Sciuridae, Gliridae and Eomyidae (Rodentia, Mammalia) from the Middle Miocene of St. Stefan in the Gratkorn Basin (Styria, Austria)

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(With 7 figures and 6 tables)

Abstract

The herein described rodent assemblage from St. Stefan near Gratkorn comprises: the flying squirrels *Albanensia albanensis* (Major, 1893), *Forsythia gaudryi* (Gaillard, 1899) and *Blackia* sp., the ground squirrel *Spermophilinus bredai* (Meyer von, 1848), the dormice *Muscardinus* aff. *sansaniensis* (Lartet, 1851) and *Miodyromys* sp., and the eomyid *Keramidomys* sp. Other vertebrate groups, i.e. various lower vertebrates, birds, large mammals, insectivores, lagomorphs and the cricetids, will be published elsewhere.

The studied rodents are interpreted to be predominantly forest dwellers. Stratigraphically they indicate the late Middle Miocene (late MN7+8), which is in good agreement with the associated Sarmatian mollusc fauna and the development of terrestrial environments in the Gratkorn Basin during the Middle Sarmatian.

Keywords: Austria, Styrian Basin, rodents, Middle Miocene, Sarmatian, biostratigraphy, Mammal Neogene zone MN7+8, forested environments.

Zusammenfassung

Die beschriebene Nagetier-Fauna von St. Stefan bei Gratkorn umfasst: die Flughörnchen *Albanensia albanensis* (Major, 1893), *Forsythia gaudryi* (Gaillard, 1899) und *Blackia* sp., das Erdhörnchen *Spermophilinus bredai* (Meyer von, 1848), die Schlafmäuse *Muscardinus* aff. *sansaniensis* (Lartet, 1851) und *Miodyromys* sp., und den Eomyiden *Keramidomys* sp. Die übrigen Wirbeltiergruppen aus der Fauna werden an anderer Stelle publiziert. Es sind: Niedere Vertebrata, Vögel, verschiedene Großsäugetiergruppen, Insektenfresser, Hasenartige und Hamsterartige.

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Die bearbeiteten Nagetiere werden vorwiegend als Waldbewohner angesehen. Stratigraphisch zeigen sie das späte Mittel-Miozän an (höhere Säugetierzone MN7+8). Diese Einstufung steht im Einklang mit der Begleitfauna Sarmatischer Mollusken und mit der Entstehung terrestrischer Lebensräume im Gratkorn Becken im Mittel-Sarmatium.

Schlüsselwörter: Österreich, Steirisches Becken, Nagetiere, Mittel-Miozän, Sarmatium, Biostratigraphie, Neogene Säugetierzone MN7+8, Waldlandschaften.

Introduction – Study Area

The locality St. Stefan is a clay pit in the Gratkorn Basin, a small satellite basin northwest of the Styrian Basin. The clay pit is situated 0.7 km east of Gratkorn (10 km northwest of Graz; N 47°08'15", E 15°20'55"). For localization see fig. 1. The investigated profile displays poorly sorted silts at the base of the clay pit (HARZHAUSER et al. 2008: fig. 3). This basal layer is overlain by a more than 15-m-thick sequence of pellites with several intercalated lignitic layers, yielding freshwater ostracods, crabs (GROSS 2008; GROSS & KLAUS 2005) and plant remains including in situ tree stumps several meters in height. The terrestrial gastropods (HARZHAUSER et al. 2008) and vertebrate fossils were collected from the basal layer of the clay pit where teeth and bones of lower vertebrates and mammals were exposed. The highly diverse vertebrate assemblage includes fishes, birds, reptiles and mammals. Among large mammals, *Deinotherium*, *Palaeomeryx* and other ruminants, the suid *Listriodon* and several carnivores are represented, but so far not studied in detail. The small mammal assemblage comprises diverse insectivores, rodents and lagomorphs. Only part of the rodents is described in the present study, i.e. the Sciuridae, Gliridae and Eomyidae. The studies on Cricetidae, Insectivora and Lagomorpha are in progress (J. Prieto, University of Munich, Section Paleontology), and the diverse assemblage of lower vertebrates is under investigation (M. Böhme, University of Munich, Section Paleontology).

Material and Methods

The vertebrate fossils were collected from the surface, when the basal layer of the clay pit was exposed. Moreover, several bulk samples (each consisting of hundreds of kg sediment) from that basal layer were washed by teams from the Landesmuseum Joanneum Graz, the Natural History Museum Vienna and the University of München. Fossil concentrations within this basal layer yielded partly articulated skeletons, mandibles and entire facial bones with dentition from small mammals and lower vertebrates. Thanks to

Fig. 1. Study area: A. Localization of the clay pit St. Stefan; modified after DAXNER-HÖCK & HÖCK ► (2009: Fig. 1); B. Simplified geological map of the north-western margin of the Styrian Basin after HARZHAUSER et al. (2008: fig.1c; data included from: KOLLMANN 1965; EBNER 1983; FLÜGEL & NEUBAUER 1984; RIEPLER 1988; KRÖLL et al. 1988; GROSS et al. 2007).
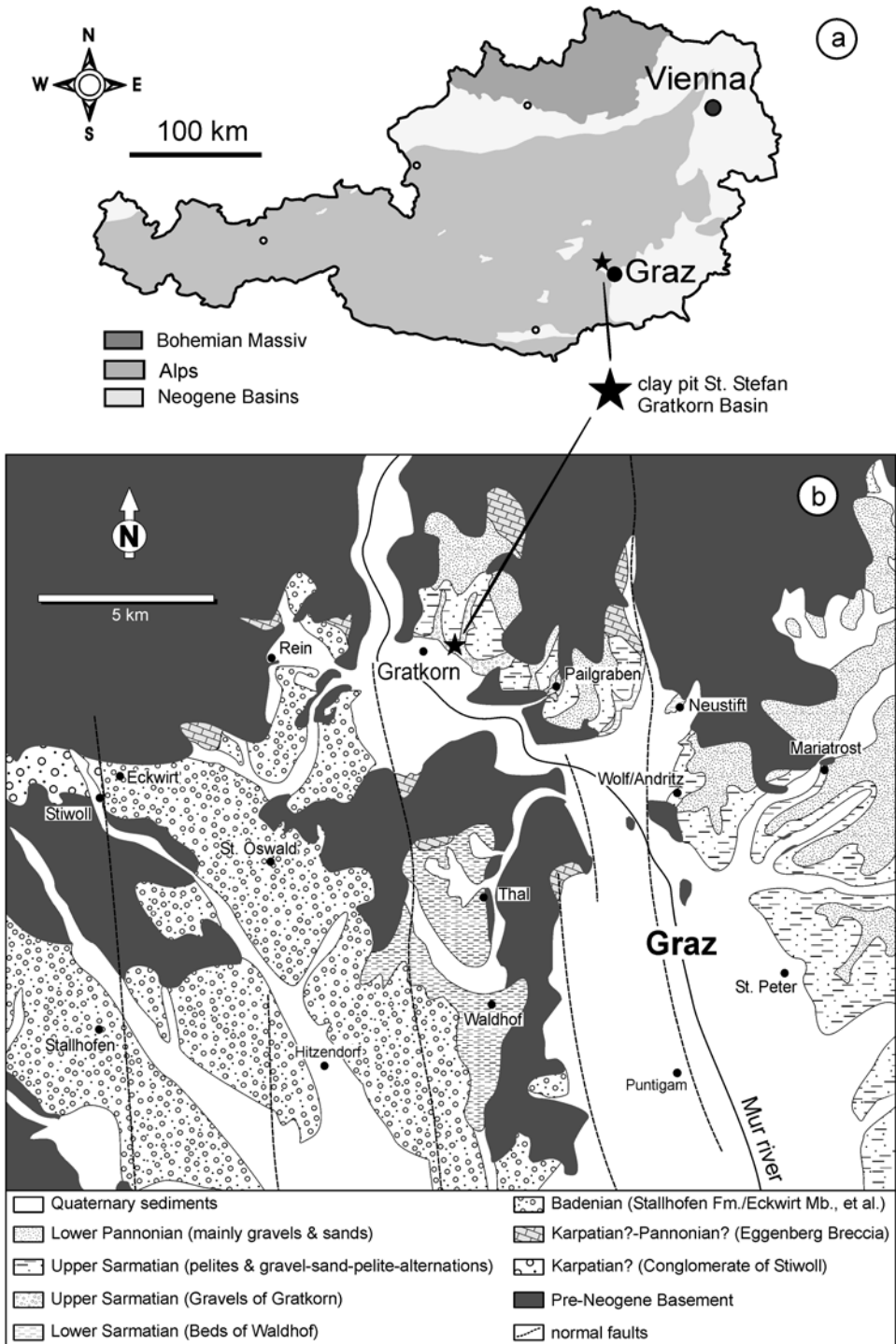
excellent preparation in the Landesmuseum Joanneum Graz, these fossils provide unique information about very rare species. Sorting of residues from washed sediment samples is still in progress.

The herein described material includes three teeth of the ground squirrel *Spermophilinus.* One tooth is available from the tiny flying squirrel *Blackia*, one lower toothrow of the medium-sized flying squirrel *Forsythia*, and several fragmentary skulls and mandibles of the large flying squirrel *Albanensia.* The dormice are represented by three molars of *Muscardinus* and by an upper toothrow and two molars of *Miodyromys*. Finally, the eomyid *Keramidomys* is represented by two teeth. As soon as sorting of the washing residue will be completed, we expect more isolated teeth from the full spectrum of taxa.

The digital photos were taken by M. GROSS and the author using digital cameras. The SEM photos were taken by E. HÖCK using the Philips XL 20 scanning microscope at the Biocenter, University of Vienna. For measurements, a light stereomicroscope (Leica-WILD M3B) was used. To facilitate comparisons, all right side teeth are figured as mirror images, and their figure numbers are underlined, e.g. fig. 2/2 (= right d4). The described material is stored in the collection of the Landesmuseum Joanneum Graz (LMJ).

For classification of Sciuridae and Eomyidae, MC KENNA & BELL (1997) is followed; for Gliridae, the classification and dental terminology proposed by DAAMS & BRUIJN DE (1995) is used. Dental terminology of Sciuridae after BLACK (1963) and of Eomyidae after ENGESSER (1990).

Abbreviations

I, i	upper, lower incisor
d4	lower deciduous tooth
p4-m3	lower permanent cheek teeth
P3-M3	upper permanent cheek teeth
♦	teeth indicated by this symbol derive from a single tooth row
MN	Mammal Neogene Zone
LMJ	Landesmuseum Joanneum Graz

Systematic part

Family Sciuridae FISCHER DE WALDHEIM, 1817

Subfamily Sciurinae FISCHER DE WALDHEIM, 1817

Genus *Spermophilinus* BRUIJN DE & MEIN, 1968

European fossil species – type localities and stratigraphic correlations:

S. besanus CUENCA BESCÓS, 1988 – Vargas 1A (Spain; Early Miocene / MN4)

S. bredai (MEYER VON, 1848)* – Oeningen (Germany; Middle Miocene / MN7+8)

S. turolensis BRUIJN DE & MEIN, 1968 – Los Mansuetos (Spain; Late Miocene / MN12)

S. giganteus BRUIJN DE et al., 1970 – Maritsa (Greece; Pliocene / MN14)

* type species

Spermophilinus bredai (MEYER VON, 1848)
fig. 2/1-2, tab.1

Material (tab. 1): 1 left M3 (LMJ 207.301), 2 right d4 (LMJ 207.313, 207.302).

Description: *Spermophilinus* has a generalized sciurid tooth pattern.

M3 (fig. 2/1) has a triangular outline with rounded corners. There are two pronounced cusps, the wide lingual protocone and the labial paracone, connected by the transverse protoloph. The narrow anterior basin is enclosed by the weak anteroloph and the protoloph. The wide posterior basin is surrounded by the protoloph, the protocone and the weak posteroloph.

d4 (fig. 2/2): The occlusal surface is subtriangular in outline because the protoconid and metaconid are situated much closer than the hypoconid and the weak entoconid. A tiny anteroconid and mesostylid are present in only one of the two specimens. The talonid basin is completely enclosed by the marginal cuspids and lophids.

Root numbers and positions: M3 has three roots, one lingual and two labial ones. No roots are preserved on the deciduous lower premolars.

Discussion: As outlined above, four species are recognized in Europe. They do not differ significantly in dental morphology but have long been known to show size increase through time (BRUIJN DE 1995). The specimens from St. Stefan very well agree with *S. bredai* from La Grive and other Middle – and Late Miocene occurrences.

Some other European occurrences of *S. bredai* are: Sansan (France: BRUIJN DE 1995; MN6), Manchones (Spain: BRUIJN DE 1995; MN6), Candir (Turkey: BRUIJN DE 1995; MN6), La Grive M, L5, L7 (France: MEIN & GINSGURG 2002; MN7+8), Barranc de Can Vila 1 (Spain: CASANOVAS-VILAR 2007: MN7+8), Anwil (Switzerland: ENGESSER 1972; MN7+8), Opole (Poland: KOWALSKI 1967; MN7+8), Rudabanya (Hungary: KRETZOI & FEJFAR 2005; MN9), Richardhof-Golfplatz, Götzendorf (Austria: MN9), Richardhof-Wald and Schernham (Aus-

Tab. 1. Measurements (in mm).

	fig.	length	width
M3 left	2/1	2.09	1.90
d4 right		1.62	1.21
d4 right	2/2	1.54	1.20

tria: MN10). The stratigraphic range is Middle Miocene (MN6-8) to early Late Miocene (MN9-10).

<div align="center">

Subfamily Pteromyinae Brandt, 1855

Genus *Blackia* Mein, 1970

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European fossil species – type localities and stratigraphic correlations:

B. ulmensis Werner, 1994 – Ulm-Westtangente (Germany; Early Miocene / MN 2)

B. parvula Baudelot, 1972 – Sansan (France; Middle Miocene / MN6)

B. miocaenica Mein, 1970 * – La Grive L7 (France; Middle Miocene / MN7+8)

B. polonica Black & Kowalski, 1974 – Podlesice (Poland; Pliocene / MN 14)

B. woelfersheimensis Mein, 1970 – Wölfersheim-Wetterau (Germany; Pliocene / MN 15)

* type species

<div align="center">

Blackia sp.
fig. 2/3

</div>

M a t e r i a l : 1 left d4 (LMJ 207.303)

M e a s u r e m e n t s (in mm): length: 1.50, width: 1.00

D e s c r i p t i o n : The d4 (fig. 2/3) is relatively long. There are four conids, the metaconid being the highest and most prominent of them. The much smaller protoconid is situated close to the metaconid. A small anteroconid is positioned anterior to the protoconid and metaconid. The small hypoconid is situated in the postero-labial corner. No entoconid is present. The talonid basin is concave and displays enamel rugosities. It is surrounded by the conids, the posterolophid and the ectolophid. No roots are preserved.

R e m a r k s : The tooth has the typical pattern of the genus *Blackia*. However, it is significantly larger than any Blackia d4. It is almost as long as d4 of *Spermophilinus bredai* from St. Stefan. Without additional material identification remains open.

<div align="center">

Genus *Forsythia* Mein, 1970

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European fossil species – type localitiy and stratigraphic correlation:

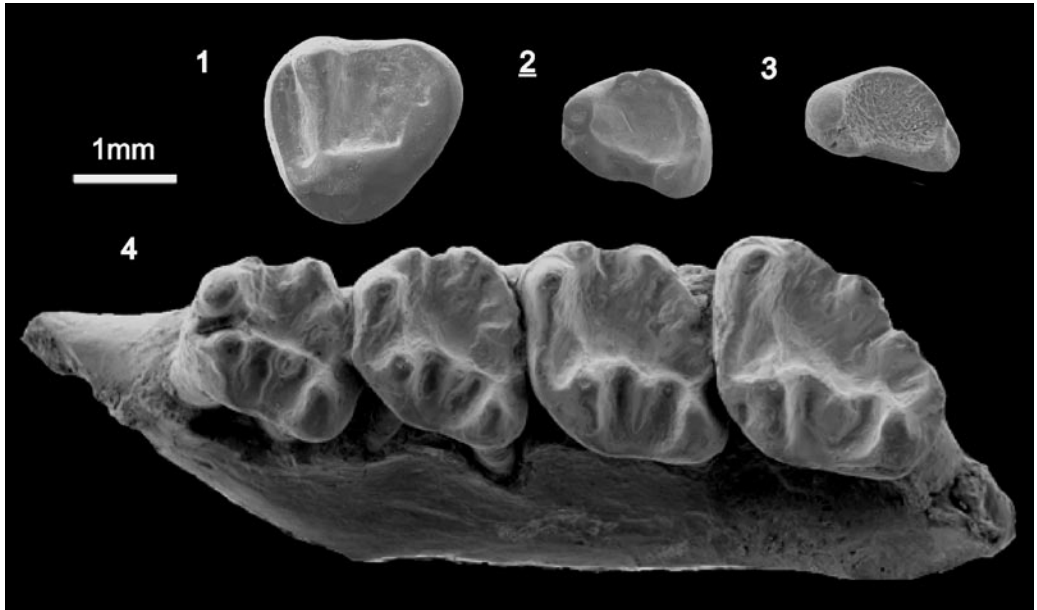*F. gaudryi* (Major, 1893) – La Grive-Saint-Alban M (France; Middle Miocene / MN7+8)

Fig. 2. Sciuridae from St.Stefan, Gratkorn Basin, Styria; Middle Miocene (MN7+8).

2/1   *Spermophilinus bredai* (MEYER VON, 1848); left M3; LMJ 207.301
2/2   *Spermophilinus bredai* (MEYER VON, 1848); right d4; LMJ 207.302
2/3   *Blackia* sp.; left d4; LMJ 207.303
2/4   *Forsythia gaudryi* (GAILLARD, 1899); left lower jaw with p4-m3; LMJ 203.592

Forsythia gaudryi (GAILLARD, 1899)
fig. 2/4, tab. 2

Material: 1 fragmentary left mandible with p4-m3 (LMJ 203.592).

Description: The tooth row (p4-m3) is 8.2 mm long (fig. 2/4). All teeth have four main conids: metaconid (antero-lingual), entoconid (postero-lingual), protoconid (antero-labial) and hypoconid (postero-labial). Both the distance between protoconid and metaconid as well as the length of the anterolophid vary as a result of the different shape of the molars, which become wider from proximal to distal. There are at least three pronounced additional conulids along the margin of the teeth: The lingual mesostylid is situated on the posterior slope of the metaconid, the mesoconid on the W-shaped ectolophid, and the hypoconulid on the strongly structured posterolophid. From the pyramidal mesoconid a crest extends towards the labial sinusoid. The labial and lingual main conids are in alternating position, giving the teeth a more or less rhomboidal shape. There is a deep notch posterior to the mesostylid and a shallower notch posterior to the entoconid. All molars have a pronounced lingual anterolophid and a weak metalophid. The lingual anterolophid

Tab. 2. Measurements (in mm).

	length	width
p4 left	1.85	1.85
m1 left	1.85	1.95
m2 left	2.20	2.20
m3 left	2.50	2.20

is the most prominent lophid of the molars. It extends from the metaconid towards the antero-labial edge, curves backwards and fuses with the anterior base of the protoconid. The short and thin metalophid extends from the protoconid-tip towards the central basin, but does not reach the metaconid. It partly separates the central basin into the small anterior trigonid-basin and the wide posterior talonid basin. From the notch posterior to the mesostylid, a wide talonid basin extends towards its postero-labial corner, where the posterolophid shows a profound notch. Rugosities of the basins are almost absent.

The p4 has short lingual and labial anterolophid arms, converging towards the anterior margin of the tooth. Metaconid and protoconid are situated close to each other. The metalophid is almost absent. The hypoconulid is pronounced.

In m1, only the lingual anterolophid is present. The distance between the anterior main conids is wider than in p4.

The m2 is larger than m1. Labial of the small hypoconulid, a second conulid is situated on the posterolophid.

The m3 is the longest molar. Only m3 has a short labial anterolophid and a small anterosinusid. The posterolophid shows deep notches on both sides of the pronounced hypoconulid.

The roots are inserted in the mandibular bone and thus not clearly visible.

R e m a r k s : *Forsythia* is an extinct flying squirrel of medium size. It is a monospecific genus with a characteristic dental pattern that does not essentially change throughout its temporal range (Middle Miocene; MN7+8). The St. Stefan specimen differs most strikingly from the original diagnosis (MEIN 1970: 33-35; fig. 43) by the pronounced hypoconulid. There is a remarkable variability in the sculptured posterolophid (hypoconulid present or not) of specimens from Anwil, La Grive (ENGESSER 1972: Abb. 3, 4) and St. Stefan. *Forsythia* is a very rare flying squirrel represented by few specimens from only a few assemblages in Europe. The intraspecific variability is therefore still poorly known. Some isolated teeth described as *F.* aff. *gaudryi* from the Early Miocene (MN4) of Petersbuch 2, Erkertshofen 1 and Rembach in Germany (ZIEGLER & FAHLBUSCH 1986) resemble *Aliveria* BRUIJN DE et al., 1980 rather than *Forsythia*. *Aliveria* is thought to be the ancestral stock (Early Miocene) from which *Forsythia* and *Albanensia* have evolved (BRUIJN DE et al. 1980; 250).

The two medium-sized flying squirrels *Forsythia* and *Pliopetaurista* Kretzoi, 1962 have a similar dental pattern. Nonetheless, some essential differences in the upper dentition and smaller differences in the lower dentition allow them to be distinguished from one another (Daxner-Höck 2004: 400). Based on recent investigations on the lower dentition, *Forsythia* differs from *Pliopetaurista* by the following characters: the smaller metaconid-protoconid distance (p4-m2) and the very wide entoconid-hypoconid distance; the strongly alternating main conids; the pronounced lingual and almost absent labial anterolophid (p4-m2); the almost absent anterosinusid; the smaller metalophid; the more oblique posterolophid (p4-m3) with profound notches; and by significantly larger teeth than in *Pliopetaurista kollmanni* Daxner-Höck, 2004 (Late Miocene; MN9-10), which is the most primitive and oldest species of *Pliopetaurista*.

Some other occurrences in Europe are: La Grive M (France: Mein 1970; MN7+8), La Grive L7 (France: Mein & Ginsburg 2002), Anwil (Switzerland: Engesser 1972; MN7+8) and Giggenhausen (Germany; Engesser 1972; = *Sciuropterus* cf. *S. gaudryi* in Black 1966; MN7+8).

The stratigraphic range is Middle Miocene (MN7+8).

Genus *Albanensia* Daxner-Höck & Mein, 1975

European fossil species – type localities and stratigraphic correlations:

A. sansaniensis (Lartet, 1851) – Sansan (France; Middle Miocene / MN6)

A. albanensis (Major, 1893)* – La Grive-Saint Alban M (France; Middle Miocene / MN7+8)

A. albanensis quiricensis (Villalta, 1950) – San Quirze de Galliners (Spain; Middle Miocene / MN7+8)

A. grimmi (Black, 1966) – Marktl (Germany; Late Miocene / MN9)

* type species

Albanensia albanensis (Major, 1893)
figs 3-5, tab. 3

Material: P3 (LMJ 207.312); anterior part of the skull with left and right I, left P3-M3 and right P3-M2 (LMJ 204.009, fig. 3/1-2); left and right maxillary bones with M1-3 left and right (LMJ 204.012, fig. 4/1-2); strongly fragmented left maxilla with P4-M3 (LMJ 204.151/3); left mandible with i p4-m3 (LMJ 204.007, fig. 5/1,4); left mandible with i, p4-m3 (LMJ 204.008, fig. 5/2,5); left p4-m3 (LMJ 204.010, fig. 5/6); right I and p4 (LMJ 204.011, fig. 5/3); right fragmentary mandible with m2-3 (LMJ 204.015/1); right
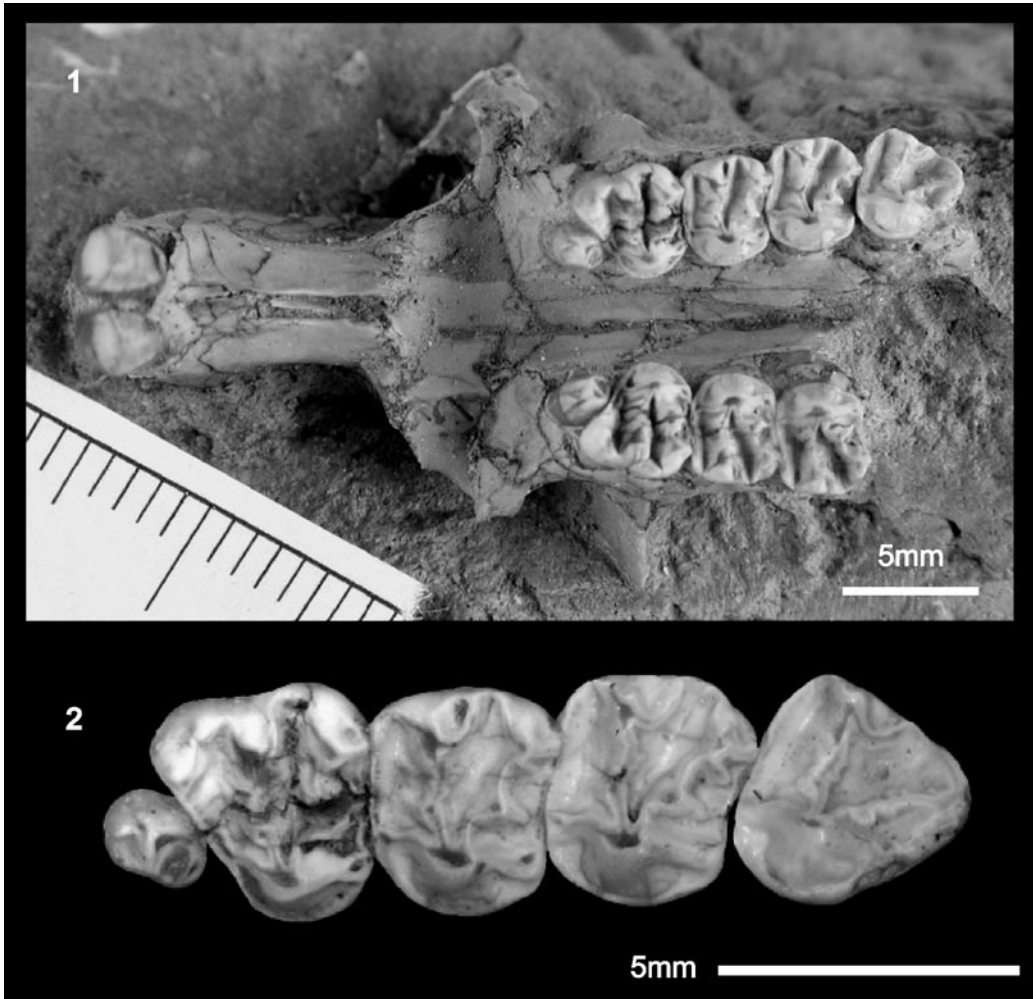
Fig. 3. *Albanensia albanensis* (MAJOR, 1893) from St. Stefan, Gratkorn Basin, Styria; Middle Miocene (MN7+8); LMJ 204.009.

3/1   anterior part of the skull with left P3-M3 and right P3-M2
3/2   left P3-M3

m1 (LMJ 204.151/2); fragmentary mandible with left I (LMJ 204.013); fragm. M (LMJ 204.046).

D e s c r i p t i o n : *Albanensia* is one of the large-sized extinct flying squirrels. Although slightly smaller, it is most similar to the living giant flying squirrel *Petaurista* concerning skull characters and dental pattern. The St. Stefan collection provides two fragmentary skulls (fig. 3/1-2 and fig. 4/1-2). One specimen (LMJ 204.009, fig. 3) consists of the rostrum with both praemaxillary bones, the upper incisors, the left and right maxilla with
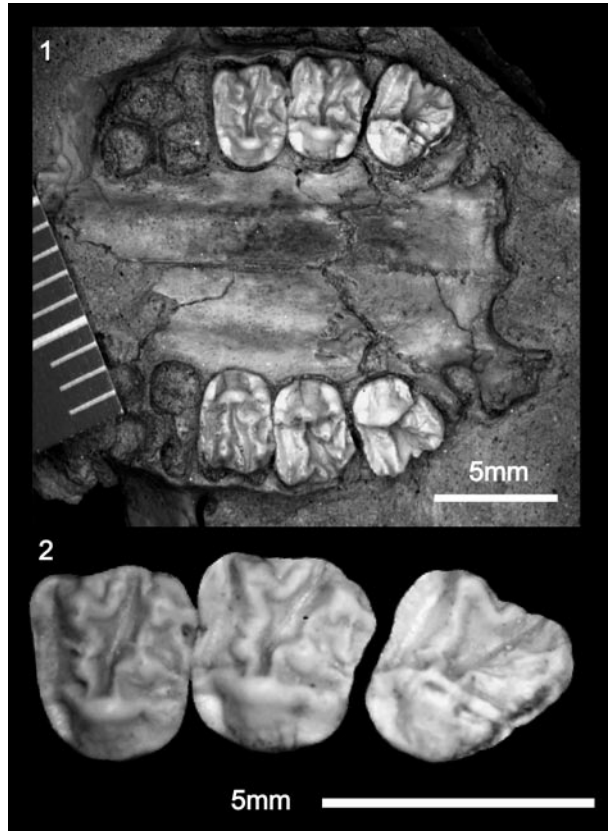
Fig. 4. *Albanensia albanensis* (MA-JOR,1893) from St. Stefan, Gratkorn Basin, Styria; Middle Miocene (MN7+8); LMJ 204.012.

4/1 palate with left and right palatine and maxilla bones and the molars
4/2 left M1-3

left P3-M3 and right P3-M2, and the palate. The incisors are robust and orthodont. The rostrum is laterally compressed and some bones are slightly dislocated. The following characters can be discerned: diastema between the incisors and the cheek teeth shorter than the length of P3-M3; incisive foramina rather small, extending from shortly behind the incisors as far as the praemaxillary-maxillary suture, incisive foramina approximately half the length of the diastema; pronounced masseteric tubercles anteromedial of the zygoma (fragmentary). The palate with left and right M1-3 (LMJ 204.012, fig. 4) is not compressed and displays maxillary and palatine bones in original shape and proportions; maxillary-palatine suture extends as far as M2. Two mandibles (LMJ 204.007, fig. 5/1, 5 and LMJ 204.008, fig. 5/2, 5) feature the ramus with incisor and the complete cheek dentition. The incisor is robust and its tip is in level with the occlusal plane of the cheekteeth (fig. 5/1). The mandibles display the following characters: diastema short, assymmetric and concave; masseteric fossa extends to below m2; mental foramen anterior to p4.

The upper tooth row (P3-M3) is 15.00 mm long, the lower tooth row (p4-m3) 13.95-14.70 mm long. Upper and lower incisors are laterally compressed. The anterior surface is slightly convex and covered by a thin, smooth enamel band. The diameter of lower

incisors is 3.30 mm (in antero-posterior direction) and 1.80 mm (in labio-lingual direction). The upper incisors measure 3.75 mm (in anterior-posterior direction) and 2.25 mm (in labial-lingual direction).

The upper teeth except for P3 are similar in their pattern (figs 3-4). Three main high cones are present, the paracone and metacone and the protocone, and a much smaller hypocone. The labial cones are connected to the protocone by the protoloph and the metaloph. Protoloph and metaloph converge in lingual direction, forming a V-shaped connection with the protocone. The metaconule is situated in the middle part of the metaloph. It is distinctly smaller than the main cones, but always larger than the protoconule, which can be absent. The sizes of the protoconule and metaconule decrease from the P4 towards the M3. Additional short but accentuated crests are present: The mesostylcrest extends from the paracone backwards and turns towards the labial margin of M1-3. Two short crests extend backwards, one from the metacone and one from the metaconule. They run in posterior direction, cross the postero-labial valley and can reach the posteroloph. The anteroloph and the posteroloph are thin and low. These marginal crests are at right angles to the endoloph. The endoloph is a prominent longitudinal ridge extending from the anteroloph towards the wide protocone (which is part of the endoloph) and backwards to the small hypocone.

P3 is the smallest, P4 the largest of all upper teeth. P3 has a simple shape and only one main cone.

Tab. 3. Measurements (in mm).

No.		length	width	length	width	length	width	length	width	length	width
sup.	fig.	P3	P3	P4	P4	M1	M1	M2	M2	M3	M3
1. P3				1.80	1.80						
2. P3-M3 left	3/1-2	1.80	1.95	4.15	4.20	3.30	4.05	3.30	4.05	3.90	4.05
2. P3-M2 right	3/1	1.80	1.95	4.15	4.20	3.30	4.05	3.45	4.05		
3. M1-3 left	4/1-2					3.30	3.90	3.60	3.90	3.75	3.75
3. M1-3 right	4/1					3.45	3.90	3.60	3.90	3.75	3.75
4. P4-M3 left				3.75	3.75	2.85	3.60	3.00	3.60	3.45	3.45
		length	width	length	width	length	width	length	width	length	width
inf.	fig.			p4	p4	m1	m1	m2	m2	m3	m3
5. p4-m3 left	5/1, 4			3.15	3.30	3.15	3.45	3.45	3.60	4.35	3.60
6. p4-m3 left	5/2, 5			3.00	3.30	3.30	3.60	3.60	3.75	4.50	3.75
7. p4-m3 left	5/6			3.30	3.15	3.15	3.45	3.60	3.60	4.50	3.60
8. p4 right	5/3			3.00	3.30						
9. m2-3 right								3.75	3.60	4.50	3.60
10. m1 right						3.15	3.75				

P4 is subtriangular in outline due to the pronounced parastyle in the antero-labial corner. It is almost as large as the three main cones (para-, meta- and protocone) and is larger than the small hypocone. There are two additional labial styli: a small one is situated between the parastyle and the paracone, the second one is the mesostyle situated posterior to the paracone. P4 has a small protoconule and a pronounced metaconule. A lingually-derected crest departs from the parastyl and merges the endoloph.

M1 and M2 are almost square in outline. M1 is smaller than M2, but similar in occlusal pattern. The mesostylcrest is pronounced, the mesostyle weak or absent.

M3 is subtriangular in outline. It is similar to M1-2 in its anterior part. The posterior part differs by the strongly oblique and short metaloph, the absence of the hypocone and metacone, and by the rugose postero-labial corner of the tooth. The protoconule is absent, the metaconule weak.

All lower cheek teeth (fig. 5) have four main conids: metaconid, entoconid, protoconid and hypoconid. The distance between protoconid and metaconid successively increases from p4 through m3. There are at least two pronounced additional conulids along the margin of the teeth, the mesostylid and the mesoconid. The pronounced mesostylid is attached to the metaconid by a strong mesostylid-crest. The pyramidal mesoconid is situated on the W-shaped ectolophid. The posterolophid is a continuous lophid that displays small conulids and a small hypoconulid on some m3. Originating from these conids and from the entoconid, more or less sharp and undulated crests run towards the talonid basin. The posterolophid is not notched. The direction of the posterolophid is almost transverse in p4, becoming increasingly oblique from m1 through m3. The labial and lingual main conids of molars are in alternating position, giving the teeth a more or less rhomboidal shape. There is a deep notch posterior to the mesostylid. From this notch a wide talonid basin extends in postero-labial direction towards the posterolophid. All molars have a pronounced lingual anterolophid. The lingual anterolophid and the posterolophid are the most prominent lophids. The lingual anterolophid extends from the metaconid towards the antero-labial edge of the tooth, curves backwards and attaches to the anterior base of the protoconid. It increases in length from m1 through m3. There is no labial anterolophid. The metalophid extends from the tip of the protoconid towards the central basin, where small crests can split from the metalophid; it then turns forwards and attaches to the metaconid. The metalophid separates the trigonid-basin from the talonid basin. The crenulation of the basins is highly variable.

The p4 is almost as long as m1, but narrow in its anterior part. There is no anteroconid, although a weak labial anterolophid is present. Excluding the anterolophid, p4 and m1 are very similar in occlusal pattern.

In m1-2 the lingual anterolophid and the metalophid are present.

The m3 is the longest tooth and has a narrow posterior part. The strongly oblique posterolophid is ornamented by one or more conulids. A hypoconulid may be present, although it is never separated by deep notches from the entoconid and from the posterolophid.
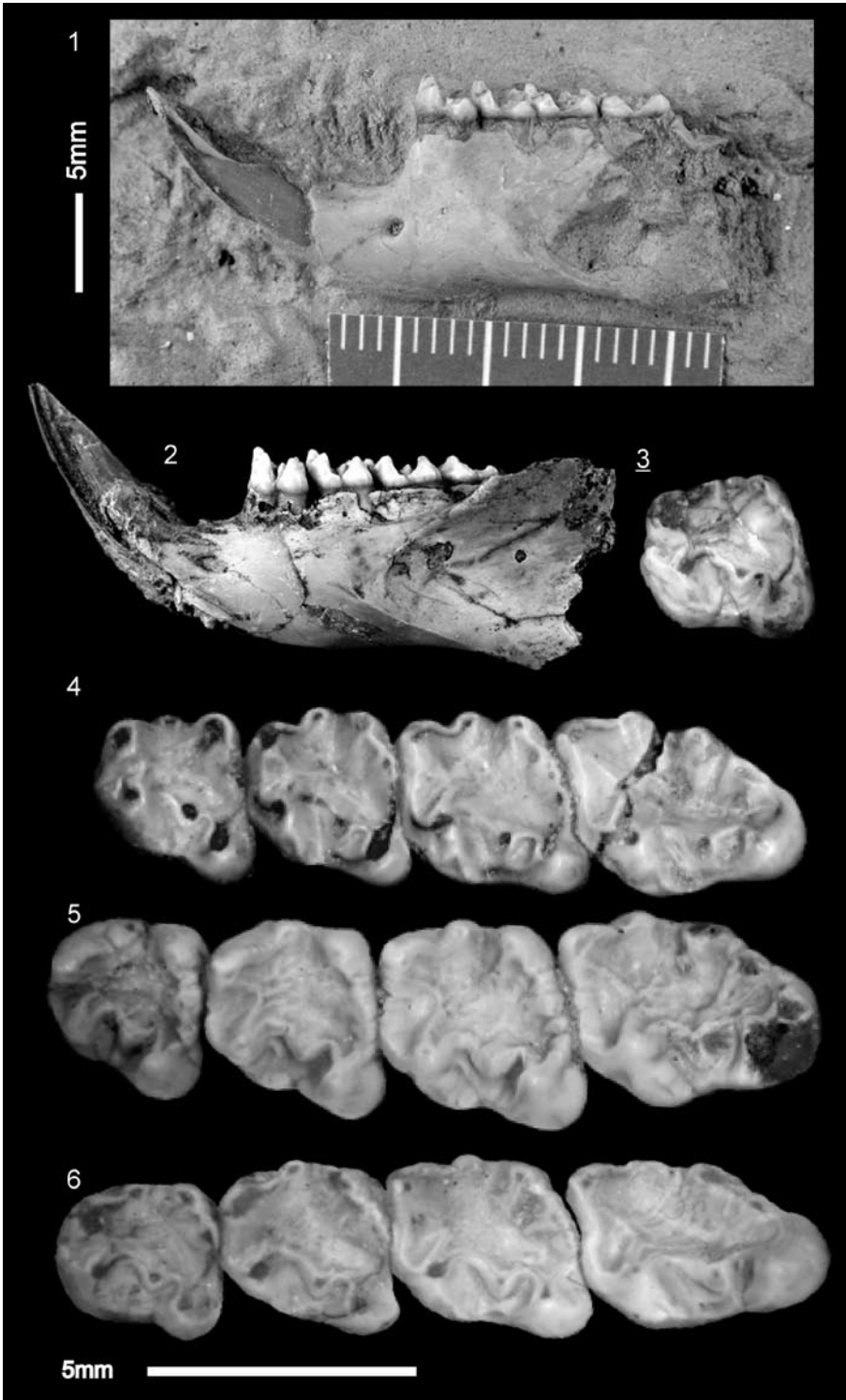
R o o t   n u m b e r s   a n d   p o s i t i o n s : The p4 has two roots, one in anterior and one in posterior position. P3 has one root, whereas P4 and M1-3 have three roots, one lingual and two labial ones.

D i s c u s s i o n : Descriptions of skulls and mandibles in more detail and comparisons to extant flying squirrels will be subject of a different paper. As outlined above, the genus *Albanensia* comprises three species and one subspecies. *A. sansaniensis* is oldest (Middle Miocene; MN6) and smaller than *A. albanensis* (Middle Miocene; MN7+8). *A. albanensis quiricensis* (Middle Miocene; MN7+8) and *A. grimmi* (Late Miocene; MN9-10) are larger and younger. In their study of the flying squirrels from Hammerschmiede in Germany, MAYR & FAHLBUSCH (1975) reported that the morphology of the lower molars from Hammerschmiede is almost identical with the type material of *Albanensia grimmi* (BLACK, 1966) from Marktl in Germany (MN9) and with the type material of *A. albanensis quiricensis* from San Quierze de Galliners in Spain (MN7+8). Consequently they considered *A. grimmi* to be synonym of *A. albanensis quiricensis*, and attributed the Hammerschmiede specimens to *A. albanensis quiricensis*.

However, the type materials of *A. albanensis quiricensis* and *A. grimmi* are very poor because no upper dentition is present in the type series, and the specific variability is unknown. Accordingly, the identity and synonymy remains questionable. We therefore treat *A. albanensis quiricensis* and *A. grimmi* as separate taxa. For the time being, the type material from Marktl (MN9), the specimens from Hammerschmiede (MN9) and the rich *Albanensia*-material from the Late Miocene (MN9-10) of Austria (DAXNER-HÖCK 2004) and Rudabanya (MN9) in Hungary (KRETZOI & FEJFAR 2004) are referred to *A. grimmi*.

Albanensia from St. Stefan resembles *A. albanensis*, and differs from *A. grimmi* and *A. albanensis quiricensis* by: the smaller dimensions, the lower and less crenulated loph(id)s and con(id)s, the smaller p4, the longer m3 with a continuous posterolophid and a small or absent hypoconulid. The maxillary teeth are also very similar to those of *A. albanensis* from La Grive and Anwil (ENGESSER 1972). They differ significantly by the following characters from the respective teeth (P4, M1, M3) of *A. grimmi* from Hammerschmiede (MAYR & FAHLBUSCH 1975: Taf. 8/1-3), Götzendorf, Richardhof-Golfplatz and Richardhof-Wald (DAXNER-HÖCK 2004: Pl.1/1-9) and Rudabánya (KRETZOI & FEJFAR 2005: text-fig. 10/1-18, Pl. 2/1-5): the significantly smaller P4, the straight (not zigzag-shaped) pro-

◄ Fig. 5. *Albanensia albanensis* (MAJOR,1893) from St. Stefan, Gratkorn Basin, Styria; Middle Miocene (MN7+8).

5/1	left mandible with complete tooth-row; labial; LMJ 204.007
5/2	left mandible with complete tooth-row; labial; LMJ 204.008
5/3	right p4; LMJ 204.011
5/4	left p4-m3; LMJ 204.007
5/5	left p4-m3; LMJ 204.008
5/6	left p4-m3; LMJ 204.011

toloph and metaloph, the absent or very small protoconule on M1-3, the less crenulated enamel, and by the presence of a small hypocone.

Some European occurrences of *A. albanensis* are: La Grive M (France: Mein 1970; MN7+8), La Grive L7 (France: Mein & Ginsburg 2002), Anwil (Switzerland: Engesser 1972; MN7+8), Opole (Poland: Mein 1970, Kowalski 1967: pl. 2, fig. 1-2; MN7+8).

The stratigraphic range of *A. albanensis* is Middle Miocene (MN7+8).

<div align="center">

Family Gliridae Muirhead, 1819

Subfamily Glirinae Thomas, 1897

Genus *Muscardinus* Kaup, 1829

</div>

European fossil species – type localities and stratigraphic correlations:

M. sansaniensis (Lartet, 1851) – Sansan (France; Middle Miocene /MN6)

M. thaleri Bruijn de, 1966 – Manchones (Spain; Middle Miocene / MN6)

M. hispanicus Bruijn de, 1966 – Pedregueras 2C (Spain; Late Miocene / MN9) (= *M. crusafonti* Hartenberger, 1966)

M. topachevskii Nesin & Kowalski, 1997 – Grytsiv (Ukraine; Late Miocene / MN9)

M. vallesiensis Hartenberger, 1966 – Can Llobateres (Spain; Late Miocene / MN9)

M. heinzi Aguilar, 1981/1982 – Montredon (France; Late Miocene / MN10)

M. pliocaenicus austriacus Bachmayer & Wilson, 1970 – Kohfidisch (Austria; Late Miocene / MN11)

M. davidi Hugueney & Mein, 1965 – Lissieu (France – Late Miocene / MN13)

M. vireti Hugueney & Mein, 1965 – Lissieu (France – Late Miocene / MN13)

M. pliocaenicus Kowalski, 1963 – Weze (Poland – Pliocene / MN15)

M. cyclopeus Agusti, Moyá-Solá & Pons Moyá, 1982 – Cala es Pou (Spain – Pleistocene)

M. dacicus Kormos, 1930 – Püspökfürdö (Hungary – Pleistocene)

<div align="center">

***Muscardinus* aff. *sansaniensis* (Lartet, 1851)**
fig. 6/1-3, tab. 4

</div>

Material: 1 right M1 (LMJ 207.304), 1 right M2 (LMJ 207.305), 1 left m2 (LMJ 207.306)

D e s c r i p t i o n : The molars have a flat occlusal surface and the typical *Muscardinus* pattern. The ridges of upper teeth are slightly tilted backwards, the ridges of lower molars are slightly tilted forwards. This is a small-sized species of *Muscardinus* with particularly short M1 and wide M2/m2 and many ridges in M2. In order to facilitate the description, the ridges have been numbered from anterior towards posterior.

M1 (fig. 6/1) is short, not as wide as M2/m2. There are 8 ridges (five long transverse ridges, three short ridges). The 1st, 2nd, 5th, 7th and 8th ridges are long (5th ridge damaged in its lingual part), the 2nd, 3rd and 6th ridges are short and in labial position. There are lingual connections of the 2nd, 7th, (? 5th) ridges to the short endoloph.

M2 (fig. 6/2) is the widest tooth. There are 10 ridges (seven long transversal ridges, three short accessory ridges). The 1st, 3rd, 4th, 5th, 7th, 9th, 10th ridges are long. The 2nd ridge is short, in lingual position. The 6th ridge is short, in labial position. The 8th ridge is short, in labial and lingual position. There are lingual connections of ridges to the endoloph.

m2 (fig. 6/3) is damaged in its postero-labial corner. There are 7 ridges, all slightly convex in anterior direction. The 1st, 3rd and 5th ridges are long (6th, 7th ridge fragmentary in their labial parts). The 2nd and 4th accessory ridges are in lingual position. There is a labial connection of the 1st and 3rd ridge.

Root numbers and positions: The M1-2 have three roots, one lingual and two labial ones. The m2 has two roots, one in anterior and one in posterior position.

D i s c u s s i o n : *M.* aff. *sansaniensis* from St. Stefan is a small-sized *Muscardinus* species. The wide and short M1, the wide M2/m2, the trapezoidal outline of m2, the many ridges of M2, the root numbers (3 roots of M1-2, 2 roots of m2) and the tooth size distinguish the St. Stefan specimens from almost all *Muscardinus*-species of the Late Miocene to the present. However, these dental characters and the identical root numbers indicate a close relationship to three *Muscardinus* species, i.e. *M. thaleri*, *M. sansaniensis* and *M. vallesiensis*.

In Spain, *M. thaleri* – the smallest and most primitive species – developed towards *M. hispanicus* (DAAMS, 1985). These two small-sized species, *M. thaleri* and *M. hispanicus*, clearly differ from the *M. sansaniensis*-group by tooth proportions (rather long and narrow molars; m2 with rectangular outline). *M. hispanicus* ranges from the late Middle Miocene to the Late Miocene in Spain, and occurred in the Late Miocene of Central Europe. In both regions the species sporadically co-occurs with *M. vallesiensis*.

Tab. 4. Measurements (in mm).

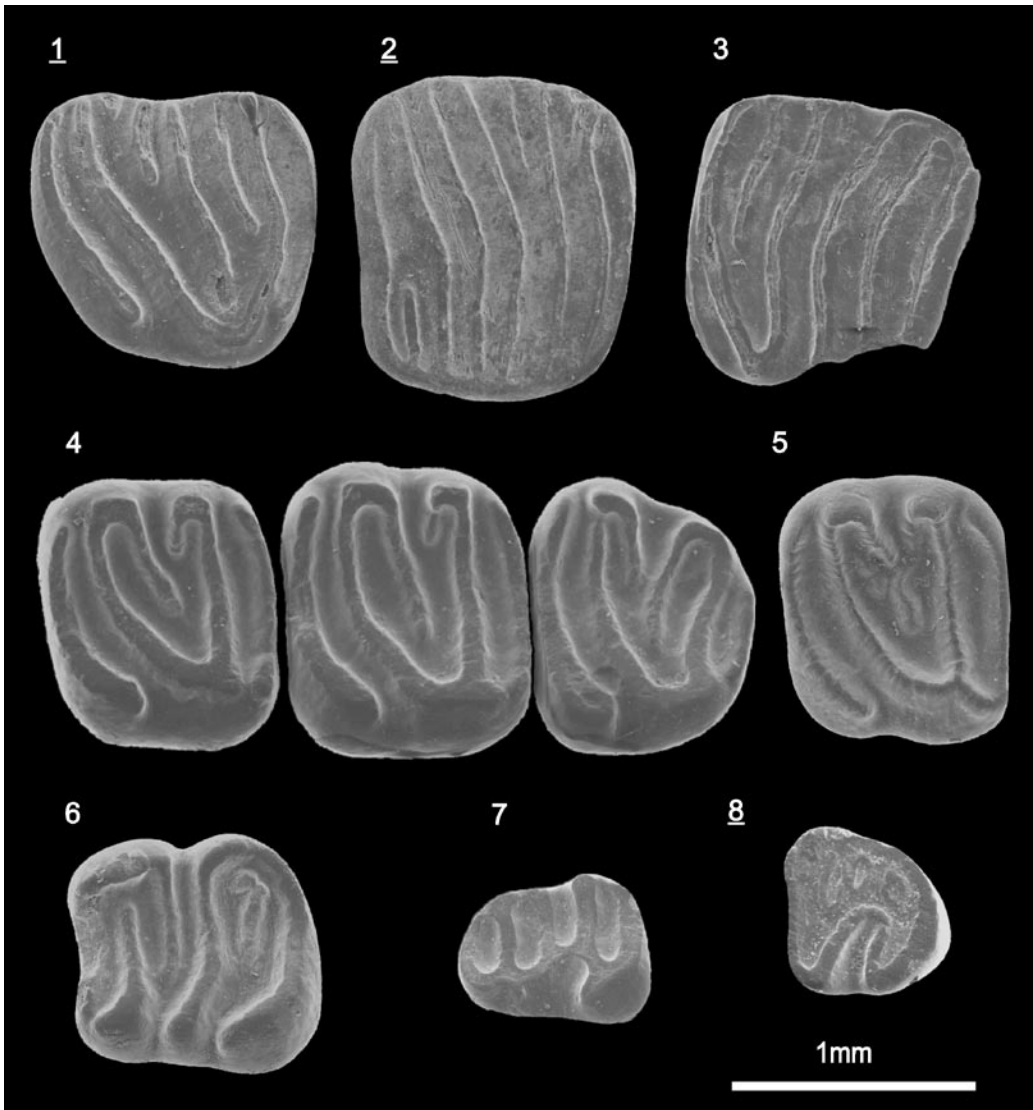|	fig.	length	width
M1 right	6/1	1.26	1.17
M2 right	6/2	1.26	1.38
m2 left	6/3	1.24	1.21

Fig. 6. Gliridae and Eomyidae from St. Stefan, Gratkorn Basin, Styria; Middle Miocene (MN7+8).

6/1   *Muscardinus* aff. *sansaniensis* (LARTET, 1851); right M1; LMJ 207.304
6/2   *Muscardinus* aff. *sansaniensis* (LARTET, 1851); right M2; LMJ 207.305
6/3   *Muscardinus* aff. *sansaniensis* (LARTET, 1851); left m2; LMJ 207.306
6/4   *Miodyromys* sp.; left M1-3; LMJ 207.307
6/5   *Miodyromys* sp.; left M1; LMJ 207.308
6/6   *Miodyromys* sp.; left m1; LMJ 207.309
6/7   *Keramidomys* sp.; left d4; LMJ 207.310
6/8   *Keramidomys* sp.; right m3; LMJ 207.311

The second evolutionary lineage developed throughout the Middle Miocene to Late Miocene, i.e. the *M. sansaniensis – M.* aff. *sansaniensis – M.* cf. *vallesiensis – M. vallesiensis* lineage. *M. sansaniensis* (from the type locality Sansan; MN6) and from Schönenberg, Eitensheim in Germany (MN5-6) is smaller than *M.* aff. *sansaniensis* (MN7+8) from St. Stefan. These specimens are also slightly larger than the corresponding teeth of *M.* aff. *sansaniensis* from La Grive (MN7+8), Anwil and Grat (MN7+8), but the M1 is equal in size with the fragmentary M1 from Nebelbergweg (KÄLIN & ENGESSER 2001; Abb. 25). As opposed to the above occurrences, *M.* aff. *sansaniensis* from Giggenhausen and Kleineisenbach (MN7+8) have higher root numbers (3 roots on m2), which could be interpreted as an advanced character.

Occurrences of *Muscardinus* cf. *vallesiensis* have been reported from Castell de Barbera (Spain: upper MN7+8). This species is evidently larger and the number of roots is higher (4 roots of m2) than of *M.* aff. *sansaniensis*. However, its similar dental pattern, such as the wide and short M1, the wide M2/m2, the trapezoidal outline of m2 and the high number of ridges of M2, indicate the probable relationship with the *M. sansaniensis – vallesiensis* – lineage. Finally, *M. vallesiensis* is known from the Vallesian: Can Llobateres (Spain: HARTENBERGER 1966; MN9), Richardhof-Golfplatz, Götzendorf and Richardhof-Wald (Austria: DAXNER-HÖCK & HÖCK 2009; MN9-10) and Rudabánya (Hungary: DAXNER-HÖCK 2005; MN9).

Some European occurrences of *M. sansaniensis / M.* aff. *sansaniensis*:

M. sansaniensis: Sansan (France: BAUDELOT 1965; MN6), Schönenberg and Eitensheim (Germany: MAYR 1979; MN5-6).

M. aff. *sansaniensis*: Anwil (Switzerland: ENGESSER 1972; MN7+8), Grat (Switzerland: MN7+8), Nebelbergweg (Switzerland: KÄLIN & ENGESSER 2001; MN9 / in my opinion MN7+8), La Grive M (France: MN7+8), Giggenhausen and Kleineisenbach (Germany: MAYR 1979; MN7+8).

The stratigraphic range of *M. sansaniensis* is early Middle Miocene (MN5-6), whereas the more advanced *M.* aff. *sansaniensis* occurrences are typical of the late Middle Miocene (MN7+8).

Subfamily Myomiminae DAAMS, 1981

Genus *Miodyromys* KRETZOI, 1943

European fossil species – type localities and stratigraphic correlations:

M. hugueneyae AGUSTI & ARBIOL, 1989 – Fraga 11 (Spain; Late Oligocene /MP30)

M. prosper (THALER, 1966) – Bouzigues (France; Early Miocene / MN2)

M. praecox Wu, 1993 – Stubersheim 3 (Germany; Early Miocene / MN3)

M. biradiculus Mayr, 1979 – Wintershof-West (Germany; Early Miocene / MN3)

M. vagus Mayr, 1979 – Hesselohe (Germany; Middle Miocene / MN5)

M. aegercii (Baudelot, 1972) – Sansan (France, Middle Miocene / MN6)

M. hamadryas (Major, 1899)* – La Grive (France, Middle Miocene /MN7+8) (see Engesser 1972; 228)

M. grycivensis Nesin & Kowalski, 1997 – Grytsiv (Ukraine, Late Miocene / MN9)

* type species

Miodyromys sp.
fig. 6/4-6, tab. 5

Material: 1 left maxilla-fragment with M1-3 ♦ (LMJ 207.307), 1 left M1 (LMJ 207.308), 1 left m1/2 (LMJ 207.309)

Description: The molars are of small to medium size. They have concave occlusal surfaces, few ridges and shallow flat valleys between ridges. The upper molars (M1-3) are almost square in outline, with M3 being narrowest in its posterior part. They have four main ridges (antero-, proto-, meta- and posteroloph). There is a lingual connection between the protoloph and metaloph, and labial connections to the paracone and meta-cone, respectively. The labial and lingual ends of the anteroloph are free. The posteroloph has a free labial end. Lingually it is connected to the short endoloph (M1, fig. 6/5), or the connection is constricted (M1-3, fig. 6/4). The anterior centrolophs are longer than posterior centrolophs in M1-2; in M3 the anterior centroloph is shorter. The centrolophs of a second M1 have an irregular shape with a Y-shaped connection, and a weak anterior extra ridge is present.

The m1/2 (fig. 6/6) is rectangular in outline and has four main ridges (antero-, meta-, meso- and posterolophid). The anterolophid is lingually connected to the metaconid; its labial end is free. The metalophid has free labial and lingual ends. The mesolophid–pos-

Tab. 5. Measurements (in mm).

	fig.	length	width
M1 left ♦	6/4	1.02	1.14
M2 left ♦	6/4	1.05	1.26
M1 left	6/5	1.05	1.22
M3 left ♦	6/4	0.95	1.20
m1/2 left	6/6	1.14	1.05

terolophid connection is lingual. The centrolophid is of medium length and is connected to the metaconid. A short posterior extra ridge is present.

Root numbers and positions: The upper molars have three roots, one lingual and two labial ones. The m2 has two roots, one in anterior and one in posterior position.

Discussion: The validity of the genus *Miodyromys* is still under discussion, and DAAMS & DE BRUIJN (1995: 21) refer to a possible synonymy of *Miodyromys*, *Prodryomys* MAYR, 1979, *Pseudodryomys* DE BRUIN, 1966 and *Peridyromys* STEHLIN & SCHAUB, 1951 based on the very similar dental pattern. Medium-sized teeth with two centrolophs in upper molars and one or more extra ridges in both upper and lower molars are attributed to *Miodyromys* (DAAMS & DE BRUIJN 1995: 20-21). However, these dental characters are also typical for *Myomimus* OGNEV, 1924, a small dormouse known to range from the Late Miocene to the present.

The St. Stefan specimens are clearly smaller and have a simpler dental pattern (i.e. fewer accessorial ridges) than *M. aegercii*, which is the most common *Miodyromys* species of the Middle Miocene. *M. grycivensis* (Grytsiv) and *M. hamadryas* (measurements from La Grive and Anwil in ENGESSER 1972; Diagramm 28) are smaller than *M aegercii*. *M. grycivensis* differs from the St. Stefan specimens by a more complex dental pattern and higher root numbers (m1 with three instead of two roots). *M. hamadryas* is more similar in dental pattern, but differs in root numbers (m1 with three roots). However, the material from St. Stefan is too scarce for definitive species identification.

Family Eomyidae DEPERET & DOUXAMI, 1902

Genus *Keramidomys* HARTENBERGER, 1966

European fossil species – type localities and stratigraphic correlations:

K. thaleri HUGUENEY & MEIN, 1968 – Vieux Collonges (France; Early-Middle Miocene / MN4-5)

K. carpathicus (SCHAUB & ZAPFE, 1953) – Neudorf Spalte (Slowakia; Middle Miocene / MN6)

K. reductus BOLLIGER, 1992 – Grat (Switzerland; Middle Miocene / MN7+8)

K. mohleri ENGESSER, 1972 – Anwil (Switzerland, Middle Miocene / MN7+8

K. anwilensis ENGESSER, 1972 – Anwil (Switzerland, Middle Miocene / MN7+8)

K. ermannorum DAXNER-HÖCK & HÖCK, 2009 – Richardhof-Golfplatz (Austria, Late Miocene / MN9)

K. pertesunatoi HARTENBERGER, 1966* – Can Llobateres (Spain, Late Miocene / MN9)

* type species

Tab. 6. Measurements (in mm).

	fig.	length	width
d4 left	6/7	0.98	0.64
m3 right	6/8	0.72	0.72

Keramidomys sp.
figs 6/7-8, tab. 6

M a t e r i a l : 1 left d4/p4 (LMJ 207.310), 1 right m3 (LMJ 207.311).

D e s c r i p t i o n : The teeth are characterized by a lophodont pattern.

d4 (fig. 6/7) has five distinct lophids and four transversaly orientated synclinids (numbered from anterior towards posterior). 1st, 2nd and 4th synclinids are closed. The sinusid points backwards.

m3 (fig. 6/8) is strongly worn. Five lophids with lingual connections can be recognized. All four synclinids are closed, the 1st being the smallest. The sinusid points backwards.

Root numbers and positions: The d4 has two roots, one in anterior and one in posterior position. The m3 has three roots, two anterior ones and one posterior root.

D i s c u s s i o n : The pronounced lophodonty of the molars from St. Stefan indicates close morphological relations with three *Keramidomys* species, i.e. *K. thaleri*, *K. mohleri* and *K. ermanorum*. The tooth sizes are larger than those of *K. thaleri*, but within the size range of *K. mohleri* and *K. ermannorum*. Other species (*K. reductus*, *K. anwilensis* and *K. pertesunatoi*) have strongly reduced dental characters and therefore can be excluded from comparisons.

The specimens are described here as *Keramidomys* sp. because the small amount of material does not allow reliable species identification.

Biostratigraphy (fig. 7)

In the present study, seven taxa are described from the locality St. Stefan:

Sciuridae

      Spermophilinus bredai

      Blackia sp.

      Forsythia gaudryi

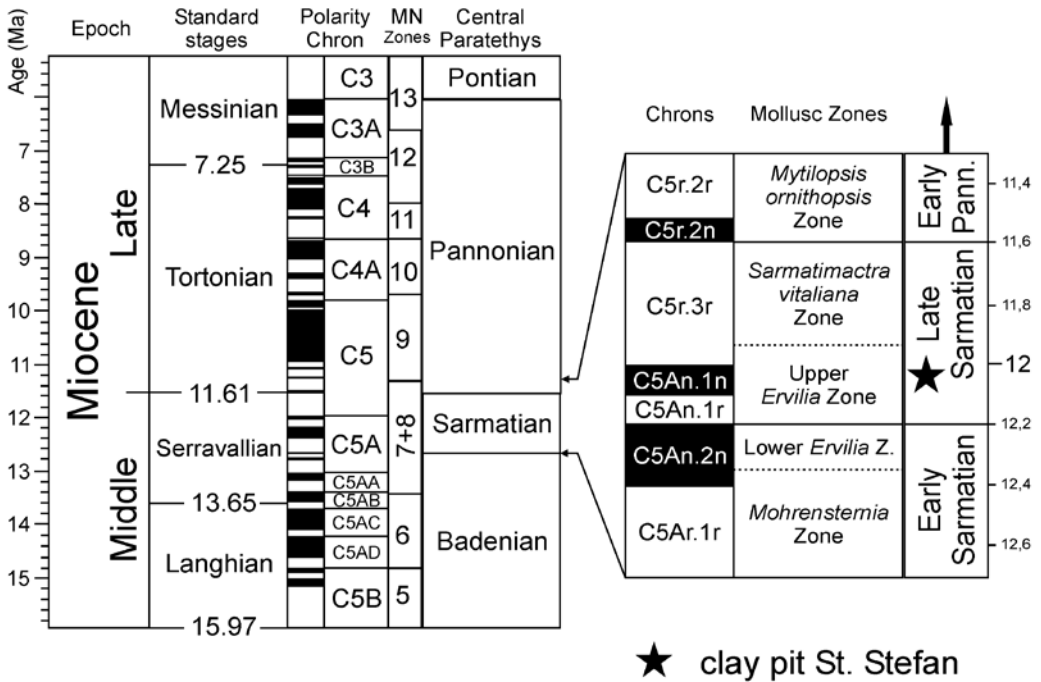   *Albanensia albanensis*

Fig. 7. Stratigraphy of the Middle and Late Miocene (especially of the Sarmatian and Early Pannonian; Styran Basin). Modified after HARZHAUSER et al. (2008: fig. 2; based on HARZHAUSER & PILLER 2004 and LOURENS et al. 2004).

Gliridae

>   *Muscardinus* aff. *sansaniensis*

>   *Miodyromys* sp.

Eomyidae

>   *Keramidomys* sp.

Three taxa cannot be determined at the species level because of the scarce material. However, three species are highly significant for the Middle Miocene of Central Europe and France. These biostratigraphic markers are: *Forsythia gaudryi*, *Albanensia albanensis* and *Muscardinus* aff. *sansaniensis* (late Middle Miocene; MN7+8). The co-occurences of these three species are rare, i.e. La Grive M, La Grive L7 (France; MN7+8), Anwil (Switzerland; MN7+8) and St. Stefan (Austria; MN7+8). One of the rare occurrences of *Forsythia gaudryi* is Giggenhausen (in Germany; MN7+8). *Muscardinus* aff. *sansaniensis* occurs also in Giggenhausen and Kleineisenbach (in Germany; MN7+8). As outlined above, *Muscardinus* aff. *sansaniensis* derived from *Muscardinus sansaniensis* (range MN5-6) and is thought to be the ancestor of *Muscardinus vallesiensis* (MN9).

The specimens from Giggenhausen and Kleineisenbach are highly advanced and are most probably the youngest among the late Middle Miocene occurrences of *Muscardinus* aff. *sansaniensis*.

St. Stefan seems to be younger than La Grive M (France) and Anwil and Grat (Switzerland). It is apparently most similar in age with Giggenhausen and Kleineisenbach (Germany). Assemblages younger than St. Stefan – ranging from the latest Middle Miocene to the early Late Miocene (latest MN7+8 to early MN9) – differ significantly in their rodent composition, e.g. *Albanensia albanensis* is replaced by *Albanensia grimmi*, and *Muscardinus* aff. *sansaniensis* is replaced by *Muscardinus cf. vallesiensis* and finally by *Muscardinus vallesiensis*. This biostratigraphic pattern can be traced in Central Europe, France (Mein & Ginsburg 2002) and parts of Spain (Casanovas-Vilar 2007).

Overall, there is a good biostratigraphic correlation of small and large mammals (late MN7+8) and of the late Sarmatian terrestrial gastropod fauna (Harzhauser et al. 2008) from the identical paleosoil horizon of St. Stefan.

Lithology and Palaeoecology

The fauna originates from a ca 0.5-m-thick paleosoil, underlain by fluvial sands and gravels and topped by ca 15-m-thick limnic pelites (Gross, 2008). Sedimentological data as well as the gastropod (Harzhauser et al. 2008) and vertebrate assemblages suggest an alluvial fan/braided river landscape (Gross et al. 2009). Root traces, ferruginous concretions and bioturbation indicate the development of a paleosoil. Woodlands with moist soil and nearby limestone-screes and sun-exposed open areas would be the favourable environments of the recorded terrestrial gastropods (Harzhauser et al. 2008).

The investigated rodents, however, are typical for forested environments, i.e. the flying squirrels *Forsythia*, *Blackia* and *Albanensia*, the dormice *Muscardinus* and *Miodyromys* and the eomyid *Keramidomys*. All extant flying squirrels are arboreal and nocturnal. The flying squirrels from St. Stefan comprise three different body sizes: the large *Albanensia albanensis* is similar to the living Red Giant Flying squirrel, *Forsythia gaudryi* is of middle size and *Blackia* sp. is smallest. More striking is the excellent preservation of *Albanensia*, indicating that long transport can be excluded. It lived apparently in the forested floodplains of the Gratkorn Basin. These environments were also inhabited by the glirids *Muscardinus* aff. *sansaniensis* and *Miodyromys* sp. and by the small eomyid *Keramidomys* sp. From living glirids we know that their preferred environments are forests with deciduous trees, thickets and dense undergrowth or open woodlands with rocky substrate. Many dormice – such as the forest-dwelling *Muscardinus* – are squirrel like in their habits. They live arboreally, are active at night and sleep in hollow trees during the day. Contrary to flying squirrels, all living glirids hibernate and can survive unfavourable climatic conditions in winter.

The Gratkorn Basin apparently provided both forested environments with high trees and dense undergrowth, as favoured by the forest dwellers, as well as sun-exposed open areas

with rocky ground and low vegetation. The latter sites were inhabited by the ground squirrel *Spermophilinus bredai* as well as by terrestrial gastropods as described by HARZHAUSER et al. (2008). A diverse assemblage of other ground-dwelling rodents from the St. Stefan assemblage, i.e. the cricetids, is under investigation (PRIETO in progress).

Conclusions

At the beginning of the field investigations stratigraphy of the clay pit St. Stefan and the age of the fossils was not clear. On the basis of the first findings of large mammals, e.g. *Listriodon*, *Deinotherium*, *Palaeomeryx*, *Anchitherium*, but no *Hippotherium*, a Middle Miocene age (MN7+8; Sarmatian or earliest Pannonian) was assumed by the author. The rodents show that biostratigraphic data of large and small mammals are in full agreement. Moreover, the late Middle Miocene age of the St. Stefan fauna was confirmed by the terrestrial gastropods, which turned out to be indicative for the Sarmatian stage (HARZHAUSER et al. 2008: tab.1). A correlation with the beginning of the Late Sarmatian and Chron C5An1n around 12 Ma is postulated by HARZHAUSER et al. (2008: fig. 2) based on geological data and on an integrated stratigraphy of the Gratkorn area.

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