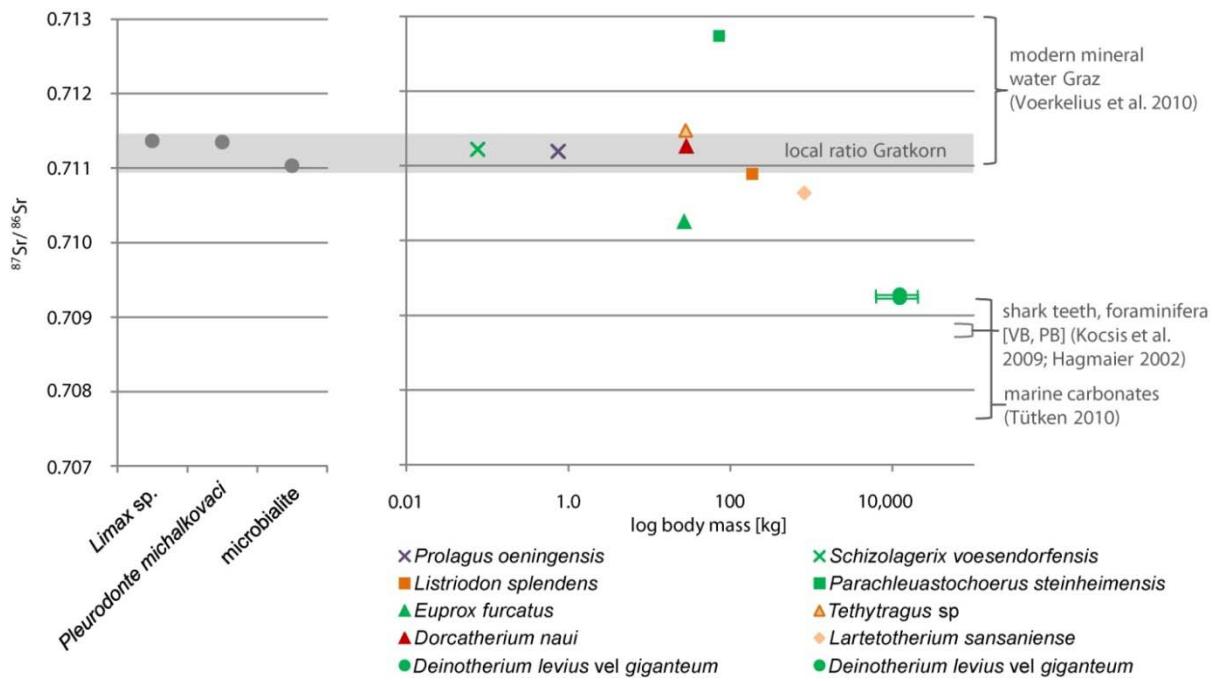
Bocherens and Sen (1998) and for *Germanomeryx* (Palaeomerycidae) from Sandelzhausen by Tütken and Vennemann (2009). Although smaller in body size than these taxa, a feeding on top canopy plants could have been possible for *Tethytragus* due to a caprine-like postcranial adaptation, which allowed climbing and tree-/rock-jumping to a certain degree (indicated for the Gratkorn specimen due to the morphology of a recorded metatarsal). Adaptation to mountainous areas was shown by Köhler (1993) for *Tethytragus koehlerae* from the Turkish locality of Çandir (Middle Miocene).

5.2. Provenance and migration of large mammals

A detailed migrational history cannot be reconstructed from ^{87}Sr/^{86}Sr ratios of the large mammals from Gratkorn (Fig. 18). However, it can be observed that *Tethytragus* sp. and *Dorcatherium naui* were more or less local residents and assumably better adapted to the seasonal variations and food supply limitations of the locality. *Parachleuastochoerus steinheimensis* lived at least temporarily in areas with higher ^{87}Sr/^{86}Sr ratios in bioavailable strontium, as e.g. the Eastern Alpine Mountain Chain. While the other large mammals, *Listriodon splendens* (only to a minor degree), *Lartetotherium sansaniense*, and *Euprox furcatus*, inhabited, at least temporarily, areas with slightly lower ^{87}Sr/^{86}Sr ratios in bioavailable strontium (early Sarmatian sediments with considerable terrestrial input), *Deinotherium levius* vel *giganteum* shows the lowest values, fitting well to fully marine early Sarmatian sediments, most likely exposed during the Middle Miocene in the Styrian basin (Fig. 18).

Especially the larger herbivores, such as the proboscidean or the rhinocerotids (see Fig. 18 for bodymasses), were dependent on a large amount of daily food supply and a limitation in the available biomass (at least during some seasons) at the Gratkorn locality might be an explanation for migration of the larger mammals.

6. Summary

The early late Sarmatian Gratkorn locality (12.2/12.0 Ma) yielded a rich large mammal community with so far 14 species of herbivorous large mammals, *Deinotherium levius* vel *giganteum, Aceratherium* sp., *Brachypotherium brachypus*, *Lartetotherium sansaniense*, *Chalicotherium goldfussi*, *Anchitherium* sp., *Listriodon splendens, Parachleuastochoerus steinheimensis, Dorcatherium naui, Micromeryx flourensianus*, ?*Hispanomeryx* sp., *Euprox furcatus*, Palaeomerycidae gen. et sp. indet., and *Tethytragus* sp.. The fossil assemblage from Gratkorn is considered to form a more or less autochthonous taphocoenosis without any significant time averaging (or faunal mixing) in terms of geologic resolution (contemporaneously deposited). Most likely the accumulation did not extant a few years or decades and was to a considerable amount the result of scavenging carnivores.

During the late Middle Miocene the Gratkorn locality (bordered by the Eastern Alpine Mountain Chain in the north and the Styrian Basin in the south) was part of an ecosystem with a predominantly C3 vegetation in a semi-arid and subtropical climate with distinct seasonality and too little precipitation (MAP of 486 ± 252 mm and a MAT of less than 15 °C; Böhme and Vasilyan 2014) for a closed canopy woodland. Gastropod, small and large mammal assemblages fit well within such a well-structured, riparian landscape (Gross et al. 2014). It provided enough diversity in plant resources to allow occupation of different niches by herbivorous large mammals (subcanopy browsing, rooting, top canopy browsing, facultative frugivory, and mixed feeding). Niche partitioning among large mammals proved to be stable comparing the data from Gratkorn with data for other localities, distinct in time and space, and seem to reflect a rather typical partitioning in a Middle Miocene faunal assemblage and less dependent on climatic frame conditions.

Most of the large mammals from Gratkorn are typical for a late Middle Miocene faunal assemblage. The presence of the tragulid *Dorcatherium naui* (more common during the Late Miocene) in contrast is one of the earliest records of this species and the richest assemblage from the Middle Miocene. It provides essential data for an assignation of this species to a more selenodont lineage among Miocene European Tragulidae, well distinct from *D. crassum*, and thus represents a key population for the evaluation of tragulid phylogeny.

Due to the rich record and the well defined frame conditions the Gratkorn locality can be well termed a benchmark locality for the terrestrial deposits from the Sarmatian *sensu stricto* of the Central Paratethys realm (Gross et al. 2011).

Fig. 19: Student excavation at the Gratkorn locality 2012

7. Acknowledgements

"Dang Eich fir ällas!"

8. Reverences

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