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Gratkorn: A benchmark locality for the continental Sarmatian s.str. of the Central Paratethys

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Abstract This paper presents one of the richest and most complete vertebrate faunas of the late Middle Miocene (~12 Ma) of Central Europe. Up to now, sixty-two vertebrate taxa, comprising all major groups (fishes, amphibians, reptiles, birds, mammals), have been recorded. Based on sedimentological and palaeobiological evidences, this *Fossillagerstätte* is assumed to originate from a floodplain paleosol formed on top of a braided river sequence. The fauna points to a highly structured, somewhat vegetated landscape with a wide array of habitats (e.g., fluvial channels, sporadically moist floodplains, short-lived ponds, savannah-like open areas and screes). It was preserved due to a rapid drowning and the switch to a freshwater lake environment. Palaeoclimatological data, derived from pedogenic features as well as from biota, indicate an overall semi-arid, subtropical climate with distinct seasonality (mean annual precipitation 486 ± 252 mm, mean annual temperature ~15°C). This underlines the late Middle/early Late Miocene dry-spell in Central Europe. From taphonomical point of view, the irregularly distributed but roughly associated larger vertebrate remains refer to an in situ accumulation of the bone bed. Splintered bones, gnawing marks as well as rhizoconcretions and root corrosion structures record some pre- and post-burial modification of the taphocoenose. However, the findings of pellet remains argue for a very fast burial and thus to a low degree of time-averaging. For this reason, the fossil fauna reflects the original vertebrate community rather well and is a cornerstone for the understanding of late Middle Miocene terrestrial ecosystems in this region. Certainly, Gratkorn will be one of the key faunas for a high-resolution continental biostratigraphy and the comprehension of Europe's faunal interchanges near the Middle/Late Miocene transition.

Keywords Vertebrate fauna · Late Middle Miocene · Sarmatian s.str. · Central Paratethys · Styria/Austria · Fossillagerstätte

Introduction

About 34 million years ago, two more or less independent palaeogeographic units appeared, which shaped Europe and its life for the following epochs: To the north of the rising Alpine orogens the Paratethys Sea emerged, whereas in the south the Neogene Mediterranean evolved (e.g., Rögl 1998; Popov et al. 2004). Diverging palaeogeography, sea level fluctuations and climate changes heavily affected aquatic and terrestrial biota alike. Consequently, a regional stage concept for the Paratethyan realm was introduced, remaining matter of debate until now (e.g., Cicha et al. 1967; Piller et al. 2007). Different stages have been established for the Central and Eastern Paratethys, between which correlations are under discussion as well (e.g.,

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Harzhauser and Piller 2007). Recent advances in astronomical tuning of sedimentary cycles and comprehensive compilations of bio-, sequence-, magnetostratigraphical and geochronological data significantly improved high-resolution correlations between regional Paratethyan and standard stages (e.g., Piller et al. 2007; Lirer et al. 2009). However, these correlations concern chiefly aquatic (marine) sedimentary sequences and linking those to terrestrial environments remains extremely challenging (e.g., Steininger et al. 1996; Aguilar et al. 2004).

For European non-marine deposits, the Mammal Neogene zone concept (MN zones; e.g., Mein 1999; Steininger 1999) served as the stratigraphical backbone during the last decades, which obviously enhanced communication between researches throughout the Old World. Nevertheless, at higher biostratigraphic resolutions (<1.5 Myr), this concept looses its practicability and mostly its meaning (for discussions see e.g., De Bruijn et al. 1992; Steininger 1999; Van Dam et al. 2001; Lourens et al. 2004; Costeur et al. 2007; Vangengeim and Tesakov 2008). Thus, clearly defined (regional) continental biozones are needed for more detailed analyses (e.g., Böhme et al. 2009). To achieve this, a much higher number of independently dated vertebrate localities are essential. This is particularly crucial for the late Middle to earliest Late Miocene epoch in the Paratethyan area, for which well-dated and taxonomically rich vertebrate faunas are hardly available (e.g., Sabol and Holec 2002; Hír 2004; Nargolwalla et al. 2006; Venczel and Ştiucă 2008; Daxner-Höck and Göhlich 2009), precluding trustworthy correlations to different parts of Europe.

Around the Middle/Late Miocene transition, Central Europe faced remarkable turnovers, on land as well as in the aquatic environments. Following the Miocene climate optimum (*c*. Middle Ottnangian to Middle Badenian), terrestrial faunas and floras of Central Europe responded intensively to a Middle Miocene climatic cooling (decrease in mean annual and especially winter temperatures, pronounced seasonality and aridity; Böhme 2003; Mosbrugger et al. 2005; Jiménez-Moreno et al. 2005; Kováč et al. 2006; Costeur et al. 2007; Erdei et al. 2007; Böhme et al. 2008). In the aquatic realm, marine faunas experienced a striking incision due to the isolation of the Paratethyan Sea from the world oceans and the formation of the highly carbonate supersaturated, alkaline Sarmatian Sea (Papp et al. 1974; Piller and Harzhauser 2005). A dramatic drop in sea level, which seems to be linked with a glacio-eustatic sea level fall around the Middle/Late Miocene boundary (~Ser 4/Tor 1 sequence boundary of Hardenbol et al. 1998), is reflected by large-scale erosion of Upper Sarmatian deposits in the Central Paratethys area (Sacchi and Horvath 2002; Harzhauser and Piller 2004; Kováč et al. 2004, 2008; Schreilechner and Sachsenhofer 2007). Due to this sea level low stand, underlying terrestrial sediments became largely eroded and are rarely preserved. This causes a substantial palaeobiological "blackout" on land for about 1 Myr (~Late Sarmatian to Early Pannonian; ~12.5–11.5 Ma; Thenius 1960; Mottl 1970; Kováč et al. 2006).

In this paper, we present a first overview of a new vertebrate fauna from south-eastern Austria (locality Gratkorn), which is exceptional for Central Europe (Fig. 1a) because: (1) It is fairly well dated to the late Middle Miocene (*c*. 12.2–12.0 Ma, earliest Late Sarmatian s.str.) and contributes therefore notably to our knowledge of vertebrate faunas just before the Middle/Late Miocene boundary; (2) it comprises a large spectrum of vertebrate groups (fishes, amphibians, reptiles, small and large mammals), which accumulated quite rapidly in a paleosol; (3) the remains include numerous, almost complete skulls or even partially associated skeletons of small vertebrates, which are of prime importance for further analyses on palaeoecology and taxonomy of single taxa. Moreover, it is part of a multidisciplinary investigation, which provides a holistic reconstruction of the palaeoenvironment; the discovered small mammals (e.g., rodents, insectivores) permit to approach more precisely the palaeobiogeographic relationships within the Central Paratethys area and beyond; and it offers the possibility to explore a complex taphonomic situation.

Geographical and geological setting

The locality Gratkorn (clay pit St. Stefan) is situated in south-eastern Austria (federal state of Styria) about 700-m east of the city of Gratkorn (15°20′56″E, 47°08′14″N). It lies in the eastern part of Gratkorn Basin, which belongs to a series of embayments along the south-eastern margin of the Eastern Alps (Fig. 1b).

Deposition in the Styrian Basin as well as in its satellite basins was, beside tectonics, strongly affected by short-term sea level changes of the Central Paratethys. This enabled the development of a detailed sequence stratigraphic concept in addition to a comprehensive aquatic biota-based biostratigraphy (Kollmann 1965; Ebner and Sachsenhofer 1991; Kosi et al. 2003; Harzhauser and Piller 2004; Schreilechner and Sachsenhofer 2007). However, in marginal basin areas, where alluvial to lacustrine sediments predominate, stratigraphic tie points are scarce (Gross et al. 2007a, b). Marine incursions, radiometrically datable volcanic ash layers as well as palaeomagnetic investigations and vertebrate faunas, are used to gain a convincing timing (e.g., Mottl 1970; Steininger 1998; Handler et al. 2006). Especially, the fossil-poor and volcanoclastics-free Neogene deposits at the northern and north-eastern fringe of the Styrian Basin (including the Gratkorn Basin) have been

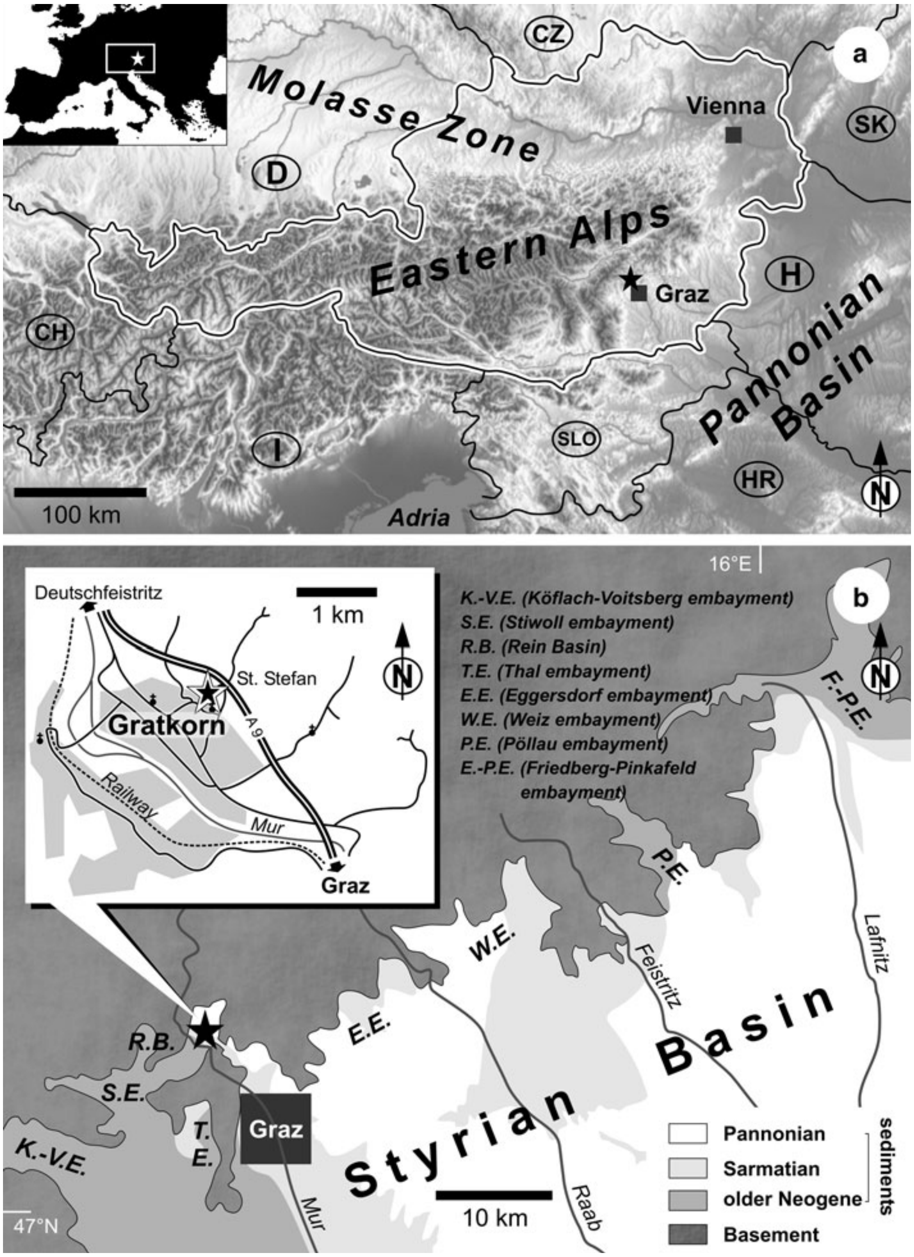


Fig. 1 Setting of the locality Gratkorn. **a** Its position in Central Europe respectively at the south-eastern margin of the Alps. **b** Its position at the northern periphery of the Styrian Basin close to the city of Gratkorn (district St. Stefan)

intensively studied during the last years. Even though outcrops are rare, and only a few shallow well logs are on hand, these investigations allowed a correlation with the high-resolution stratigraphic framework of the open Styrian Basin and beyond (Gross et al. 2007a, b; Harzhauser et al. 2008; Fig. 2).

Litho- and biostratigraphy

In the eastern Gratkorn Basin, polymict gravels/conglomerates (Gratkorn Gravel; containing the herein presented vertebrate-bearing paleosol on its top) are the lowermost exposed sediments. Whereas fluvial coarse clastics and debris flows are abundant, intercalations of sandy and pelitic layers are rare (Gross et al. 2007a, b). This general lithofacies distribution argues for a braided river system, influenced by distal alluvial fans as depositional setting (gravel-bed braided river with sediment-gravity-flows sensu Miall 1996).

Below the Gratkorn Gravel, reduced marine pelites of Early Sarmatian age (Rollsdorf Formation, *Elphidium reginum–Elphidium hauerinum* zone) are present at the transition to the Styrian Basin. Above the Gratkorn Gravel follow up to 25-m thick, commonly plant-bearing limnic pelites (Peterstal Member, Gleisdorf Formation; Flügel 1997; Gross et al. 2007b). Typical biotas of the Sarmatian

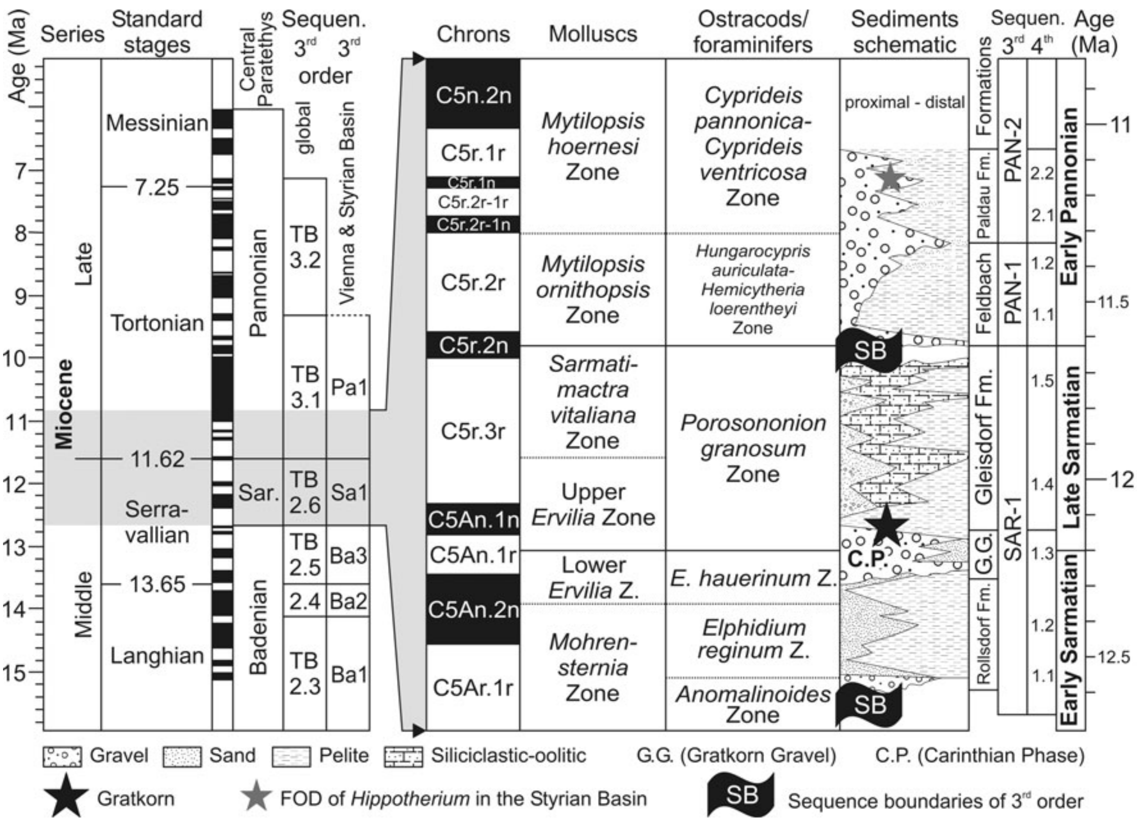


Fig. 2 Stratigraphical correlation and position of Gratkorn (based on Harzhauser and Piller 2004; Lourens et al. 2004; Gross et al. 2007b; chrons modified after Hüsing et al. 2007, sequence stratigraphical correlation adapted after Strauss et al. 2006; Schreilechner and Sachsenhofer 2007); biostratigraphical zonation after Papp 1951, 1956; ostracod zones after Jiříček and Riha 1991)

Sea or the Pannonian Lake are completely absent (Gross 2008). However, the numerous findings of the fossil legume *Podocarpium podocarpum* at the locality Gratkorn (pelites above the vertebrate horizon; Meller and Gross 2006) gave first indications for a dating of the Peterstal Mb. older than Late Miocene (Hably 1992; Erdei et al. 2007). Later on, the terrestrial gastropod fauna from the vertebrate horizon at Gratkorn turned out to be indicative for the Late Sarmatian (Harzhauser et al. 2008).

In the hanging wall of the fine clastic Peterstal Mb. variegated alternations of gravels/conglomerates, sands and pelites (Lustbühel Member, Gleisdorf Fm.) are developed. In addition to scarce marine microfaunas, thin, but highly characteristic oolites (Piller and Harzhauser 2005) are intercalated in that level and confirm their Late Sarmatian age (*Porosononion* zone; Gross et al. 2007b).

Sequence stratigraphical frame and age correlation

Based on its position between biostratigraphically dated underlying Lower Sarmatian strata (Rollsdorf Fm.) and Upper Sarmatian hanging wall sediments (Gleisdorf Fm.), deposition of the Gratkorn Gravel (and the Gratkorn vertebrate fauna) is obviously related with a wide-ranging sea level fall at the end of the Early Sarmatian (Fig. 2). This so-called Carinthian Phase (Winkler 1927; Winkler-Hermaden 1957) is recorded throughout the Pannonian Basin (Harzhauser and Piller 2004; Strauss et al. 2006; Schreilechner and Sachsenhofer 2007; Kováč et al. 2008). Some of these authors link the Carinthian Phase to enhanced up-lift of the Eastern Alps, which triggered the erosion of underlying rocks and a basinward progradation of alluvial/deltaic systems. The Eastern Alpine embayments fell dry and turned into terrestrial habitats. However, also a strong astronomical forcing of the entire 3rd order Sarmatian sequence (approximately corresponding to the TB 2.6 cycle of Haq et al. 1988) as well as its 4th order parasequences has repeatedly been suggested (e.g., Harzhauser and Piller 2004; Kováč et al. 2008; Lirer et al. 2009).

The subsequent initial Late Sarmatian flooding caused sedimentation of monotonous pelites with scarce marine faunas in distal basin areas of the Styrian Basin (Kollmann 1965). At the northern basin periphery, limnic pelites were deposited (Peterstal Mb.; lower Gleisdorf Fm.). For these fine clastics normal magnetic polarity is recorded (clay pit St. Stefan; Moser 1997), which implies a correlation to Chron C5An.1n (*c.* 12.16–12.07 Ma after Hüsing et al. 2007).

Thus, by integrating all stratigraphic data for the vertebrate locality of Gratkorn, formed around the Early/Late Sarmatian boundary, an age of about 12.2–12.0 Myr is proposed (Gross et al. 2007a; Harzhauser et al. 2008). This age estimation is in good agreement with the astronomically tuned age of the Early/Late Sarmatian boundary (*c*. 12.2 Ma; Lirer et al. 2009).

Section Gratkorn

At the locality Gratkorn (clay pit St. Stefan), calcareous pelites are mined for cement production. The vertebrate-bearing strata represent the base of the current raw material exploitation and provide an ideal setting for systematic area excavations. The sediment succession below the working level could be studied in prospecting holes only (Fig. 3a).

Detailed section below working level

At the base, grey to orange, horizontally bedded gravels (1), a few cm thick, yellowish, massive sandy (2) and a grey, slightly laminated silty fine sand layer (3) are observed. Several wisps of the silty fine sand bed (3) penetrating the underlying (2) as well as the overlying sandy units (4), making its boundaries diffuse. The yellowish, faintly horizontally bedded sandy layer (4) in the hanging wall starts with a gravel lag at the base, fines upward and borders with irregular boundary to grey, diffusely laminated silty fine sand (5). Above, a yellowish, thin sand layer (6) is topped by a wavy level with ferruginous nodules, which form the base of a bright grey–yellowish calcic horizon (7). The carbonate-impregnated horizon itself contains several ferruginous nodules (some might be rhizoconcretions) as well as calcified meniscate burrows (several cm in length and around 2 cm wide). The carbonate nodules are discrete or amalgamated to each other. Following upon a very diffuse, irregular boundary, a grey–orange mottled pelitic layer (8) includes lots of ferruginous nodules and some meniscate burrows. The subsequent, 0.3–0.4-m thick, yellowish, crudely horizontal bedded sandy unit (9) displays diffuse upper and lower boundaries and is indistinctly fining upward. Prominent are up to dm long, some cm wide meniscate burrows, frequently affected by slickensides. This layer merges into orange–reddish, strongly bioturbated silty fine sand with many ferruginous nodules (?rhizoconcretions) and grey coloured burrows of variable shape and size (10).

Upsection, these layers continue into a *c*. 0.4-m thick, olive grey, angular blocky structured fine clastic horizon (11a) with many ferruginous nodules, some septaria-like glaebules, numerous oxidized root traces, hackberry endocarps (*Celtis*) and very rare phosphatic coprolites (?hyaenids). It evolves gradually into an olive–dark grey, slightly laminated, platy structured and intensively mottled, fine sandy silt (11b). This stratum contains many oxidized root traces, snails, pits of *Celtis* and sometimes accumulated owl pellets. Beside *Celtis*, infrequently gyrogonites of the charophyte *Lynchnothamnus* were found. Only rarely, slightly silicified, autochthonous lignitic stumps (*c*. 1 m in diameter) were observed during mining. The herein discussed vertebrate fauna derives from layers 11a and 11b.

Generalized section of mined hanging wall pelites

The base of clay mining is formed by a 7-cm thick, grey or yellowish, laminated calcareous pelite layer (Fig. 3a) with a large amount of carbonaceous or diagenetically oxidized leaf litter (e.g., *Salix*, *Potamogeton*) and wood remains. Pedogenic features are almost absent except very rare traces of roots.

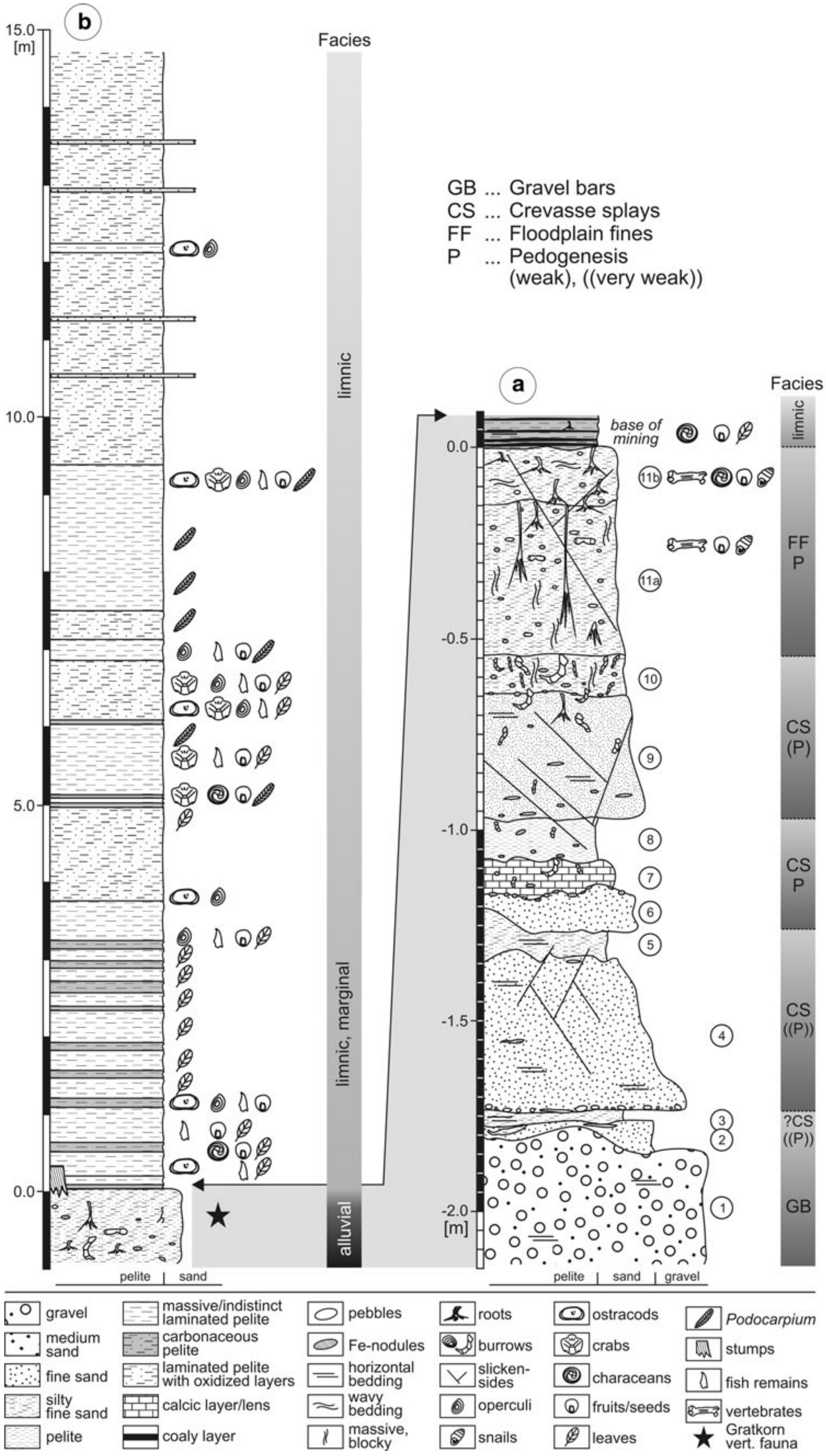
In the northern part of the clay pit, an up to 1.2-m thick, grey, matrix-supported, slightly inverse graded gravel rests upon the vertebrate-bearing layers. It makes up a remarkable humpy, convex-up relief and contains irregular calcareous filaments. Pebbles are frequently carbonatic coated on their underside. This coarse clastic layer tapers off towards the south (excavation area).

Further up, more than 15-m thick, grey–bright grey, calcareous pelites are exposed (Fig. 3b). Especially in the lower part, lignitic layers (plant litter) are frequent. Sandy intercalations are rare and thin throughout the entire outcrop. Whereas diversity of the fossil leaf flora is quite low, dozens of seed and fruit taxa, beside a few ostracod species are documented from several levels (Meller and Gross 2006; Gross 2008). Some layers enclose numerous seeds and leaves of *Podocarpium podocarpum* as well as claws and exuviae of freshwater crabs (Klaus and Gross 2010). Freshwater gastropods (e.g., *Bithynia* operculi), characean gyrogonites and fish fragments (bones) are sometimes abundant in these fine clastics. Unionid bivalves are rarely present in the hanging parts of the section.

Lithofacies interpretation of the section

The gravel layer at the base (layer 1) represents most probably gravel bar deposits of a braided river system. A general decrease in grain size (2, 3) argues for flash flood deposits (crevasse splays) in overbank areas or low-stage water sedimentation (bar top assemblage). Soft sediment deformation (dewatering) and pedogenic processes may have overprinted these beds to some extent thereafter. The sandy/pelitic sequence above (4–10) is interpreted as post-sedimentary altered deposits of succeeding flooding events (crevasse splays). An enclosed moderately developed calcrete (7) hints to an arid/semi-arid climate with seasonal

Fig. 3 Lithology and facies interpretation of the locality Gratkorn. **a** Detailed section of sediments below working level (the vertebrate fauna originates from layer 11a and 11b) **b** Generalized section of the mined clay deposit



rainfalls (Retallack 2001). Large meniscate burrows (especially of 9–10) resemble possible freshwater crayfish burrows described from the Bavarian Upper Freshwater Molasse (Schmid 2002).

The fine-clastic, vertebrate-bearing horizons (11a, b) are interpreted as a floodplain paleosol, which is influenced only sporadically from the braided river system during flash floods. Due to its rather uniform appearance (no distinct soil horizons), in combination with the excellent preservation of the vertebrate remains (see below) as well as very rare findings of coprolites, a rapid accumulation is proposed. Duration of soil formation is suggested to be in the order of 10^1–10^2 years, more probably lasting for only a few decades (see Schmid 2002 for similar calculations for paleosols of the North Alpine Molasse Basin). The co-occurrence of calcic and ferric nodules, hackberry pits, aragonitic valves of land snails and vertebrate remains directs to transient water logging during soil development and thus to alternating wet and dry periods (Retallack 1997, 2001). Relict bedding, intense mottling and drab colouring of the upper part (11b) argues for a more pronounced hydromorphic setting and a shorter inference of pedogenic processes in comparison with the lower part (11a). In particular, the preserved pellet remains indicate a very fast (<1 year?) burial of layer 11b. Because of the great abundance of *Celtis* endocarps, most probably medium-sized hackberry trees have been growing on the fossiliferous substratum. Larger trees must have been present too as several metre-thick, autochthonous tree stumps were found.

In the northern part of the clay pit, the paleosol is covered by matrix-supported gravels, which were formed by a debris flow. Tiny calcareous filaments (pseudomycelia) and pebbles coated with carbonate on their lower surface give indications for an initial calcrete formation within a generally, at least ephemeral dry setting (Retallack 1997).

Layer 11b already signalizes a rising water table. The sedimentation of laminated calcareous pelites (mined hanging wall strata) records that a remarkable switch from alluvial to lacustrine environment took place. Also immediately above the debris flow deposit in the north of the clay pit, lignitic, calcareous pelites rest upon and document the rapid changeover to limnic facies. Ostracod faunas as well as potamid crabs indicate the development of a shallow freshwater lake environment (Gross 2008; Klaus and Gross 2010).

A very similar situation was observed in adjacent outcrops (Gross et al. 2007b). There, debrites or coarse fluvial gravels (Gratkorn Gravel) are superimposed by up to 25-m thick, lacustrine pelites (Peterstal Mb.) and could be mapped out by more than 12 km into the Styrian Basin. Based on well logs and seismic investigations, this unit seems to be even more widespread (Kollmann 1965; Harzhauser and Piller 2004; Gross et al. 2007a). Consequently, this rock column is clearly not linked with a local floodplain pond or oxbow lake formation but is related to a significant transgressional event at the beginning of the early Late Sarmatian.

Taphonomy of vertebrate remains

Sampling and material

The vertebrate-bearing basal paleosol (layers 11a, b) of the clay pit St. Stefan was systematically excavated in the southern part of the pit in an area of *c*. 150 m^2 down to approximately 0.4 m. All in situ excavated fragments were documented and mapped in their finding position. To date, around 800 kg of sediment was wet sieved (sieve size >0.3 mm) using diluted hydrogen peroxide for a better disintegration. However, not only larger vertebrates but also the bulk of the small vertebrates were already collected in the field, thus avoiding fracturing and disintegration during the screen washing process.

Pedogenic features of vertebrate remains

The majority of vertebrate remains (especially these from layer 11a) is rubiginous stained, adhering ferruginous rhizoconcretions and coatings, as well as root corrosion structures (see Fig. 4a). Usually, ferric coating is more pronounced and traces of roots are more frequent on the upper side of bones.

Staining and incrustation might be explained by varying redox-conditions, where Fe^{2+} is mobilized during wet periods and subsequently oxidized to Fe^{3+} in drier phases. This led to the cementation of attached roots and the coating of the bones (Brewer 1976; Retallack 1997). These features are generally assumed to be typical for hydromorphic, weakly/moderately developed soils in warm, seasonal climates (Bao et al. 1998). Selective bleaching of bones due to fibrous, drab-haloed root traces (Fig. 4b) also hints to a fluctuating hydromorphy (Retallack 1997). Moreover, the presence of the adhering root traces indicates that these vertebrate remains were already shallowly buried and the soil surface was vegetated in some way.

Nevertheless, several remains (especially from the upper layer 11b) are light beige and a few are nearly coloured black. This variable colouring possibly reveals changing moisture of the paleosol. Perhaps, even within one season, water logging of the soil varied significantly laterally due to the local topography of the floodplain. In addition, diverging surface exposure times or the mode of accumulation (see below) might have played an important role as well as post-burial diagenesis.

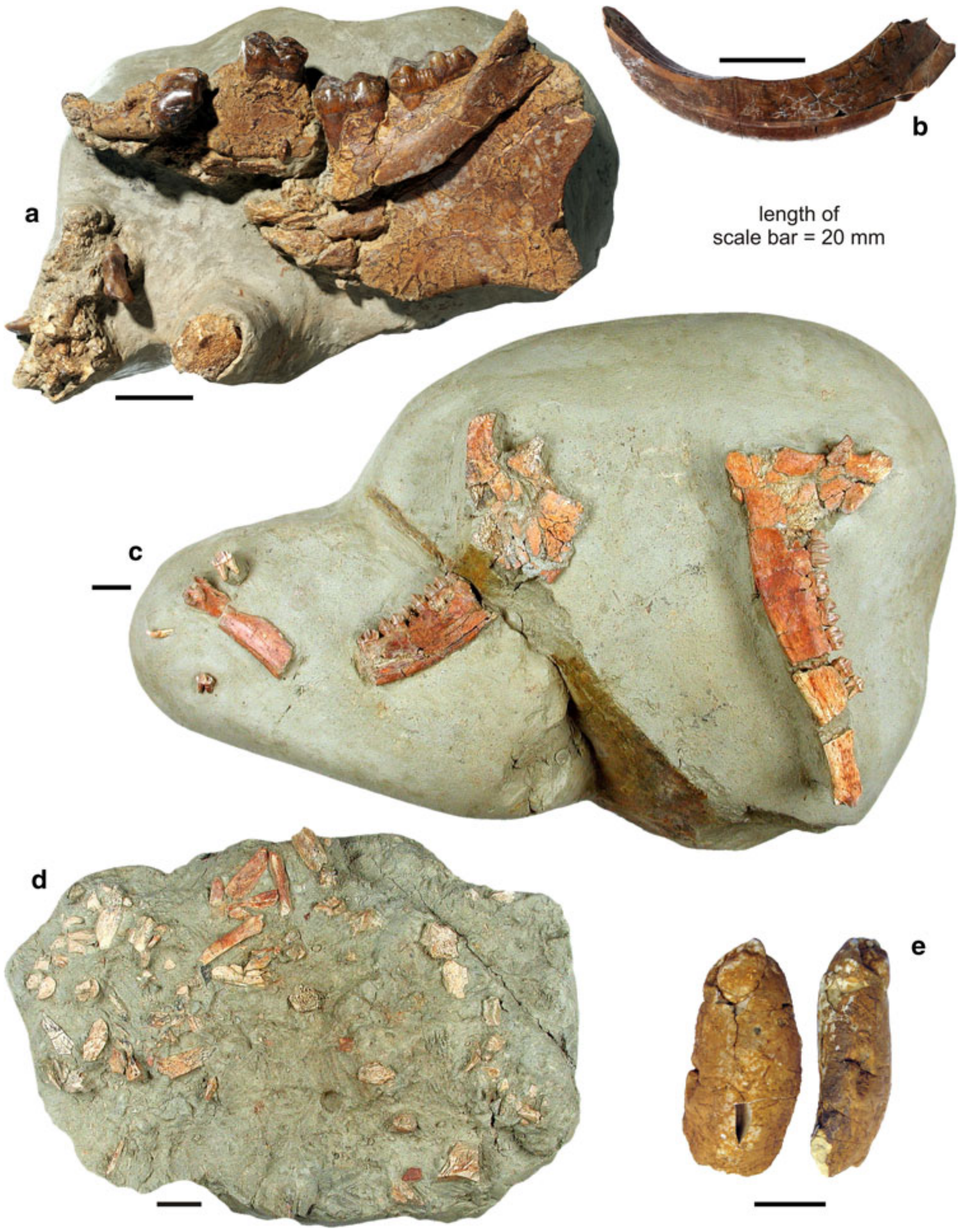


Fig. 4 Examples for the preservation of the Gratkorn vertebrate fauna. **a** Left suid mandible (*Conohyus* sp.; UMJGP 203698) with attached ferruginous rhizoconcretions; the anterior portion is broken and teeth are turned into an upright position probably due to trampling. **b** Left male canine of the suid *Listriodon splendens* (UMJGP 203699) with fibrous, drab-haloed root traces. **c** Mouse deer (left and right mandibles in juxtaposition, affected by a slickenside afterwards; *Dorcatherium naui*; UMJGP 203737). **d** Splintered bones of an unknown animal (UMJGP 203704), indicating pre-burial activity of predators/scavengers. **e** Coprolite (UMJGP 209210), indicating the presence of carnivores

Taphonomy of larger vertebrates

At the beginning of the excavations, large fragments of a *Deinotherium* skeleton attracted attention. Post-cranial elements (ribs, limb bones, vertebras) and isolated teeth were scattered within an area of several square metres (Fig. 5). In general, the bones are weakly permineralized and experienced some post-depositional damage due to compaction. Some bones are clearly affected by slickensides, others were heavily decomposed, indicating a longer surface exposure and weathering of the carcass (Behrensmeyer 1978). However, several specimens might have suffered damage because of trampling like inferred by the embedding position of suid jaws (see Fig. 4a). All *Deinotherium* elements appear to belong to one individual, since no element was found twice. Many long bones are lacking epiphyses. Occasionally isolated epiphysis fragments are unearthed with a granular epiphysis plate preserved. The associated teeth are completely unworn. These observations point to a young *Deinotherium* individual (for studies on recent *Elephas maximus* see Shoshani and Eisenberg 1982).

Although all skeletons of larger vertebrates were found disarticulated, many skeletal parts belonging to the same individual are embedded in short distances from each other (see Fig. 4c). The material displays no obvious signs of abrasion (e.g., rolling) or re-working due to, e.g., fluvial transportation and lacks any preferred orientation.

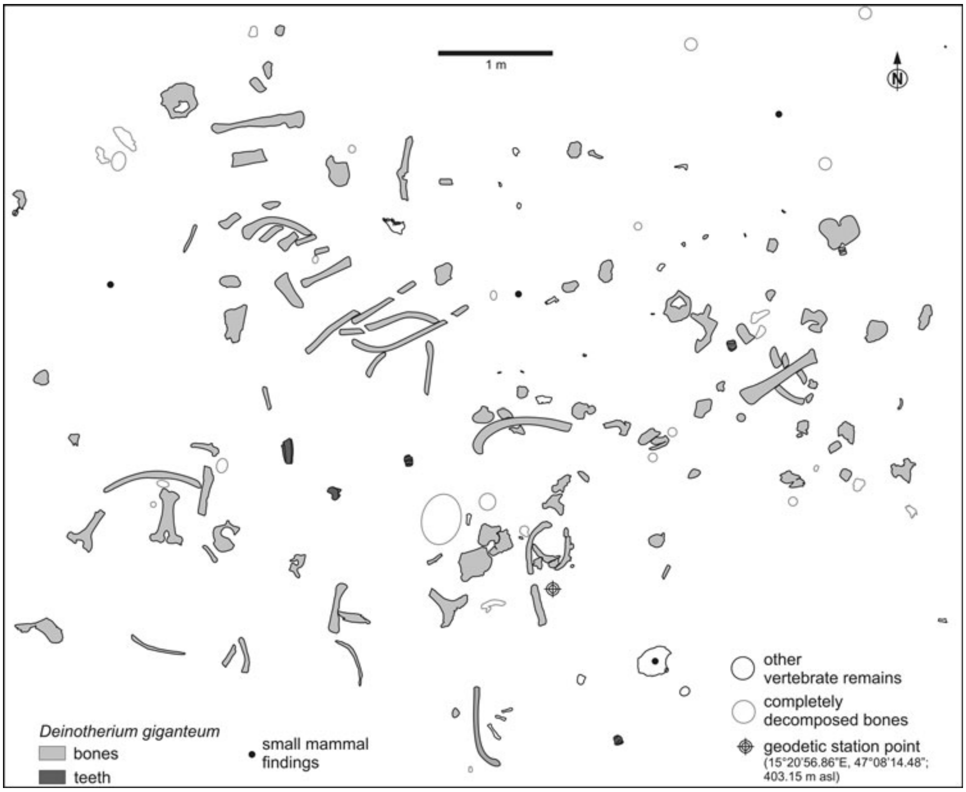


Fig. 5 Distribution of vertebrate remains in the main excavation area

Particularly, the bones of medium-sized animals (e.g., turtles, tragulids) show a high degree of primary fragmentation and are often heavily splintered (Fig. 4d). These cracked bones infer the activity of predators and/or scavengers, which might be partially responsible for local accumulation and/or dislocation, and were maybe responsible for some taphonomical biases. The high percentage of skulls and jaws leads to the same conclusion (e.g., Behrensmeyer 1991; Bertoni-Machado and Holz 2006). Although the record of carnivores is very rare, coprolites (Fig. 4e) and a few teeth indicate their presence. Due to the findings of *Varanus* sp., this large-sized monitor lizard might have been represented a significant predator/scavenger within this terrestrial food web additionally.

Frequently, the bone splinters itself bear minute biting traces. Equally, many tortoise plates and mammalian bones exhibit similar, several mm long and ~mm wide, more or less parallel series of grooves, affecting regularly the complete margins of these bones (Fig. 6a). These marks resemble well the ichnogenus *Machinus* (Mikuláš et al. 2006). They are assumed to be traces of gnawing produced by rodents and/or insectivores (e.g., squirrels, hamsters or shrews) to obtain nutrients (collagen and vitamins) from the bones. Alternatively, such animals simply could have used it to sharpen their teeth. Additionally, randomly arranged, several mm long and wide scratches sometimes occur on compact bones. These marks are very similar to structures related by Fejfar and Kaiser (2005) to traces of osteophagous termite activity (note that termites are still present in the Styrian Basin around that time; Engel and Gross 2009).

Taphonomy of small vertebrates

In the first excavation campaign, small vertebrates were only scarcely found (see Fig. 5). Afterwards in an area of about two square metres a few dozen of gymnures, hamsters and ectothermic vertebrate skeletons and associated elements (skulls, jaws, extremities) were discovered in the upper part of the paleosol (layer 11b; Fig. 6b). Bones and teeth are generally very well preserved, most often only insignificantly corroded and mainly beige coloured (Prieto et al. 2010a). Prieto et al. (2009, 2010a) explain such extreme local concentration of small vertebrate remains as the result of pellet accumulations at feeding/resting places of birds of prey, in more detail of owls. In contrast to, e.g., diurnal raptors or mammalian carnivores, owls cause only minor effects of digestion (Mayhew 1977; Denys et al. 1995; Terry 2007). Thus, the low grade of corrosion, the extreme concentration and the roughly equal co-occurrence of cranial and post-cranial elements (e.g., Andrews 1990; Matthews 2002) point to accumulated owl pellets. Those pellets reflect more or less the local small vertebrate fauna around the locality. Taxonomical biases may have occurred

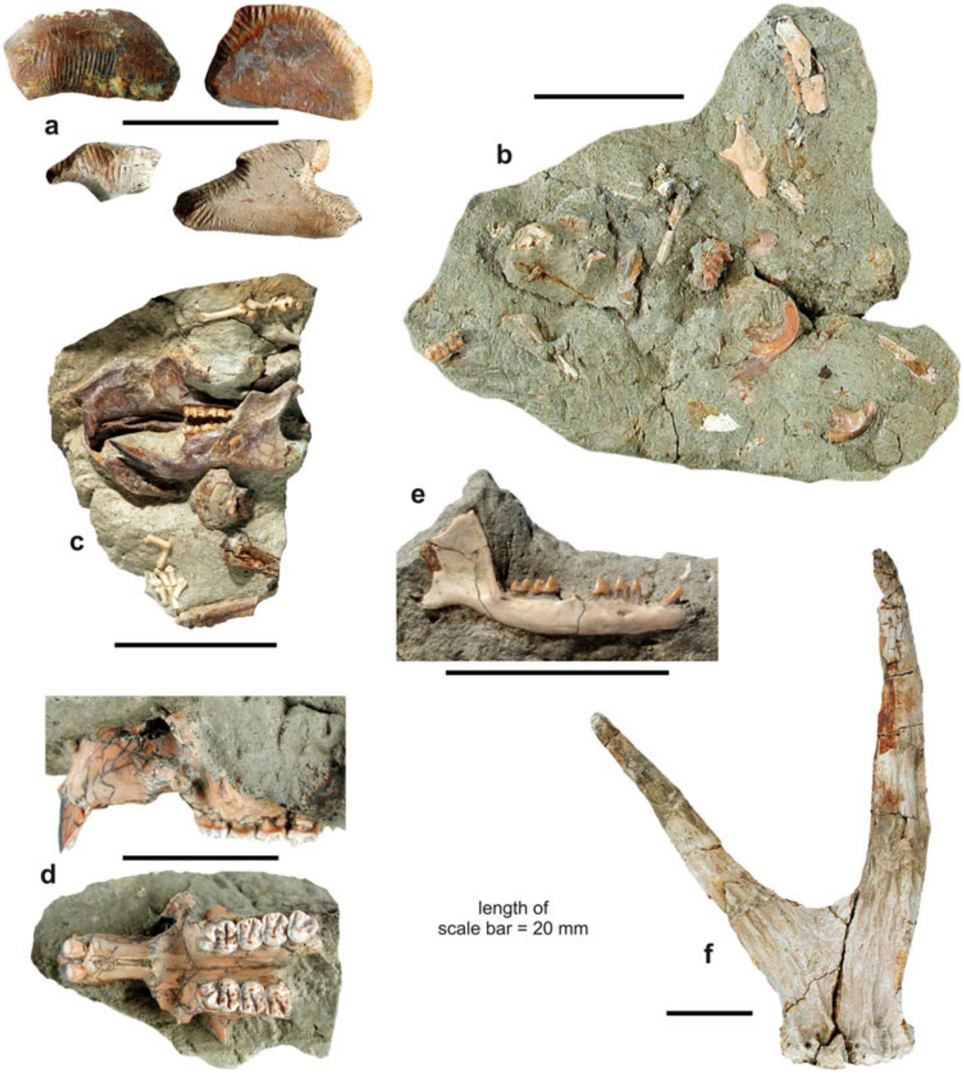


Fig. 6 Indications for the pre-burial activity of small mammals (**a**), probable pellet accumulation by owls (**b**) and examples for preservation (**c**–**f**). **a** Gnawing marks (UMJGP 204099 and 204724). **b** Concentration of cranial and post-cranial elements of two micromammalian individuals: the gymnure *Schizogalerix voesendorfensis* and the rodent "*Cricetodon*" *fandli* (UMJGP 204700). **c** Hamster (fragmentary skull, *left* and *right* mandibles and limb bones; "*Cricetodon*" *fandli*; UMJGP 204240). **d** Flying squirrel (anterior part of the skull; *Albanensia albanensis*; UMJGP 204009). **e** Gymnure *Schizogalerix voesendorfensis* (right mandible; UMJGP 203984). **f** Antler of *Euprox furcatus* (UMJGP 204062)

due to alimentary preferences of the owl as well as the abundance of prey (Prieto et al. 2010a).

Moreover, the presence of pellets excludes a considerable post-depositional dislocation or a long surface exposure and therefore underlines a rapid deposition (<1 year?) of the upper part of this paleosol (layer 11b). Perhaps, some single microvertebrate skeleton associations might be persevered in situ, maybe in their burrows (e.g., spadefoot toads, glass lizard, hamsters or talpids). Unfortunately, such burrows are not recorded up to now, making this suggestion tentatively. However, the abundant presence of the snuggle snail *Testacella* (Harzhauser et al. 2008), which today lives subterranean and preys on earthworms, give a clear indication for vital faunal life in the floodplain soil.

The occurrence of a very few cyprinid fish vertebras (which may belong to only one or two individuals; the lack of resorbed cyprinid pharyngeal teeth, which otherwise indicate in situ life) and one single gobiid otolith are considered to be related to allochthonous deposition (Böhme 2010), maybe as part of prey. Likewise, the record of rare charophyte gyrogonites (*Lynchnothamnus*) is most probably an allochthonous one and may have entered the sediment via passive dispersal (e.g., water birds). Nevertheless, both fish and gyrogonites may indicate the nearby existence of permanent, but short-lived shallow water bodies (see Haas 1994; Bhatia et al. 1998).

Altogether, this vertebrate taphocoenose experienced a variety of pre-depositional modification, and after burial, compaction (in early phases probably also trampling) and subterranean life as well as abiotic soil forming processes acted on it. However, the weak stage of soil development and the observed taphonomic features point to a rather low extent of time-averaging of the fossil community (maybe only or even less than tens or hundreds of years). The presence of pellet remains even indicates a much more rapid burial for the upper part of the paleosol (layer 11b).

In a strict sense, this is definitely not an example for an "event horizon", like a sudden mass mortality event (e.g., Turnbull and Martill 1988), and the structure of the taphocoenose is certainly obscured to some degree. Nonetheless, we are facing to an in situ evolved *Fossillagerstätte*, which developed quite rapidly.

The vertebrate fauna of Gratkorn

Several publications are in progress dealing with the so far recorded vertebrate fauna (Daxner-Höck 2010; Prieto et al. 2010a, b and submitted). Here we present a general overview, which will be extended by specific works later. Up to now, 62 vertebrate taxa are recognized at this locality (Table 1).

Most of the specimens are housed in the collection of the Universalmuseum Joanneum, Abteilung für Geologie & Paläontologie (Graz; abbreviated UMJGP). Some reference specimens are stored in the Bayerische Staatssammlung für Paläontologie und Geologie (Munich) and in the palaeontological collection of the University Tübingen.

Table 1 Gratkorn vertebrate faunal list

	Order	Family	Taxon
Pisces	Cypriniformes	Cyprinidae	Cyprinidae indet.
	Perciformes	Gobiidae	Gobiidae indet. (otolith)
Amphibia	Urodela	Salamandridae	*Triturus* aff. *vulgaris*
			Chelotriton aff. *paradoxus*
			Salamandra sp.
	Anura	Ranidae	*Pelophylax* sp.
			Rana sp.
		Discoglossidae	*Latonia* sp.
		Bufonidae	*Bufo cf. viridis*
		Pelobatidae	*Pelobates* aff. *sanchizi*
Reptilia	Scincomorpha	Scincidae	Scincidae indet.
		Lacertidae	*Lacerta* sp. *1*
			Lacerta sp. *2*
			Lacerta sp. *3*
			Miolacerta sp.
			?Edlartetia sp.
		Gekkonidae	Gekkonidae indet
	Anguimorpha	Anguidae	*Ophisaurus* sp.
		Varanidae	*Varanus* sp.
	Serpentes	Elapidae	*Naja romani*
		Colubridae	Colubrinae sp. 1
			Colubrinae sp. 2
			Natricinae indet.
	Testudines	Testudinidae	*Testudo* sp. *1*
			Testudo sp. *2*
		Chelydridae	*Chelydropsis* sp.
		Emydidae	Emydidae indet.
Aves	?Coliiformes	fam. indet.	?Coliiformes indet.
	?Anseriformes	fam. indet.	?Anseriformes indet.
	Strigiformes	fam. indet.	Strigiformes indet. (pellets)
Mammalia	Rodentia	Cricetidae	*Megacricetodon minutus*
			Democricetodon sp.
			Eumyarion sp.
			"Cricetodon" fandli
		Gliridae	*Muscardinus* aff. *sansaniensis*
			Miodyromys sp.
		Eomyidae	*Keramidomys* sp.
		Sciuridae	*Albanensia albanensis*
			Forsythia gaudryi
			Blackia sp.
			Spermophilinus bredai
		Castoridae	Castoridae indet.
	Lagomorpha	Ochotonidae	*Prolagus oeningensis*
			Eurolagus sp.
	Lipotyphla	Erinaceidae	*Schizogalerix voesendorfensis*
			Galericinae indet
	Soricomorpha	Talpidae	*Desmanodon fluegeli*
		Soricidae	*Dinosorex* sp.
	Chiroptera	Vespertilionidae	cf. *Myotis* sp.
	Perissodactyla	Chalicotheriidae	*Chalicotherium goldfussi*
		Rhinocerotidae	*Lartetotherium* sp.
			Dicerorhinus sp.
			Brachypotherium sp.
		Equidae	*Anchitherium* sp.
	Artiodaclyla	Suidae	*Listriodon splendens*
			Conohyus sp.
		Tragulidae	*Dorcatherium naui*
		Moschidae	*Micromeryx flourensianus*
		Cervidae	*Euprox furcatus*
		Palaeomerycidae	*Palaeomeryx* sp.
	Carnivora	?Hyaenidae	?Hyaenidae indet. (coprolite)
	Proboscidea	Deinotheriidae	*Deinotherium giganteum*

Ectothermic vertebrates

A total number of 27 species belonging to all major groups of ectothermic vertebrates (fishes, amphibians, reptiles) have been recorded. Reptiles represent by far the most numerous group. Fish remains are very rare and comprise only ten vertebrae and one otolith. They belong to small-sized cyprinids (minnows) and gobiids (gobies).

Tailed amphibians are represented by disarticulated specimens of a small-sized newt (*Triturus* aff. *vulgaris*), a salamander (*Salamandra* sp.) and a skeleton association of a crocodile newt (*Chelotriton* aff. *paradoxus*). Frogs are known by five species (*Rana* sp., *Pelophylax* sp., *Latonia* sp., *Bufo* cf. *viridis*, *Pelobates* aff. *sanchizi*), of which *Rana* sp., documented by two ilia, represents the most interesting taxon. The morphology of the bones indicates a member of the brown frog group (*Rana temporaria* group), the record of which goes back into the Early Miocene (Böhme 2001). The Gratkorn material represents the second evidence of brown frogs in the Miocene of Europe. The burrowing spadefoot toad *Pelobates* aff. *sanchizi* is known, apart from disarticulated remains, from a skeleton association.

The most diverse and abundant ectothermic vertebrate group are scincomorph reptiles (lizards), of which more than thirty jawbones belonging to six taxa (Scincidae indet., *Lacerta* sp. 1–3, *Miolacerta* sp., ?*Edlartetia* sp.) have been recognized. In contrast to lizards, geckos (Gekkonidae indet.) are relatively rare. Anguimorphs are represented by a large monitor lizard (*Varanus* sp.) and a small-size species of *Ophisaurus* (glass lizard), both represented by associated skeletons. The related vertebrate column of the monitor lizard (vertebra and ribs) points to an individual of about 1.5 metres in total length.

The snake material recorded so far is rather scarce (about twelve better-preserved trunk vertebra), but relatively divers. Four taxa can be identified; beside a large-sized cobra (*Naja romani*), two small-sized colubrines (Colubrinae sp. 1, 2) and a natricine (Natricinae indet.) occur.

Chelonians are known by four taxa: two aquatic turtles and two terrestrial tortoises. The latter are recorded with three partially preserved shells, from which two show similarities to *Testudo* (s.l.) *steinheimensis* (*Testudo* sp. 1). The second tortoise (*Testudo* sp. 2) belongs to a very robust and thick-shelled species, resembling *T.* cf. *kalksburgensis* described from Steinheim (Staesche 1931). Both turtle species (*Chelydropsis* sp., Emydidae indet.) are documented by a few isolated plates only.

Aves

Birds are represented by a few bones and bone fragments (?Coliiformes, pers. comm. U. Göhlich; ?Anseriformes) and one fractured eggshell. The presence of owls (Strigiformes indet.) is indicated indirectly by pellet remains.

Small mammals

Rodents, lagomorphs, insectivores and one chiropteran constitute the small mammal fauna (in total 19 species up to now) from Gratkorn.

Five families of rodents are recorded. The Cricetidae are documented by four species: *Megacricetodon minutus*, *Democricetodon* sp. nov. (sensu Kälin and Engesser, 2001), *Eumyarion* sp. and the new species "*Cricetodon*" *fandli* (Prieto et al. 2010b). Apart from isolated teeth, well-preserved cranial and post-cranial material has been found for the last two species at least (Fig. 6c).

The Sciuridae are represented by four genera: the flying squirrels *Albanensia albanensis*, *Forsythia gaudryi* and *Blackia* sp., as well as with the ground squirrel *Spermophilinus bredai* (Daxner-Höck 2010). The material of *Forsythia*, *Blackia* and *Spermophilinus* is rather limited. In contrast, *Albanensia* is nicely documented with fragmentary skulls (Fig. 6d), maxillaries and mandibles, which were discovered concentrated within a small area.

Two species of dormouse (Gliridae: *Muscardinus* aff. *sansaniensis*, *Miodyromys* sp.) are occasionally found in the paleosol of Gratkorn. Very rare is the small eomyid rodent *Keramidomys* sp. (Daxner-Höck 2010). Beavers (Castoridae) are recorded by some fragmentary mandibles and maxillaries. Pikas (Ochotonidae) are represented by *Prolagus oeningensis* (Prieto et al. submitted) and *Eurolagus* sp.

Insectivores are the most abundant small mammal group at this locality (Prieto et al. 2010a). Especially the gymnure *Schizogalerix voesendorfensis* is very common and has been regularly found along the excavation surface (Fig. 6e). A second, larger gymnure (Galericinae indet.) is documented from one upper molar only and could not be determined in more detail (although some morphological characteristics remember *Parasorex socialis*). Shrews (Soricidae) are nearly absent, except the large *Dinosorex* sp., which is documented by an extremely well-preserved mandible. A new mole species (Prieto et al. 2010a), *Desmanodon fluegeli* is the only representative of the Talpidae. Bat remains (cf. *Myotis* sp.; a few isolated teeth) are insufficient for a closer determination (Prieto et al. 2010a).

Larger mammals

Among the 13 larger mammal taxa the Perissodactyla are only rarely present. They include *Chalicotherium goldfussi*, three taxa of rhinos (pers. comm. K. Heissig) and the horse *Anchitherium* sp.

More frequent are cranial and post-cranial elements of the suids *Listriodon splendens* (Fig. 4b) and *Conohyus* sp. (Fig. 4a). However, the ruminants are the dominant large mammal group at Gratkorn. Mouse deers (Tragulidae) with *Dorcatherium naui* (Fig. 4c), musk deers (Moschidae) with *Micromeryx flourensianus*, as well as deers (Cervidae: *Euprox furcatus*) are regularly documented with more or less complete mandibles, maxillaries, antlers (*Euprox*; Fig. 6f) and also with post-cranial bones.

Few post-cranial bones document the Palaeomerycidae (*Palaeomeryx* sp.). The presence of carnivores is indicated by rare teeth and by coprolites. The largest mammalian taxon is the proboscidean *Deinotherium giganteum,* which is recorded by one disarticulated skeleton.

Discussion

Preliminary palaeoenvironmental implication of the mammalian fauna

The flying squirrels *Albanensia*, *Forsythia* and *Blackia* are supposed to be typical for forested environments, like recent arboreal and night-active Pteromyinae (Daxner-Höck 2010). Van der Meulen and De Bruijn (1982) defined the "flat molar group" of dormice, in which the genus *Muscardinus* is included, and proposed as biotope for these forms undergrowth, thickets and arboreal vegetal environments. Following this approach, *Miodyromys* ("asymmetrical group") could have been a ground-living genus, requiring open environment. Similarly, the ground squirrel *Spermophilinus* probably inhabited more open, sun-exposed environments with rocky ground and low vegetation (Daxner-Höck 2010).

The palaeoecological demands of ground dwelling Galericini (e.g., *Schizogalerix*) are still unclear (moist forested habitats *vs*. open habitats; for discussion see Prieto 2007 and Prieto et al. 2010a). The mole *Desmanodon* seems not to be extremely adapted to subterranean life and probably avoided very wet environments (Prieto 2010). Confident proves of the ecological preference of large-sized shrew *Dinosorex* (Heterosoricinae) are unknown (Van den Hoek Ostende 2001). However, at least some members of this extinct subfamily were assumed to be forest dwellers (Doukas 1986).

Considering that the *Democricetodon* species from Gratkorn has a long mesoloph in the M2, the species could have required a more humid environment (Wessels and Reumer 2009). The ecology of the genus *Eumyarion* is difficult to deduce from the fossil record. Indeed, several species with similar size and dental morphology can co-occur in a single locality suggesting different adaptations for each species in its biotope (De Bruijn 2009). Small-sized *Megacricetodon* species are usually more opportunistic (Kälin 1999; Prieto 2007). Due to their semi-aquatic mode of living, the presence of beavers points to the existence of permanent water bodies surrounded by some kind of forest (Daxner-Höck 2004; Daxner-Höck and Bernor 2009; Stefen 2009).

Along with the larger mammals *Chalicotherium* (Heissig 1999, 2009; Coombs 2009), the equid *Anchitherium* (Kaiser 2009; Tütken and Vennemann 2009), the mouse and musk deers *Dorcatherium* and *Micromeryx* as well as the cervid *Euprox* and *Palaeomeryx* (Gentry et al. 1999; Hillenbrand et al. 2009; Merceron 2009) argue for forested, at least partially moist environments. More open, savannah-like conditions can be deduced from the occurrence of the suids *Listriodon* and *Conohyus* (Thenius 1960; Mottl 1970; Van der Made 2003).

Although much more investigations are needed (e.g., isotopic investigation, micro- and meso-wear analyses), the found mammalian assemblage points, similar to the gastropod fauna, to a well-structured landscape (Harzhauser et al. 2008; Daxner-Höck 2010), which offered a wide range of habitats (active and abandoned channels, moist floodplain soils, ephemeral ponds as well as nearby dryer, open areas and limestone screes of the surrounding Palaeozoic basement).

Palaeoclimate derived from ectothermic vertebrates

The rich record of ectothermic vertebrates allows the estimation of both temperature and precipitation for the Gratkorn locality. Several thermophilous ectothermic vertebrates, which characterized the Miocene climatic optimum, are absent from Gratkorn and other comparable localities of the Sarmatian in the Central Paratethys (Böhme 2003). In particular, these missing groups are the crocodiles, chamaeleonids, cordylids, pythonids and the giant tortoises, all living today in areas with over 15°C in the annual mean. The temperature requirements of many recorded reptiles (e.g., scincomorphs) are difficult to estimate on an actualistic approach, because their taxonomic relationships remain obscure and thus the nearest living relatives are unknown. *Varanus* sp. probably represents the most thermophilous vertebrate of the Gratkorn fauna.

Monitor lizards are known since the Ottnangian (*c*. 18 Ma) of the North Alpine Foreland Basin and survive the Middle Miocene cooling in Central and Eastern Europe (Böhme 2003). Based on the requirements of the recent representatives of the family Varanidae, the occurrence of *Varanus* suggests mean annual temperatures (MAT) above 14.8°C (Haller-Probst 1997; Böhme 2003), indicating for Gratkorn a subtropical thermal regime with MAT around 15°C. Comparable temperature estimations based on freshwater crab (coldest month mean temperature >0°C) and ostracod findings (subtropical) in the hanging wall pelites are discussed by Gross (2008) and Klaus and Gross (2010).

The calculation of the palaeoprecipitation is based on relative frequencies of defined ecophysiological groups within the herpetofauna and was calibrated on a recent dataset covering most parts of the Old World (for details see Böhme et al. 2006). Twenty-one out of 25 recorded amphibians and reptiles of the present fauna (excluding non-fossorial snakes; Böhme et al. 2006) are grouped according to their assumed ecologic and physiologic adaptations into five ecophysiological groups (Table 2). Using the mean of the ecophysiological indices and equation 1 from Böhme et al. (2006) results in a mean annual precipitation value (MAP) of 486 ± 252 mm. Compared to the recent precipitation in that area (MAP 840 mm; climate station Graz-Thalerhof; Müller and Hennings 2009), the earliest Late Sarmatian MAP-estimation represents about 58% of present-day rainfall and indicates a semi-arid, significantly drier climate than today.

Table 2 Amphibian and reptile taxa from Gratkorn, their supposed ecophysiological groups, and calculation details for the estimation of palaeoprecipitation (according to Böhme et al. 2006)

Taxon	Ecophysiologic group	Index
Triturus aff. *vulgaris*	Peri-aquatic	0.3918
Chelotriton aff. *paradoxus*	Peri-aquatic	0.3918
Salamandra sp.	Pen-aquatic	0.3918
Latonia sp.	Peri-aquatic	0.3918
Pelobates aff. *sanchizi*	Fossorial	0.0917
Bufo cf. *viridis*	Heliophil	0
Pelophylax sp.	Semi-aquatic	0.513
Rana sp.	Pen-aquatic	0.3918
Emydidae indet.	Full aquatic	1
Chelydropsis sp.	Full aquatic	1
Testudo sp. 1	Heliophil	0
Testudo sp. 2	Heliophil	0
Gekkonidae indet.	Heliophil	0
Lacerta sp. 1	Heliophil	0
Lacerta sp. 2	Heliophil	0
Lacerta sp. 3	Heliophil	0
Miolacerta sp.	Heliophil	0
?*Edlartetia* sp.	Heliophil	0
Scincidae indet.	Heliophil	0
Ophisaurus sp.	Heliophil	0
Varanus sp.	Heliophil	0
Ecophysiologic index		0.21732
Mean annual precipitation (mm)		486
95% prediction interval (mm)		252

The obtained MAP value fits very well with the reference curve presented by Böhme et al. (2008) and confirms the assumption of a dry climate during the (Late) Sarmatian again. Moreover, a semi-arid climate for the Late Sarmatian s.str. agrees with earlier observations based on fossil floras and vertebrate communities (e.g., Berger and Zabusch 1953; Thenius 1960; Kollmann 1965; Mottl 1970) as well as with data from the marine environments (e.g., Harzhauser et al. 2007).

Biostratigraphic implication of the vertebrate fauna

The age of the Gratkorn vertebrate fauna is set to the early Late Sarmatian (*c.* 12.2–12.0 Ma) based on integrated stratigraphy (Gross et al. 2007a; Harzhauser et al. 2008). As it is dated independently from the vertebrates themselves, it provides a valuable tie point for calibration of several vertebrate taxa ranges.

In general, cricetid rodents are of prime importance for terrestrial high-resolution biostratigraphy due to their rapid evolution (e.g., Kälin 1999). Prieto et al. (2010b) highlight the biostratigraphical inference of the Gratkorn material in detail. This discussion clearly demonstrates the value of the locality Gratkorn in terms of continental biozonations (based on phylogenetical lineages) as well as its geographical key position for the understanding of faunal interchanges between western and (south-)eastern Europe. To date, the species *Megacricetodon minutus* and *Democricetodon* sp. nov. (sensu Kälin and Engesser, 2001) indicate a dating to the late Middle Miocene (Late Sarmatian) up to the early Late Miocene (Middle Pannonian). Specimens of *Eumyarion* are left in open nomenclature. The occurrence of this genus ranges from Early Miocene (Ottnangian) up to the Middle Pannonian (Daxner-Höck 1996, 1998). However, the new hamster species "*Cricetodon*" *fandli* from Gratkorn is probably an ancestor of the Late Sarmatian *Cricetodon klariankae* from Northern Hungary (locality Felsőtárkány-Felnémet; Hír 2006; Prieto et al. 2010b). This would match very well with the postulated slightly older age of the Gratkorn site.

Among the sciurid and glirid rodents, *Albanensia albanensis*, *Forsythia gaudryi* and *Muscardinus* aff. *sansaniensis* are indicative for the late Middle Miocene (Daxner-Höck 2010).

Based on investigations on the insectivore fauna (Prieto et al. 2010a), the occurrence of the gymnure *Schizogalerix voesendorfensis* is the oldest known (stratigraphical range now: Late Sarmatian to Middle Pannonian, restricted to Central Europe). Although morphological characters relate the new mole species *Desmanodon fluegeli* to the Anatolian *Desmanodon minor–Desmanodon major* lineage (stratigraphical range: Middle to early Late Miocene;

Table 3 Selected large mammal faunas from the Late Badenian to Early Pannonian of the Styrian, Lavanttal, Vienna and the North Alpine Foreland Basin, and the Pannonian Basin (taxonomic data according to: 1) Heizmann and Reiff 2002; 2) Berger and Zabusch 1953; Thenius 1955, 1960; 3) Mottl 1964; 4) this paper; 5 and 6) Mottl 1970; 7) Daxner-Höck and Göhlich 2009; 8) Thenius 1982; 9) Papp and Thenius 1954; Vislobokova 2005; 10) Bernor et al. 2004)

	Steinheim Late Badenian	**Vienna B.** Early+Late Sarmatian	**Lavanttal B.** Early Sarmatian	**Gratkorn** Late Sarmatian	**East Styria** Late Sarmatian	**East Styria** Early Pann. Zones B+C	**Atzelsdorf** Early Pann. Zone C	**Mariathal** Early Pann. Zone C	**Vösendorf** Middle Pann. Zone E	**Rudabanya** Late Pann. Zone F
Anchitherium aurelianense	▬	▬	▬	sp.		▬	▬	▬		
Hippotherium ssp.						▬	▬	▬	▬	▬
Alicornops simorrense	▬									
Lartetotherium sansaniense	▬			sp.						aff.
Dicerorhinus steinheimensis	▬	?sp.	cf. *germanicus*	sp.	cf. *germanicus*	▬			sp.	
Brachypotherium brachypus		▬	▬	sp.	▬					
Brachypotherium goldfussi						▬	▬			
Hoploaceratherium belvederense										▬
Hoploaceratherium bavaricum								▬		
Aceratherium incisivum		sp.			▬	▬	▬		▬	▬
Metaschizotherium fraasi	▬									
Anisodon grande		▬	▬			?				
Chalicotherium goldfussi				▬			▬	▬		aff.
Tapirus priscus										▬
Listriodon splendens	▬	▬	▬	▬	▬					
Conohyus simorrensis	▬	▬		sp.	?					
Albanohyus pygmaeus	▬						cf.			
Propotamochoerus palaeochoerus						▬		▬	▬	▬
Parachleuastochoerus kretzoii							▬			▬
Lagomeryx parvulus			▬						cf.	
Micromeryx flourensianus	▬			▬			▬			▬
Amphiprox anocerus								▬		
Euprox furcatus	▬	▬	▬	▬			sp.			
Euprox dicranoceros									▬	
Heteroprox larteti	▬									
Hispanomeryx sp.	▬									
Palaeomeryx eminens	▬		?	sp.			cf.			
Lucencia aff. *pierensis*										▬
Dorcatherium crassum	▬		▬							
Dorcatherium naui				▬		▬	▬	▬		▬
Eotragus sansaniensis		▬								
Miotragocerus monacensis		▬								
Miotragocerus pannoniae						▬	vel *Tethytragus*	▬	▬	sp.
Tragocerus sp.					▬					
Protragocerus chantrei		▬			▬					
Austroportax latifrons		▬								
Gazella stehlini		▬								
Gomphotherium angustidens		▬	▬			▬				
Gomphotherium steinheimense	▬									
Tetralophodon longirostris					▬	▬	cf.	▬	▬	▬
"Stegotetrabelodon" grandincisivum					aff.					
"Stegotetrabelodon" gigantorostris										▬
Zygolophodon turicensis		▬				cf.				
Deinotherium giganteum		aff.	aff.	▬		▬	▬	▬	▬	▬
Data from:	1)	2)	3)	4)	5)	6)	7)	8)	9)	10)

Engesser 1980), the Gratkorn species cannot be directly integrated into this lineage.

Within the large mammal fauna, the presence of *Euprox furcatus*, *Listriodon splendens* and *Conohyus* suggests a Sarmatian age (Table 3). These species are well known from Sarmatian and are absent from Pannonian sediments of the Styrian Basin (Mottl 1970) and the Vienna Basin (Thenius 1955, 1960; Table 3). The tragulid *Dorcatherium naui* is in Gratkorn for the first time recorded from the Late Sarmatian. This species was previously only known from the Pannonian (Hillenbrand et al. 2009).

The equid *Hippotherium*, which occurred in Central Europe during the Early Pannonian (∼ 11.2 Ma; Woodburne 2009) and in the Styrian Basin in the upper part of the Paldau Fm. (Mottl 1970; Gross 2003; Fig. 2), is not present in Gratkorn, as are typical Pannonian suids (*Propotamochoerus palaeochoerus* and *Parachleuastochoerus kretzoii*) and bovids. Boselaphid bovids are not only characteristic elements of the Pannonian in the Central Paratethys (Vislobokova 2005), but also characteristic elements in the Sarmatian of the Vienna Basin (Thenius 1955, 1960) and the Late Sarmatian of the Styrian Basin (Mottl 1970). If their absence from Gratkorn is related to environmental reasons has to be investigated in the future.

Beside the mammal record, the lack of the usually common, large-size anguin *Pseudopus* from the Gratkorn fauna might be of stratigraphical importance too. This may support the hypothesis of Klembara et al. (2010), who discuss that after the extinction of the Early to Middle Miocene species *Pseudopus laurillardi* and before the immigration of *Pseudopus pannonicus* (Tempfer 2009) representatives of this genus are missing in the late Middle Miocene of Central Europe.

Conclusions

The vertebrate fauna of Gratkorn is one of the very few qualitatively and quantitatively rich localities known from the late Middle Miocene (Sarmatian s.str.) of the Paratethyan realm. Founded on lithostratigraphical correlation and biostratigraphy based on molluscs, ostracods, foraminifers, mammals and plants, it is matched with the high-resolution sequence stratigraphy of the Styrian Basin. Supplemented by palaeomagnetical data an absolute age of *c*. 12.2–12.0 Ma is most plausible.

The vertebrate-bearing horizon represents a floodplain paleosol formed on the top of a fluvial succession. Lithofacies assemblages point to a braided river system, which is sometimes influenced by debris flows of adjacent alluvial fans. Mollusc and vertebrate faunas reflect a variety of habitats within the alluvial plain, which was covered by some kind of pioneer vegetation at least. Afterwards a freshwater lake environment immediately replaced this alluvial landscape.

Pedogenic features of the paleosol provide indications for pronounced wet and dry periods/seasons in an overall semi-arid climate. This interpretation is supported by the palaeoclimatological analysis of the herpetofauna, resulting in an estimated MAP of 486 ± 252 mm. Biota-based (especially on reptiles) temperature estimations point to a subtropical thermal regime with a MAT of around 15°C.

The taphonomical situation excludes a significant time-averaging of the fauna. Splintered bones and gnawing marks document the pre-burial activity of predators/scavengers, micromammals as well as insects, pointing to a certain period of surface exposure. After burial, subterranean life (e.g., plant roots) as well as abiotic soil forming processes (e.g., compaction, coating) affected the taphocoenosis additionally. Nevertheless, accumulation of the Gratkorn vertebrate fauna in total is estimated to range in the order of tens to hundreds of years only. However, the findings of owl pellet remains in the upper part of the paleosol argue for a much faster burial. Hence, further studies on the bone bed of Gratkorn will enable to confer about the palaeocommunity structures of the late Middle Miocene much more precisely than many other locations.

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