

Taphonomical and ichnological considerations on the late Middle Miocene Gratkorn locality (Styria, Austria) with focus on large mammal taphonomy

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Abstract At the Gratkorn locality (Styria, Austria), a highly diverse, late Middle Miocene (late Sarmatian *sensu stricto*; 12.2–12.0 Ma) faunal assemblage is preserved in a palaeosol. It represents the first systematically excavated and well-documented continental Sarmatian site in Central Europe. Taphonomical analysis of the 700 large mammal specimen excavated so far has led to the following conclusions: (1) the level of diagenetic alteration is low, as primary (aragonitic) mineralisation in gastropod shells is preserved and teeth and bones of large mammals in general show a relatively low total REE content; (2) the high degree of disarticulation and fragmentation in large mammal bones is induced by hunting, scavenging, trampling, and neotectonics; (3) there are no signs for fluvial transportation due to the general preservation features of the bones (e.g. no record of abrasion) and the still roughly associated fragments of individual bones and skeletons; and (4) local accumulation of large mammal bones is the result of scavenging. The fossil assemblage 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).

Keywords Vertebrate taphonomy · REE-pattern · Middle Miocene · Scavenging · Palaeosol

Introduction

Taphonomical analysis is the fundamental tool for estimations on the role of ecological and sedimentological (e.g. diagenetic) influences on a fossil assemblage and its preservation. Circumstances of deposition, erosion, and diagenesis have a reasonable impact on the fossil record available for the reconstruction of ancient ecosystems (see e.g. Lyman 1994; Martin 1999). Invertebrate and vertebrate taphonomy in terrestrial sites is mainly influenced by disarticulation, fracturing, and transportation of shell or bone elements (by biotic as well as abiotic processes; for details, see discussions in Behrensmeyer and Kidwell 1985; Behrensmeyer 1988, 1991; Lyman 1994; Martin 1999). Estimations on the degree of diagenesis and recrystallisation in bones, teeth, and invertebrate shells are indispensable for the application of analytical methods, like e.g. isotopic measurements (Rink and Schwarcz 1995; Kohn et al. 1999). The site Gratkorn (Styria, Austria; Middle Miocene, Sarmatian *sensu stricto*, 12.2–12.0 Ma) must be considered a particular site for taphonomic analysis as it houses a mostly contemporaneous, autochthonous community (see Gross et al. 2011). Since 2005, more than 1,000 vertebrate remains (700 attributed to large mammals) have been recovered in excavations from one single layer by the Universalmuseum Joanneum Graz and the Eberhard Karls Universität Tübingen at the clay pit St. Stefan near Gratkorn. This community was investigated by classical taphonomical/palaeoecological methods (Voorhies-Analysis; estimations of completeness, weathering, disarticulation, fracturing, and

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degree of scavenging; taxonomic, body-mass, and age distribution) and geochemical/mineralogical methods (REE-content and patterns, stable isotope analysis, XRD carbonate analysis). Additionally, ecological circumstances, sedimentology of the host sediment, and the geographic position in the context of regional geology have been taken into consideration.

Geologic overview

The site Gratkorn is situated at the southern rim of the Eastern Alps (Fig. 1; Gross et al. 2014, this issue). A Neogene clastic sedimentary section (“Gratkorn Formation” according to Flügel et al. 2011) is lying discordantly on top of Palaeozoic carbonates and siliciclastics from the “Grazer Paläozoikum” (see Flügel et al. 2011). The fossil-bearing palaeosol on top of a coarse-grained braided river sequence (see Gross et al. 2011; layer 11 a and b in Gross et al. 2014, this issue) was discovered by M. Gross in 2005, during geological mapping of the area. It reaches a thickness of up to 55 cm and lithology consists of a green-grey (sometimes brownish oxidized), moderately solidified, silty-sandy clay to clayey silt/fine sand with very low primary carbonate content (for detailed information, see Gross et al. 2011, 2014, this issue), and is interpreted as a floodplain palaeosol, influenced sporadically by a braided river system during floods (Gross et al. 2011). From base (lower part of palaeosol) to top (upper part of palaeosol), a gradual decrease in grain size and slight enrichment in the carbonate content can be observed. Gravels (generally scarce; most frequent in the lower part) in the palaeosol show a predominance of igneous and metamorphic rocks in the source area (Gross et al. 2014, this issue), which crop out abundantly in today’s hinterland of the locality (Gleinalpe 20 km NW of Gratkorn; Flügel et al. 2011). Maturity of the

sediment is high (low carbonate content, well-rounded grains), grain size sorting well (fine to medium sand with small gravels). Maturity of the palaeosol is low and stratification is missing (particularly in the lower part). The upper part of the palaeosol displays more hydromorphic conditions than the lower part. The soil is overlain by marly lacustrine sediments (Peterstal Member of Gleisdorf Formation with a total thickness of at least 25 m; Gross et al. 2011).

Palaeosol formation

The palaeosol can be subdivided in an upper, clayey part (10 cm), and a lower, more sandy part (45 cm). Pedogenic carbonate glaebules are rarely observed in the lower part of the palaeosol, while microbialites up to few centimetres in diameter have been sporadically detected in the uppermost part. The time span for deposition of the primary sediment of the palaeosol was supposedly very short and is interpreted as sedimentation of a crevasse splay on a flood plain (Gross et al. 2011; 2014, this issue). The time span for soil formation was suggested to be in the range of 10^1 – 10^2 years, more likely lasting only a few decades (Gross et al. 2011). Pedogenic features (mottling, carbonate concretions, stratification, lessification, and clay cutanes) are weakly developed. This would indicate either less intense soil-forming processes or a shorter time span for formation. Since the climate during the late Sarmatian (Böhme et al. 2008, 2011), especially as recorded in Gratkorn (Gross et al. 2011; Böhme and Vasilyan 2014, this issue; based on estimations by ectothermic vertebrates) was warm-temperate to subtropical, with sub-humid conditions (seasonal changes in precipitation), the latter explanation is more plausible. Autochthonous horizontal rhizoms and roots up to several metres in length and 10 cm in thickness are preserved. Gross et al. (2011) mentioned still vertical, xyloid lignitic, partially silicified stumps of trees excavated during active mining. They are attributed to the family Cupressaceae (*Taxodioxylon*; A. Selmeier, personal communication). Those trees were most likely just rooting in the palaeosol and represent vegetation growing at the time of the lake formation. Otherwise, plant remains in the soil layer are more scarce, comprising smaller roots and rootlets, rhizomes, and *Celtis* fruits. Up to now, there have been no sedimentological signs for desiccation or flooding in the palaeosol, but, above it, laminated, calcareous, silty marls rich in leaves (“leaf layer”) comprise the basal 3 m of the lake deposits (for detailed section, see Gross et al. 2011). Only at the northern part of the outcrop on top of the palaeosol, a matrix supported gravel was observed, which is missing completely in other parts (debris flow; see Gross et al. 2011; 2014, this issue). Between 20 and 300 cm above the palaeosol, leaves associated with characean oogonia are most abundant (see Gross et al. 2014, this issue). Invertebrate remains in the palaeosol are

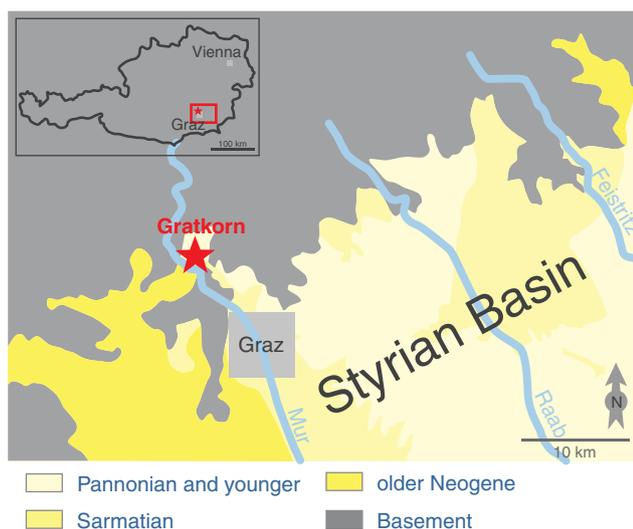


Fig. 1 Geographic position of Gratkorn and geological overview of the surroundings of the site

predominantly terrestrial gastropod shells (including slugs; Harzhauser et al. 2008), while articulated arthropods have only been detected in the lacustrine marls above (see Gross 2008; Klaus and Gross 2010; Gross et al. 2014, this issue). Vertebrate findings are restricted to the

palaeosol itself and only occur very sporadically in the lacustrine marls (these were not considered for taphonomical analysis). The most important taphonomic, ecologic and sedimentologic features of the Gratkorn locality are summarised in Table 1.

Table 1 Main taphonomic, ecologic and sedimentologic features of the Gratkorn locality (Styria, Austria)

Variable	Features observed at Gratkorn locality
Outcrop informations	
Sample size	1,000 vertebrate specimens (700 large mammals)
Surface excavated	220 m ² (2011–2013 continuous surface) and 120 m ² (2006–2010 on different sites)
Bone distribution	Grouped, no current alignment, no size separation
Articulated elements	Small mammals, one cervid vertebral column, proboscidian partial skeleton
Large mammal assemblage	
Number of species	13 (excluding carnivores)
Percentage of indeterminable bone fragments	47 %
MNI	48
NISP	363
Age profile (exluding carnivores)	
Juvenile specimen	25 % (MNI=12)
Adult specimen	60 % (MNI=29)
Senile specimen	15 % (MNI=7)
Predominant taxonomic groups	Cervidae, Tragulidae, Moschidae, Suidae
Predominant skeletal elements	Teeth, jaws, antlers
Predominant Voorhies Groups (VG)	VG III (63 %), VG I (18 %)
Pedological/sedimentological information	
Grain size	Fine clastic (silt, fine sand)
Sorting	Good (except of isolated gravels)
Redox conditions	Predominantly not oxydised, except of fossil roots and rhizomes
Carbonate content	Low (less than 10 %)
Pedogenic carbonates	Present, but only sporadically dispersed up to a few centimetres in size
Roots/rootlets/rhizoms	Frequent, up to several metres long
Bioturbation	Different kinds of presumably insect bio-turbation are frequent
Maturity	Of sediment high, of pedogenesis low
Interpretation	Palaeosol in crevasse splay on flood plain
Bone/shell biostratinomic information	
Breakage	Very common, most long bones crushed, many islated teeth
Weathering	WS 0–5
Abration	No
Diagenetic corrosion/incrustation	Iron hydroxide incrustations, different colour pattern in long bones
Bioerosion	Very common, insects, small mammal gnawing, large mammal bite marks
Bone/shell diagenetic information	
Gastropod shell mineralisation	Original aragonitic/calcitic composition
REE content	Low with no enrichment in mREE
Stabel isotope investigations	Biogenic values (Aiglstorfer et al. 2014a)
Palaeoenvironment	
Palaeoprecipitation	486±252 mm/ year(Gross et al. 2011, Böhme and Vasilyan 2014)
Climate	Temperate subtropical, (MAT=15 °C; Böhme and Vasilyan 2014)
Palaeogeography	At the rim of Eastern Alps; northern border of Styrian Basin

MNI minimum number of individuals, *NISP* number of identified specimen, *WS* weathering stage, after Behrensmeier (1978)

Materials and methods

Excavation technique

The excavation technique chosen for documentation of the faunal assemblage consist in systematic open area excavations recording the exact position of each finding by drawings and digital photography. Vertebrate findings larger than 1 cm were documented in detail (centimetre scale) in excavation plans based on a 1-m-square grid (scale 1:20) and photographed. Since 2011, it has been possible to excavate a continuous area (see overview in Gross et al. 2014, this issue) which was extended up to 2013 on a surface of 220 m². As the palaeosol is solidified to a certain degree, only the uppermost 10–20 cm could be excavated every year, while deeper strata were dug in the following year after surface weathering. For taphonomic analysis, results of excavation campaigns 2005–2012 were considered, while first data from campaign 2013 were only partially available. The exact stratigraphic position of specimens (basal lacustrine marls, and upper and lower parts of palaeosol; see section in Gross et al. 2014, this issue) was documented and considered, if possible. Due to considerable amounts of neotectonics (faults), a gradual lithofacial change along the section from base to top, and biotic influences on the deposition of vertebrate remains, the subdivision of an upper and a lower part of the soil can only be given approximately in many cases.

Coordinates given in figures follow Austrian Grid (BMN M34–GK) without using abbreviations.

Large mammal taphonomy

The terms ‘small mammals’ and ‘large mammals’ are used in different ways in the literature (body mass or taxonomically). We used a taxonomical definition and thus distinguish the groups of rodents, insectivores, and lagomorphs (small mammals) from perissodactyla, artiodactyla, proboscidea, and carnivora (large mammals). Expanded Voorhies analysis of vertebrate remains follows Behrensmeyer (1975). Minimum numbers of individuals (MNI) have been reconstructed for large mammals following the concept by Lyman (1994, p. 100 ff.). Besides the singularity of every anatomical element, attrition of teeth was also taken into consideration. Body mass estimations follow Merceron et al. (2012), Costeur et al. (2013), and Aiglstorfer et al. (2014b, d, this issue).

Age classes were defined as follows: juvenile (deciduous dentition), adult (permanent dentition), and senile (trigonid of m1 completely worn). Due to the clear abundance of tooth remains and the scarcity of well-preserved postcranial material or articulated skeletons, a more detailed subdivision considering tooth wear combined with fusion of postcranial long bones is not realistic for the Gratkorn material. Young adult specimens, such as, e.g. a *Deinotherium levius* vel *giganteum*

partial skeleton, with not fully fused epiphyses, are therefore not disclosed separately but included in adult specimens. A delayed fusion of the long bones and continuation of growth beyond sexual maturity has been observed in modern proboscideans (Poole 1996; in males even up to the age of 30–45 years; see discussion in Aiglstorfer et al. 2014b, this issue). Specimens only documented by postcranial elements are considered adult in all cases, if fusion of long bones is completed and no signs of attrition indicate a senile age.

REE analysis with LA-ICP-MS

Analysis of powder only delivers an average composition of bone or tooth (Trueman 2007) and is more at risk of contamination by filling of microcracks or haversian canals. Laser ablation-inductively coupled plasma-mass spectrometry (LA-ICP-MS) in contrast is distinguished by minimum sample preparation (and the possible contamination during this process) and allows a precise space-resolved sampling, helping to reduce the degree of contamination and allowing to exactly sample the desired tissue (see, e.g. Rogers et al. 2010 for discussion and references). As pointed out by Rogers et al. (2010), LA-ICP-MS has so far only rarely been applied in palaeontological research, but as it has proved to be an ideal analytical tool in work with complex materials such as fossil bones and teeth, it has been used more in recent years (see, e.g. Herwartz et al. 2013). A total of 23 samples, including 11 bone fragments and 12 tooth fragments, were analysed for REE-composition and Sr-content using LA-ICP-MS. Of the tooth fragments, 12 samples were gained from dentine, and 9 from enamel. Specimens were set in epoxy blocks, ground, and polished with agglomerated alpha alumina suspension in order to prepare a plane surface. Blocks were cleaned with distilled H₂O and placed directly in the sample chamber of the LA-ICP-MS system (resonetics RESolution M-50, coupled with a Thermo Scientific iCAP Q ICP-MS). The samples were analysed with a spot size of 33 µm, a repetition rate of 5 Hz and an energy density of 3.5 J/cm². Time per measurement was scheduled as 120 s. Measured lines were positioned in an area of less than 2 mm distance from the outer bone rim. The course of the line scans was visually controlled to avoid contamination due to, e.g. Haversian canal fillings and fractures or microcracks, where possible. Time-resolved ICP-MS spectra showed variations of REE content related to heterogeneous composition and microcracks. In these cases, scans were reduced to areas with stable REE contents. Measurement conditions in the Thermo Scientific iCAP Q ICP-MS were: rF Power 1,550 W, carrier gas flow (He) 0.6 l/min+0.003 l/min N₂, makeup gas (Ar) 0.88 l/min. For calibration, the following standards were used: NIST 611 and NIST 613 (The National Institute of Standards and Technology), as well as T1-G (MPI-DING reference glass, MPI Mainz) for control of quality. For bones and teeth, ⁴³Ca was used as an internal standard to calculate absolute element concentrations from signal intensities. Following Herwartz

et al. (2013), calcium content was assumed to be 36 wt% based on typical Ca contents measured for fossil bones. Most bone samples are assumed to have a Ca content within 2–3 % (Herwartz et al. 2013). Therefore, these 2–3 % need to be added to the external precision of the LA-ICP-MS element concentrations, which is typically better than 5–10 % (Herwartz et al. 2013). Detection limits for the dataset are generally 0.1–0.5 ppm for REE. All samples were standardised with Post-Archaean Australian Shale (PAAS) values of Taylor and McLennan (1985).

Mineralogical analysis

For a non-invasive determination between calcite and aragonite in the gastropod shells, X-ray μ -diffraction analysis was performed using a BRUKER D8 Discover θ/θ GADDS microdiffractometer with a beam diameter of app. 300 μm , due to the used monochromator optic and a large VÅNTEC-500 two-dimensional detector (μ -XRD²) covering 40° in the 2 θ and chi range (Berthold et al. 2009).

Material repository

Material is stored at the Universalmuseum Joanneum, Graz, section for geology and palaeontology (UMJGP), and at the Palaeontological Collection of Eberhard Karls Universität Tübingen (GPIT).

Results and discussion

Plant preservation

The various parts of the soil and the lacustrine marls display different kinds of plant tissue preservation. In the whole palaeosol, calcitic fructifications of *Celtis* are locally abundant, frequently preserved in groups of dozens of specimens. In the lower, more sandy part of the palaeosol roots and rhizomes up to several metres long and 10 cm in diameter were excavated. While the roots and rhizoms themselves are preserved as oxidized organic material or completely decomposed, early diagenetic, brownish iron hydroxide concretions grew around them, preserving the course of the root and its uncompact cast. Adherent sediment is frequently oxidized up to 50 cm around roots. Noteworthy pyrite or coal layers, indicating anoxic conditions, were not detected. In the upper part of the palaeosol, rhizomes are preserved as oxidized organic material, but without any iron hydroxide concretions (GPIT/IC/253; Fig. 2d, black arrow). With the typical alignment of nodes and rootlets, the rhizomes (Fig. 2f) are attributable to Poales (D. Uhl, personal communication), comprising grasses and sedges. Because of their size (diameters up to 5 cm), giant forms must be assumed, similar to extant *Arundo*,

which reaches several metres in height. They are interpreted as deeper rhizomes of plants growing at the time of deposition of lacustrine marls above the palaeosol. In the uppermost part of the palaeosol, only rootlets, up to 2 mm in diameter, are preserved as brownish impressions. Above the palaeosol, leaves occur frequently, comprising both terrestrial and aquatic species and related fructifications (*Potamogeton*, Characeae, *Salix*, *Alnus*, and other taxa). But cuticular preservation is largely missing, especially in the southern part of the pit. In the uppermost part of the palaeosol, several carbonate nodules have been excavated, ranging in diameter from 10 to 25 cm and showing a clearly flattened, suboval shape with an irregular, cauliflower-like surface (GPIT/LI/731; Fig. 2a). In thin sections (Fig. 2b), internal lamination was observed, but no pillar-structures, as expected, e.g. in freshwater stromatolites or laminated cyanobacterial mats in general (see classification in Gerdes 2007). Therefore, the structures were identified as non-cyanobacterial biomats, or generically as microbialites. Isotopic composition of the microbialites compared to the sediment in the upper part of the palaeosol shows a depletion in ¹³C from $\delta^{13}\text{C} = -7.7\text{‰}$ (sediment) to $\delta^{13}\text{C} = -12.6\text{‰}$ VPDB (microbialite), which may be interpreted as a biological fractionation, whereas the $\delta^{18}\text{O}$ -values are very similar [7.2‰ (sediment), 7.7‰ VPDB (microbialite); values from Aiglstorfer et al. 2014a, this issue]. Carbonate content in nodules is high (85 %), whereas it is very low in the sediment (0.1 %; values from Aiglstorfer et al. 2014a, this issue). Charophytes of the species cf. *Nitellopsis meriani* are documented as abundant from a layer 50 cm above the palaeosol, in the laminated lake sediments. After interpretation in Bhatia et al. (1998), this taxon is indicating water depths of 4–12 m.

Invertebrate taphonomy and ichnology

Gastropods

Gastropod shells are abundant, especially in the upper part of the palaeosol, and consist of the so far endemic *Pseudidyla martingrossi* Harzhauser et al. 2008 and *Pleurodonte michalkovaci* Binder and Harzhauser, 2008, and 13 additional species of predominantly terrestrial shell bearing pulmonata (including only two fragments of two different aquatic taxa), and slugs (Harzhauser et al. 2008). While the large shells of *Pleurodonte michalkovaci* (diameter up to 3 cm) are heavily crushed due to lithostatic pressure (GPIT/GA/5044; Fig. 2c), the smaller (up to 5 mm high) gastropods, such as *Pseudidyla*, or isolated nuclei of different species, are almost uncrushed. Most likely, the higher clay content in the upper part of the palaeosol in contrast to the lower part, and the therefore resulting higher degree of compaction during diagenesis, caused crushing of the large, fragile shells. Apparently, there

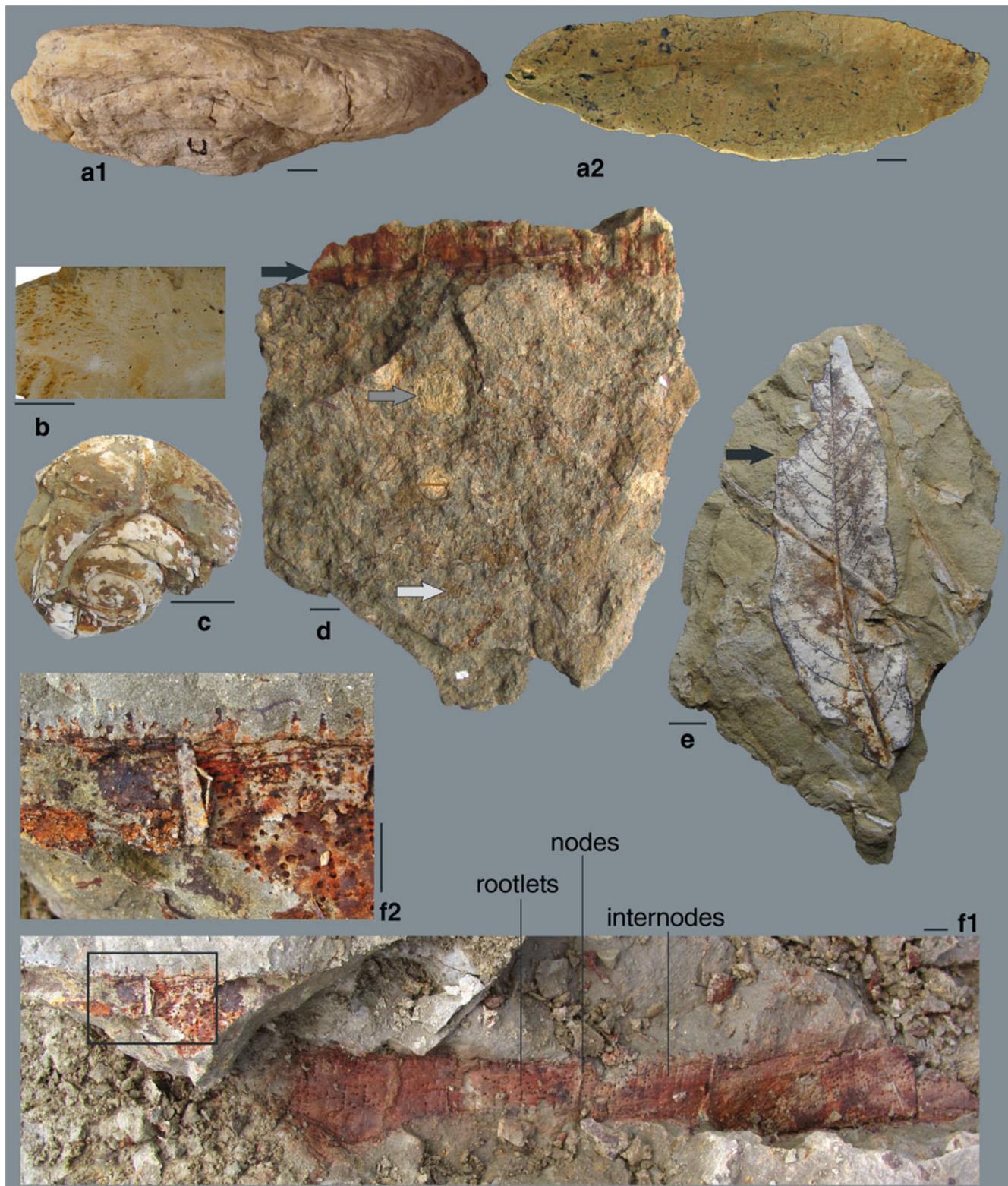


Fig. 2 Preservation of plants and invertebrates at Gratkorn locality: **a** microbialite in side view (1) and in transversal section (2; GPIT/LI/736), **b** thin section of (a) with laminar structures, **c** diagenetically crushed shell of *Pleurodonte michalkovaci* (GPIT/GA/5044), **d** horizontal surface of a sample from the upper part of the soil layer with a fossil root (dark

arrow), back-filled burrows (grey arrow) and sand lenses (white arrow; GPIT/IC/253), **e** leaf of *Salix*, showing signs of margin feeding by insects (leaf-layers approx. 15 cm above the top of palaeosol; GPIT/PL/761), **f** horizontal rhizome of Poales gen. et sp. indet. (1) and detail with rootlets and node (2); scale bar 1 cm

is no gastropod record from the lower part of palaeosol, as it represents a deeper horizon of the whole palaeosol and thus was not accessible for gastropods. Frequent findings of the more compact slug shells, attributed to *Testacella schuetti* Schlickum 1967 and *Limax* sp., do not show signs of compression in contrast to the pulmonate shells. Furthermore, there are no indications for prolonged transportation observed in the gastropod record, such as fragmentation (e.g. Hanley and Flores 1987).

The level of recrystallisation in gastropod shells is very low, as XRD analysis tested primary aragonitic shell composition for the surface of *Pseudidyla martingrossi* and *Pleurodonte michalkovaci*. The mineralogical composition of slug shells, such as *Limax* sp., consists in calcite crystals similar the extant *Limax maxima* (Furbish and Furbish 1984). Unfortunately, information on the shell structure and mineralogy of extant taxa of this genus is rather scarce (Tompa 1980) and interspecies differences in crystallite sizes rather than recrystallisation can therefore not be excluded for the slug shells at Gratkorn. In any case, primary carbonate (aragonitic) shell preservation of other gastropod shells at Gratkorn indicates a low level of diagenetic recrystallisation, and therefore makes a secondary decalcification of the palaeosol unlikely, leading to the interpretation of a primarily carbonate-depleted sediment according to bedrocks exposed in the source area.

Arthropods and ichnology

The arthropod fauna from Gratkorn consists of a thin-shelled limnic ostracod fauna (11 species; Gross 2008), in freshwater crabs of the genus *Potamon* (Klaus and Gross 2010) and in a very few land-living arthropods, all preserved in the lacustrine siltstones and marls above the palaeosol. Articulated terrestrial arthropods are preserved as brownish impressions in the leaf-rich, laminated siltstones up to 1 m above the palaeosol. So far, they comprise one woodlouse (Oniscidea) and one shieldbug (Pentatomoidea) (undescribed). Signs of insect feeding (margin feeding) have been observed on a few leaves, but cannot be assigned to specific taxa (GPIT/PL/761; Fig. 2e). Skeletisation and other kinds of feeding marks on leaves are not clear enough to be classified in detail.

Although in the palaeosol itself no body fossils of insects are preserved, abundant ichnofossils have been recorded and classified as fodichnia and domichnia of different species (nomenclature after Seilacher 1964). Fodichnia, in terms of scavenging marks, were observed on some vertebrate specimens, such as, e.g. on the root of a rhinocerotid tooth (UMJGP 203459; Fig. 3d), and indicate the presence of osteophagous insects. The marks on the tooth root are similar in size and orientation to those described by Fejfar and Kaiser (2005) and interpreted as gnawing marks of termites, but strongly differ from those observed in the Pliocene of

Tanzania and the Holocene of South Africa, as the scratches are not as strictly concentric in the former (for comparison, see figures in Fejfar and Kaiser 2005; Backwell et al. 2012). Given a record of termites in slightly younger sediments from the Styrian Basin (Lower Pannonian, 11.3 Ma; Engel and Gross 2009), the presence of termites damage does not seem unlikely for Gratkorn, but we can only attribute the scavenging marks to termites with reservations. An additional indication of the presence of social insects is given by sand-filled burrows of a few millimeters to 3 cm in diameter, where the sediment is oxidized (Fig. 2d; light grey arrow). The burrows are reticular and thickened in the parts where they meet. Therefore, they are interpreted as domichnia, similar in shape to different kinds of social insect burrows (e.g. ants or termites), but, due to the high variability and the few descriptions of comparable extant structures available (Tschinkel 2003), a more detailed classification is not possible.

Other kinds of bioturbation, again representing fodichnia, consist of vertical back-filled burrows up to 1.5 cm in diameter (Fig. 2d; dark grey arrow). As only cross-sections of burrows are preserved and no chambers are known up to now, a designation to a certain ichnogenus is limited. However, due to their morphology, they could be interpreted as traces of deposit-feeding soil invertebrates, like, e.g. beetles and cicada (Hembree and Hasiotis 2008 and citations therein). They correspond well in size and shape to *Beaconites kytosichnus*, an ichnogenus emended by Hembree and Hasiotis (2008) for burrows observed in a Miocene palaeosol from Colorado in sandy siltstones with rhizolites. A designation to this ichnogenus can be given only tentatively, as the diagnostic cocoon-bearing chamber is missing and therefore a distinction from other ichnogenera like *Taenadium*, *Muensteria*, and *Anchorichnus* is almost impossible.

Large mammal taphonomy

Overview

Vertebrate findings are mostly restricted to the palaeosol itself and occur only sporadically in the overlying lacustrine marls. They consist of large and small mammals as well as birds, reptiles, amphibians, and scarce remains of fishes (fishes only in the lacustrine marls; for detailed faunal composition, see Gross et al. 2011; Aiglstorfer et al. 2014a, b, c, d, this issue; Böhme and Vasilyan 2014, this issue; Göhlich and Gross 2014, this issue; Prieto et al. 2014, this issue; Van der Made et al. 2014, this issue). Large mammals comprise the proboscidean *Deinotherium levius* vel *giganteum*, three rhinocerotid species, *Aceratherium* sp., *Brachypotherium brachypus*, *Lartetotherium sansaniense*, and the chalicothere *Chalicotherium goldfussi*, while equids are only recorded by few bones of *Anchitherium* sp.. Most abundant are ruminants, with the most frequent species *Euprox fureatus* and the second



Fig. 3 Preservation of large mammal remains at Gratkorn locality (scale bar 1 cm): **a**,2 modern analogue: left humerus of *Capreolus capreolus* (extant) showing clear signs of gnawing by *Vulpes vulpes* and **b**,2 left humerus of *Euprox furcatus* (GPIT/MA/2418) showing similar biting marks; **c** distal fragment of ruminant right femur with tooth puncture (UMJGP 210695), note the iron oxide crust on surface, **d**1,2 *Lartetotherium sansaniense* left m/1 (UMJGP 203459): insect bioerosion marks on the root of tooth and detail with redrawing of marks, **e** bone fragment (GPIT/MA/4519) with clear signs of digestion such as dissolution of the surface (**e**2) but still showing the structure of spongiosa inside (**e**1), **f** *Listriodon splendens* right M2/(GPIT/MA/2757), 1 broken into several pieces, and 2 after preparation, **g** unidentified long bone (GPIT/MA/3852) heavily fractured by trampling, **h** fragment of deinothere ?scapula (UMJGP 204103) with gnawing marks by a large carnivore, **i** semiarticulated vertebral column and pelvis? of ruminant (UMJGP 210804; scale bar 1 cm)

most frequent *Dorcatherium navi*. The bovid *Tethytragus* sp., the moschid *Hispanomeryx* sp., and a large palaeomerycid are rare. The ‘smallest’ large mammal, the moschid *Micromeryx flourensianus*, is recorded with six specimens. Two different species of suids are part of the Gratkorn large mammal community: the more bunodont *Parachleuastochoerus steinheimensis*, and the more lophodont *Listriodon splendens*.

Distribution, disarticulation and decomposition of skeletal elements

Though assignment to different levels of the palaeosol is restricted due to the gradual change from the lower to the upper part, and due to strong neotectonic activities (represented by frequent slickensides of normal faults; Gross et al. 2011) resulting in a strong unevenness of the palaeosol, field experience tentatively allows the following observation on the abundance of certain taxa in single parts of the soil: partly articulated/associated fossorial herpetofauna (Böhme and Vasilyan 2014, this issue) and small mammals (Prieto et al. 2014, this issue) are restricted to the upper part of the palaeosol, and cervids are more abundant therein, while suids and heavyweight large mammals are more frequent in the lower part. Nevertheless, all findings must be considered to be deposited in a short time span, maximally several decades, as, for example bone fragments from the same skeletal element of a single individual were excavated in different horizons of the palaeosol. Trampling must be considered a very important burial, as well as fracturing mechanism for large mammal bones.

Large mammal remains are not randomly distributed in the palaeosol but locally concentrated (density illustrated on metre scale in Fig. 4). While excavation campaigns in 2011 and 2012 recovered several jaws of ruminants, during the campaign in 2010 only a very few large mammal bones and jaws were detected, though a similar-sized area was excavated. Large mammal remains are mostly

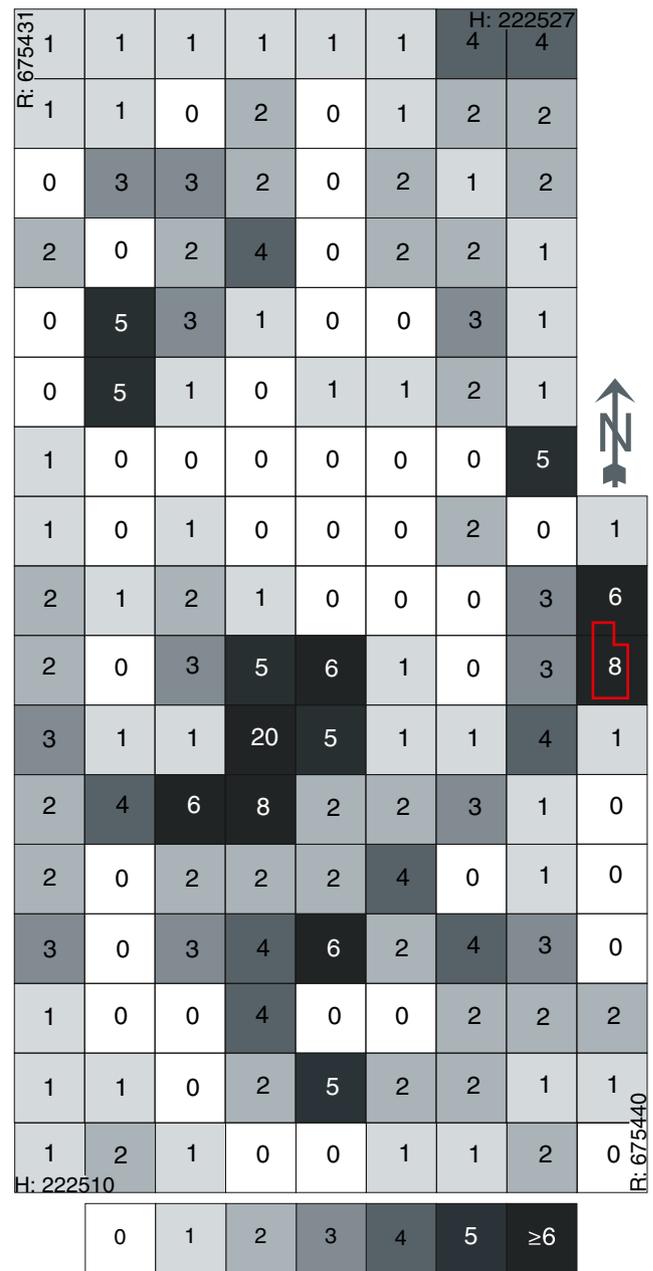


Fig. 4 Excavation map of campaigns 2011 and 2012 with additional data from 2013 showing the heterogeneous concentration of large mammal specimen per square metre. Numbers indicate the number of objects excavated; coordinates are in Austrian Grid (BMN M34–GK), red line shows outline of Fig. 5

disarticulated. Only one partial skeleton of *Deinotherium levius* vel *giganteum* (Aiglstorfer et al. 2014b, this issue), and some postcranial ruminant material (UMJGP 210804; Fig. 3i) are partially articulated. Assuming a dislocation of carcasses by carnivores, this would rather point to scavengers than to predators (Palmqvist and Arribas 2001). Palmqvist and Arribas (2001) based their distinction between predators (leopards) and scavengers (hyaenas) on data generated from recent ecosystems. They characterised

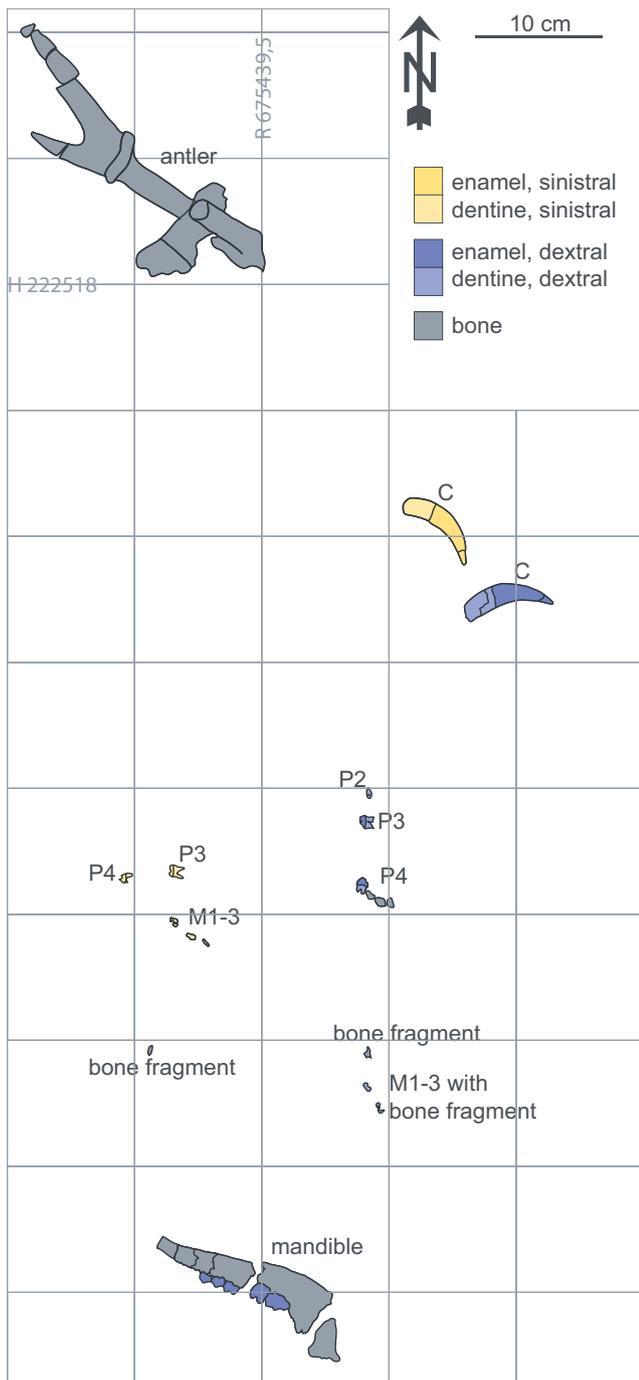


Fig. 5 Detail of excavation map of the campaign 2012 showing fragments of the skull of one individual of *Euprox furcatus* scattered over a large surface due to trampling (antler UMJGP 210955; skull fragments and teeth GPIT/MA/2736)

primary assemblages (collected by predators) as rich in articulations, and secondary assemblages (collected by scavengers) as poor in articulations, except of metapodials and vertebra. Such a secondary assemblage corresponds to the record from Gratkorn (Fig. 3i). Rough assemblages of individuals are more common, and in many cases skull

fragments or tooth rows, especially in ruminants, were found in relative proximity and are clearly assignable to single individuals (Fig. 5; see also Gross et al. 2011). Long bones are commonly fractured into several splinters by longitudinal and transverse as well as helical fractures in a single specimen (nomenclature after Haynes 1983). Long bone fragments, which were excavated in adjacency, show perfect fitting without any signs of abrasion or erosion on the fracture surface (GPIT/MA/3852; Fig. 3g). Heavy breakage of bones could be explained by the following mechanisms: trampling, scavenging, weathering, and tectonics. Trampling by larger herbivores shortly after deposition is often observed in modern large mammal assemblages. Lyman (1994) states that breakage of bones by trampling is more likely after some weathering when the bone is no longer so durable, and that fitting of contiguous fragments, as observed in Gratkorn, would indicate trampling rather than breakage prior to final deposition. Furthermore, dipping of bones (typically for trampling; Shipman 1981; Haynes 1983; Badiola et al. 2009) can be observed for several long bone fragments at Gratkorn. In Fig. 3g, a large mammal long bone (presumably a ruminant) is shown, broken into splinters with clear dislocation of few centimetres and dipping fragments. Another biotic factor for strong fragmentation is gnawing and scavenging by carnivores. Some bone crushing possibly results from sediment compaction, and in other cases neotectonics lead to vertical movements up to 10 cm (see, e.g. fig. 5c in Gross et al. 2011).

Different degrees of weathering stages (Behrensmeyer 1978) can be observed in the large mammal record from Gratkorn, but are difficult to quantify as in many cases diagenetic iron hydroxide incrustations and diagenetic alteration overprint the primary weathering stage. Those impregnations on bones and splinters of different large mammal remains can be up to 1 mm thick. The partial skeleton of *Deinotherium levius* vel *giganteum* comprises many bones, which are strongly weathered (weathering stage 5; after Behrensmeyer 1978) and often the bone compacta is not preserved, but only bone spongiosa. It shows clear signs of a prolonged exposure, such as fragmentation on the surface and scavenging of larger carnivores (see discussion below; Fig. 3h; and Aiglstorfer et al. 2014b, this issue). This could be explained by the size of the bones, which are much larger than in all other species from Gratkorn, and therefore the skeleton was probably not covered so soon and bones not dislocated as deep into the palaeosol as observed in other specimens. This is well in accordance with recent decomposition data in modern elephants (Coe 1978; Conybeare and Haynes 1984; see discussion in Aiglstorfer et al. 2014b, this issue). Furthermore, the deinotherere remains are sticking out over the top of the palaeosol and many remains were recovered from the uppermost part of it, which led to longer exposure

near or on the surface and therefore stronger weathering during early diagenesis. Such boundaries between lithologies with different fluid flow ratios often provide ideal conditions for groundwater permeability. Such diagenetic fluids influence preservation of the Gratkorn large mammal remains (at least near or on the surface) to a certain degree as, e.g. shown by the iron hydroxide incrustation described above (Fig. 3b, g, h).

Other remains, for example some ruminant long bones, are fractured but still possess a smooth surface and do not show any signs of, e.g. flaking or chemical weathering (weathering stage 0 or 1; after Behrensmeyer 1978). Different degrees of weathering stages in the Gratkorn assemblage indicate that the faunal assemblage did not result from a mass mortality, but rather from accumulation over some years or decades (Behrensmeyer 1978).

Besides fracturing of bones, teeth are also disrupted (e.g. M2 dex. of the suid *Listriodon splendens* GPIT/MA/2757; Fig. 3f), with splinters found clearly distant from each other (some up to several decimetres) still showing perfect fittings. This is more likely for teeth that are broken by trampling, as weathered, splitting teeth would be more likely to lose small pieces that would prevent perfect re-fitting (A.K. Behrensmeyer, personal communication). Fracturing of teeth can be observed at Gratkorn in robust teeth with thick enamel (e.g. molars of *Listriodon splendens*) and more fragile teeth with thinner enamel, as, e.g. in cervids. While tooth fragmentation in the more fragile teeth can easily result from sediment compaction (comparable to preservation of gastropod shells described above) and trampling, tooth disruption of, e.g., suid molars is more likely to result from weathering and trampling. Tooth splitting when desiccating at the surface was described by Behrensmeyer (1978) for extant mammal remains of the Amboseli basin (Kenya). As she observed differences in weathering more dependent on the individual morphology and characteristics of the tooth (eruption, stage of wear, enamel thickness) than on surface exposure and climatic conditions, she stated that weathering stages are not as applicable to teeth as they are to bones. Keeping in mind that molars of *Listriodon splendens* possess a rather thick enamel, and including observations of longitudinal tooth splitting on a camel skeleton in Abu Dhabi (Andrews and Whybrow 2005) it seems likely, that longer surface exposure and increased aridity (low absolute humidity; as commonly observed in desertic environments; M. Böhme personal observation) might have enhanced splitting of the suid teeth. A peculiarity of the Gratkorn site is the frequent occurrence of transversal fragmentation of teeth besides longitudinal fragmentation (Fig. 3f), which cannot be explained by long surface exposure or desiccation, but probably by neotectonic activities (see dislocation of the lower part of tooth in finding position in Fig. 3f).

Current alignment of long bones, size sorting or abrasion was not observed in bones from the Gratkorn locality. Small and large mammal remains as well as small and large bone

splinters are preserved in vertical as well as horizontal adjacency. A prolonged transportation (e.g. fluvial, see below) of bones or teeth after skeletisation and disarticulation of the animal can be excluded due to the described perfect fittings of fragments and the lack of any indications of transport (see also discussion in Badiola et al. 2009).

Bioerosion

Signs of bioerosion by invertebrates and vertebrates are present on many large mammal remains from Gratkorn, and comprise insect osteophagy, scavenging of different kinds and small mammal gnawings. Bioerosion by insects was observed in a few cases, and is possibly attributed to termites (see “Arthropods and ichnology”). Small mammal gnawing marks of the ichnogenus *Machinus* are very frequent on many large mammal bones as well as on turtle shell fragments (Gross et al. 2011). As a description of these trace fossils is in progress, this topic will not be discussed in detail here.

As mentioned above, gnawing and scavenging by carnivores plays a major role in the fracturing and fragmentation of long bones. The preferred accumulation of tooth material in comparison to long bones or axial skeleton elements could be explained by the general consumption sequence (e.g. discussion in Lyman 1994) and enhanced trampling. While postcranial flesh is consumed first, mandible and maxilla flesh are often last to be consumed by carnivores (Blumenshine 1987; Lyman 1994). Most large mammal long bones discovered comprise distal or proximal epiphyses with most of the shaft missing. Most of the femora excavated comprise more or less only the distal articulation. Extensive marrow consumption could explain this kind of fragmentation and would rather point to an accumulation by scavengers than by predators (Palmqvist and Arribas 2001). In fact, in the consumption sequence of marrow by Blumenshine (1987), femora are consumed first, followed by most long bones, and last are pulps of the skeletal elements (especially skull and mandible). On a humerus of the cervid *Euprox furcatus* (GPIT/MA/2418; Fig. 3b), bite marks (puncture marks) at the proximal epiphysis can be observed. Similar bite marks by *Vulpes vulpes* can be observed on a humerus of the extant *Capreolus capreolus* (Fig. 3a) and indicate that a medium-sized carnivore was responsible for some of the bite marks from Gratkorn. Bite marks on the distal fragment of a ruminant femur (UMJGP210695; Fig. 3c) fit well to size and morphology of the tricuspid P4 of an yet undescribed carnivore discovered at Gratkorn locality. Besides bite marks, chewing marks of an unknown larger carnivore can be observed on a fragment of the scapula of *Deinotherium levius vel giganteum* (UMJGP 204103; Fig. 3h).

Only one bone fragment from Gratkorn could be interpreted as digested (GPIT/MA/4519; Fig. 3e). Because of the strong alteration of bony material and the high but irregular degree of “surface rounding” on this specimen, we

consider it to represent a coprolite or a regurgitated bone (in any case, a partially digested bone fragment). This interpretation is supported by the visible damage to the microstructure of spongiosal bone material in a cross-section of the specimen (Fig. 3e1). Another specimen with evidence of rounding could be explained by gnawing of micromammals and scavengers. One single phosphatic coprolite (Hyaenidae? UMJGP 209210) has been excavated has so far (Gross et al. 2011). Considering Thulborn (1991) and literature cited therein, preservation of coprolites in a palaeosol is most probably restricted to at least temporarily arid climates. Humid conditions would quickly destroy coprolites. The reconstructed seasonality and precipitation ratios of 486 ± 252 mm/year

(Gross et al. 2011) could well favour the preservation of coprolites, assuming a burial of this coprolite prior to the wet season. As there are no visible septaria-like cracks, the assumption of a rapid covering is supported and an extended pre burial desiccation of the coprolite itself can be excluded.

Voorhies analysis

A total of 363 out of 700 large mammal remains were analysed in an expanded Voorhies classification (expanded Voorhies groups: I, I-II, II, II-III, III, according to Voorhies 1969 and expanded by Behrensmeyer 1975) for obtaining an estimate of possible fluvial transportation. As the Voorhies classification is limited to anatomically designable objects, undetermined splinters or fragments are not considered (Fig. 6a). Furthermore, according to classifications of Voorhies (1969) and Behrensmeyer (1975), different parts of bones have to be classified into different groups, because of their morphology, e.g. isolated articulation surfaces (if broken off or if resulting from not completely closed symphysis; juveniles) should be classified in a different way than more complete long bones. The results of the analysis, additionally resolving the anatomical position of the specimens analysed are shown in Fig. 6b. As the sample was taken from material discovered during well-documented excavations, we expect this result to be representative for the whole fossil-bearing palaeosol at the Gratkorn site. Although all Voorhies groups are present in the sample, 63 % of bones are attributed to Voorhies group III, which is considered to contain bones resistant to prolonged fluvial transportation, such as teeth, jaw fragments, and astragali. Apparently isolated teeth are heavily over-represented (146 isolated teeth, 30 assignable fragments), and frequently associated with skull fragments or antlers (in ruminants). But there is also a remarkable number of specimens attributed to Voorhies group I (e.g. vertebra, ribs). These elements are considered to be non-resistant to transportation, because of their shape. The Voorhies data gained from Gratkorn are in agreement with data from the

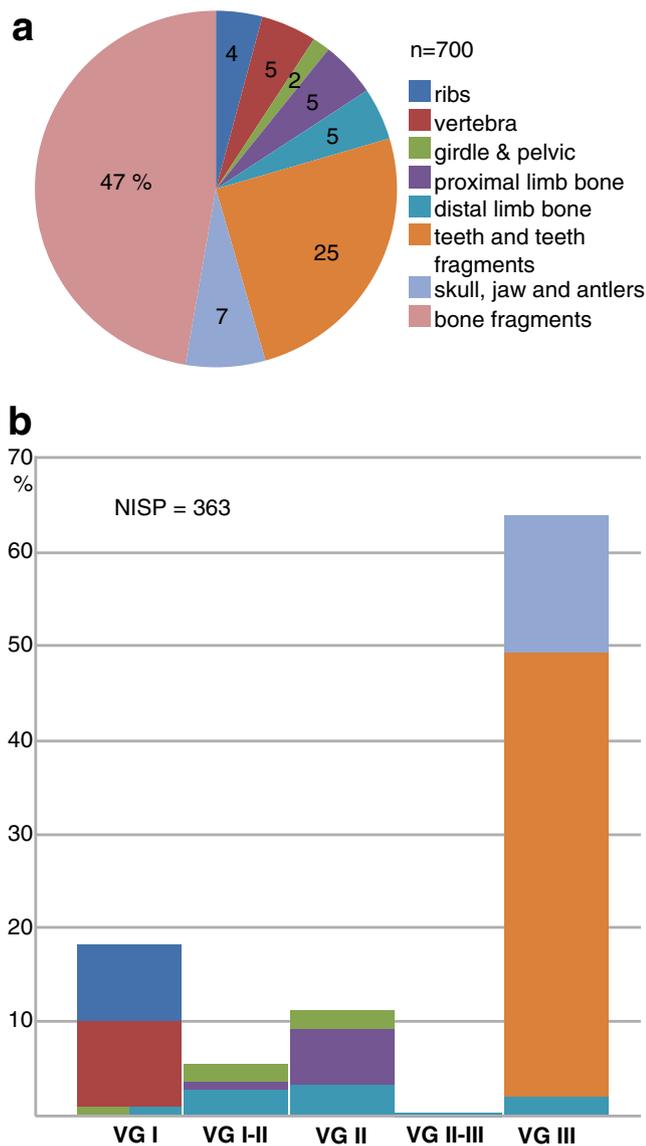


Fig. 6 Distribution of skeletal elements of large mammals. **a** Relative abundance of elements in percent, **b** expanded Voorhies analysis based on a NISP of 363 from all excavation campaigns up to 2012 at the Gratkorn locality; in percent of total amount (colours correspond to anatomical classification in **a**)

Table 2 Expanded Voorhies analysis of large mammal remains from the Gratkorn locality compared with the Zambrana locality (data from Badiola et al. 2009)

Voorhies group	Gratkorn	Zambrana
VG I	18 %	17 %
VG I-II	6 %	4 %
VG II	11 %	7 %
VG II-III	1 %	10 %
VG III	63 %	61.5 %
VG III teeth	48 %	55 %

Data from Zambrana are medium values between samples I and II VG Voorhies group,

Zambrana locality, (late Eocene, Spain; Table 2) described by Badiola et al. (2009). In two different samples from excavations at this site, Badiola et al. (2009) grouped 14 and 20 %, respectively, of the sample to group I and 60 and 63 %, respectively, to group III with a similar overweight of teeth in the samples (225 out of 375 NISP and 210 out of 420 NISP; Badiola et al. 2009, fig. 6). A similar taphonomic pattern for the Gratkorn site as observed in Zambrana can therefore be assumed. As both, elements grouped in Voorhies group I (“no prolonged fluvial transportation possible”) and III (“prolonged fluvial transportation possible”), were well represented, a prolonged transportation has to be excluded. Furthermore, there are no signs of rounding by fluvial transportation, which is in accordance with observations on gastropod shell preservation, sedimentology, and pedogenic features.

Also, the anatomical distribution (Fig. 6a) shows clear similarities to the Zambrana locality: after bone fragments with 47 %, teeth and teeth fragments are the second most abundant group of elements (25 %), while postcranial material is definitively underrepresented with a total of 21 %. The high relative abundance of teeth can possibly be

explained by carnivore behaviour (see discussion above). Comparing different ways of bone collecting by predators and by scavengers, Palmqvist and Arribas (2001) observed a lower ratio of vertebrae and ribs versus girdle and limb bones as typical for scavengers (1:9 in contrast to 1:4 in predators). The almost equalized ratio (1:1.25) observed at Gratkorn would therefore point more to a predator assemblage. As most of the vertebrae and ribs coded in the Voorhies analysis originate from the deinothere skeleton, which is unlikely to be transported by any of the carnivores but most probably died at the place of its deposition (compare to Coe 1978 and excavation map in Aiglstorfer et al. 2014b, this issue), it has to be excluded from this comparison. The ratio (1:8.7) for isolated remains of all the other large herbivorous mammals, excluding the proboscidean, clearly points to collecting by scavengers.

Taxonomic and body mass distribution

Small mammals including rare semiarticulated skeletons are the most common vertebrate remains from the Gratkorn locality. With a MNI of 34, ruminants are the most abundant large mammals (Fig. 7), dominated by the cervid *Euprox furcatus* (16), followed by *Dorcatherium navi* (9) and the small moschid *Micromeryx flourensianus* (6), while additional taxa *?Hispanomeryx*, *Tethytragus* sp. and *Palaeomerycidae* gen. et sp. indet. are only represented by single individuals. Suidae are frequent with at least 7 individuals. Carnivores are rare with only 3 MNI (6 % of all large mammals). Perissodactyla (4) and the only proboscidean *Deinotherium levius* vel *giganteum* (2) are less common. This distribution corresponds to an accumulation of the remains by scavengers, as does the generally wide range of body mass and the high diversity of the species (Palmqvist and Arribas 2001). Besides ecological considerations (Aiglstorfer et al. 2014c, this issue), the abundance of small mammals and the rarity of specimens with a body mass of more than 1,000 kg (Fig. 7a) excludes sorting by fluvial transport and emphasises the assumption of a more or less autochthonous taphocoenosis (Gross et al. 2011). In a regime dominated by fluvial transportation, one would expect to find a distinct abundance of species with large body mass in comparison to low or medium weight species (Behrensmeier 1988; see also data for the fluvial-dominated Eppelsheim Formation described in Sommer 2007).

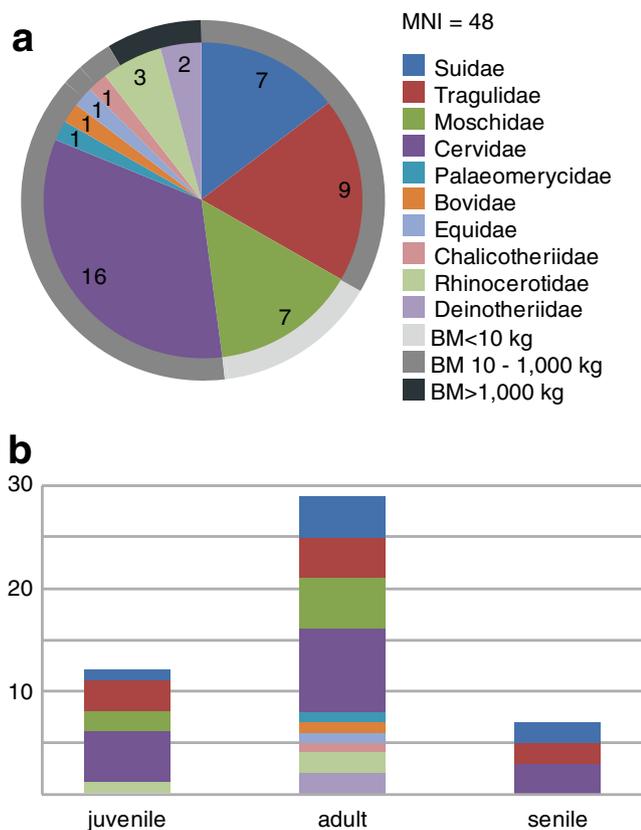


Fig. 7 Faunal composition of the Gratkorn large mammal taphocoenosis: **a** MNI of herbivore large mammals on the family level based on the number of similar anatomical elements and tooth enamel consumption (body mass, BM, following categories given in Costeur et al. 2013), **b** age model of large mammals based on enamel consumption (juvenile: deciduous dentition; adult: permanent dentition, senile: trigonid of m1 completely worn) and apophyseal growth (colours correspond to Fig. 8a)

Age profile

Large mammal specimens from Gratkorn show a clear dominance of (prime) adult specimens (MNI=29; 60 %), while juvenile specimens are less frequent (MNI=12; 25 %) and senile ones are rarest (MNI=7; 15 %). Though we are well

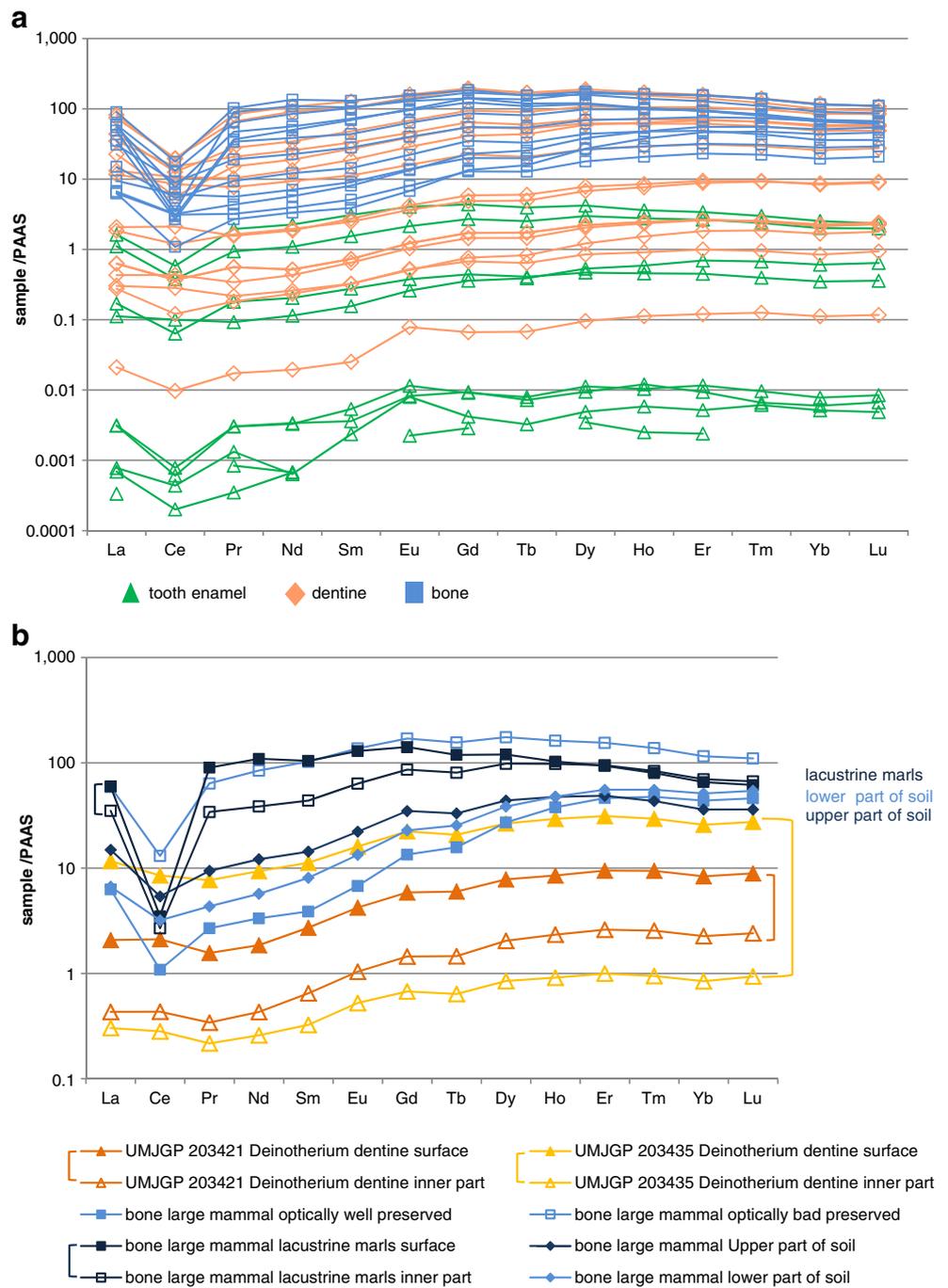
aware that these numbers are far from statistical significance, and that interpretations on age–frequency distribution are speculative to a certain degree (Lyman 1994 and references therein), the age profile from Gratkorn still allows some interpretations. Following Lyman (1994) and references therein, two basic types of mortality pattern can be distinguished. An attritional/normal mortality pattern is U-shaped, comprising an overrepresentation of juvenile and senile specimens, which are more susceptible to hazards than prime adults. A catastrophic/mass mortality pattern is L-shaped representing the age profile of the live community with fewer senile specimens. Surprisingly, the pattern observed at Gratkorn does not fit to the attritional/normal mortality one would expect for a site where different populations of large mammals meet for drinking or feeding, and where young and inexperienced or old individuals are more likely to become the prey of cursorial predators or prone to other hazards. The Gratkorn assemblage in contrast shows an L-shaped pattern (in the sense of Lyman 1994 and references therein), with a clear dominance of prime individuals. Such a pattern could be observed as a result of mass mortality (Lyman 1994). This interpretation is not suitable for Gratkorn, as we do not have any sedimentological signs for desiccation or flooding, as should be expected in such a case. Following Stiner (1990), an L-shaped pattern could also be caused by ambush predators such as Felidae. Even though neither Felidae nor Barbooufelidae have been recorded from Gratkorn or from other Sarmatian localities of the Central Paratethys realm (Morlo 2006), their presence in this ecosystem is possible, as there is a record from Atzelsdorf (Austria; Nagel 2009) and from different localities in the North Alpine Foreland Basin (Morlo 2006). An L-shaped pattern can also be explained by collecting by scavengers (secondary assemblage) to which corresponds the level of disarticulation and the anatomical distribution of skeletal elements of prey animals observed at Gratkorn (Palmqvist and Arribas 2001).

REE analysis

During lifetime, bones show very low absolute contents of rare earth elements (REE; levels of ~0.1 ppm or even in the range of ppb; Tütken 2003; Trueman 2007), but a rapid post mortem incorporation is observed (e.g. ~1,000 ppm for fish teeth younger than 10,000 years; Trueman 2007). REE are therefore considered a useful tool for taphonomical considerations (Trueman 2007). A strong enrichment in total REE values generally points to a stronger diagenetic alteration of the original tissue, while a lower REE content indicates minor diagenetic alteration. The vertebrate remains from Gratkorn show total REE contents ranging from below the detection limit (0.07 ppm) to 13,484 ppm, with bones (values between 989 and 13,484 ppm) and dentine (values between 4 and 12,510 ppm) comprising, in general, higher contents than enamel [values from below detection limit (0.07 ppm) up to 284 ppm; Online resource 1]. This shows lower

diagenetic alteration for tooth enamel than for dentine and bone. The shapes of REE distribution patterns have often been used for estimations of the degree and time of diagenetic alteration of vertebrate remains (see, e.g. Trueman 2007; Badiola et al. 2009; Rogers et al. 2010) with a flat pattern [no considerable medium-sized rare earth elements (MREE) enrichment] indicating weak or early diagenesis (Badiola et al. 2009), while a bell-shaped pattern would imply more extensive or late diagenesis (Reynard et al. 1999). However, recent works on REE contents in fossil bones and teeth (see, e.g. Kocsis et al. 2010; Herwartz et al. 2013; Trueman 2013) have shown a more complex process of REE uptake, fractionation, and protracted content alteration, and question the assumption that recrystallisation can be more or less synonymised with a late diagenetic alteration. Both adsorption and recrystallisation could represent early and late diagenetic processes (Herwartz et al. 2013). In any case, all samples from Gratkorn show flat REE distribution patterns and MREE enrichment is generally poor (Fig. 8a), indicating a minor degree of recrystallisation. Intrabone and intradentine fractionation from the surface (more enriched in REE) to inner parts (less enriched in REE) can be observed for the Gratkorn specimens (Fig. 8b; Online resource 1; fitting well to observations of Tütken et al. 2008; Herwartz et al. 2013) and indicate a chemically less altered preservation of the inner parts of skeletal tissues than on the surface. Optically categorised “well preserved bone” and “badly preserved bone” differ in total REE amounts, being respectively less (1,014 ppm) and more (10,025 ppm) enriched in REE contents, and encompass all values for the bones of different levels (Fig. 8b). Upper and lower parts of soil comprise quite similar values, thus re-enforcing the assumption of a generally “uniform” history for the vertebrate-bearing palaeosol. Trueman et al. (2006) and Trueman (2013) showed that REE composition still preserves broadly environment-specific REE patterns, implying that the REE composition retains the early diagenetic signal to a considerable degree and is not significantly overprinted by late diagenesis (see discussions in Kocsis et al. 2010 and Herwartz et al. 2013). With shale-normalised ratios ranging between 0.337 and 1.6198 for La/Sm and between 0.1302 and 0.9903 for La/Yb (Online resource 1), all values are well within the range of “terrestrial samples” (Trueman et al. 2006; Herwartz et al. 2013), and in general plot with the pattern described for soils by Trueman (2013). Most specimens comprise a negative Ce anomaly, which is often used to evaluate redox conditions in REE studies of fossil bones and teeth (e.g. Metzger et al. 2004; Domingo et al. 2011). Herwartz et al. (2013), however, observed that only a few bones in their study comprised Ce anomalies actually related to redox conditions, and further observed an intrabone shift from a negative to a positive Ce anomaly. The biogenic apatite from Gratkorn mostly displays negative Ce anomalies and does not show intrabone or intradentine inverse of anomalies, but a decreasing negative anomaly can be observed in one bone from the outer surface to the inner part of the cortex (Fig. 8b), well in agreement with the

Fig. 8 Distribution of rare earth elements (REE) of fossil bone, dentine, and enamel from Gratkorn (for details, see Online resource 1): **a** total distribution patterns for tooth enamel, dentine and bones, **b** distribution pattern of different bone samples from different parts of the vertebrate-bearing palaeosol and from different parts of one sample (intradentine and intrabone sampling indicated with brackets)



observations of Herwartz et al. (2013), which could be explained by changing fluid composition during diagenesis.

Conclusions

Almost all vertebrate and most invertebrate remains originate from one palaeosol layer, and the community preserved is considered to be more or less contemporarily deposited and therefore representing an autochthonous taphocoenosis.

Bioturbation, roots, and rhizomes emphasise the interpretation of the fossil-bearing horizon as autochthonous palaeosol, as does the diverse, rich, and predominantly terrestrial gastropod fauna. The general grade of diagenetic alteration is low, as shown by primary aragonitic gastropod shells and the REE pattern in enamel, dentine, and bones. Therefore, especially enamel is very likely to have preserved in vivo signals for isotopic measurements (Aiglstorfer et al. 2014a, this issue). Taphonomical considerations on small mammals need to be treated independently as completely different mechanisms,

e.g. predation by birds (Gross et al. 2011) is of importance. The large mammal age profile from Gratkorn could be explained by mass mortality or the accumulation by scavengers. However, a mass mortality community can be excluded due to the following observations: (1) different weathering stages, (2) inhomogeneous dispersal inside the vertebrate-bearing palaeosol, and (3) anatomical separation (except of the proboscidean partial skeleton). Fluvial transport of bones and teeth can be excluded, as there is no sign of abrasion, no alignment of long bones, no size sorting, and bone fragments of individual bones are in close proximity. Furthermore, the Voorhies analysis showed a clearly bimodal distribution including groups I and III. Nevertheless, the level of disarticulation is high, supposedly caused by predation, scavenging, trampling, and bioerosion, together with post-depositional neotectonics (simple faults on slickensides). The accumulation of large herbivorous mammal remains most likely represents a secondary assemblage, transported by scavengers, as indicated by a low ratio of vertebrae and ribs in comparison to girdle and limb bones, a scarcity of diaphyses and completely preserved long bones, a low MNI for carnivores, a low proportion of juvenile specimens, a high species diversity, and a wide range in bodysize (Palmqvist and Arribas 2001). Furthermore, there are different signs of gnawing and bite marks observed, confirming activity of carnivores and osteophagy by small mammals and insects.

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