

Complement to the study of the pikas (Lagomorpha, Ochotonidae) from the Middle Miocene of Gratkorn, Austria

Chiara Angelone · Jérôme Prieto · Martin Gross

Received: 1 October 2013 / Revised: 27 November 2013 / Accepted: 16 December 2013 / Published online: 24 January 2014
© Senckenberg Gesellschaft für Naturforschung and Springer-Verlag Berlin Heidelberg 2014

Abstract An update about the Middle Miocene ochotonids (Lagomorpha, Mammalia) from Gratkorn, Austria, is presented. The presence of *Prolagus oeningensis* (König, 1825), previously attested based on the description of two well-preserved lower mandibles is confirmed, and complementary material is added. In addition, isolated teeth of a rooted ochtonid allow the recognition of the presence of cf. *Eurolagus fontannesii* (Depéret, 1887). A third ochtonid (Ochotonidae indet.), characterised by large-sized and ever-growing teeth, is another new element of the Gratkorn assemblage, although it cannot be taxonomically assigned, even at the genus level, because of the lack of diagnostic material. The fossil community is discussed in the central and eastern European context during Sarmatian times.

Keywords Styrian Basin · Late Middle Miocene · Sarmatian s. str · *Prolagus* · *Eurolagus* · Ochotonidae

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

C. Angelone
Grup de recerca de Faunes del Neogen i Quaternari, Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICP, Campus de la UAB s/n, 08193 Cerdanyola del Vallès, Barcelona, Spain
e-mail: chiara.angelone@icp.cat

J. Prieto (✉)
Department of Earth- and Environmental Science, Palaeontology, Ludwig-Maximilians-University Munich, Richard-Wagner-Str. 10, D-80333 Munich, Germany
e-mail: j.prieto@lrz.uni-muenchen.de

M. Gross
Department for Geology and Palaeontology, Universalmuseum Joanneum, Weinzöttlstrasse 16, 8045 Graz, Austria
e-mail: martin.gross@museum-joanneum.at

Abbreviations

AA	Partial width
L	Length
Ltrig	Trigonid length
LJ	Lower jaw
NAFB	North Alpine Foreland Basin
PH	Hypoflexus depth
TH	Distal hypercone length
UJ	Upper jaw
W	Width
Wtrig	Trigonid width
Wtal	Talonid width

Introduction

The palaeofauna from Gratkorn is one of the richest and most complete of the European late Middle Miocene (Gross et al. 2011). The Austrian locality is situated east of the city of Gratkorn, at the eastern part of the Gratkorn Basin (satellite basin of the Styrian Basin), and derives from a paleosol which has yielded some well-preserved (jaws and skulls), and sometimes semi-articulated small mammal remains (e.g. Prieto et al. 2010). Prieto et al. (2012) reported two mandibles of the pika *Prolagus oeningensis*. We analyse here some new ochotonid findings that increase the knowledge of the Gratkorn assemblage in their central and eastern European context.

Materials and methods

The fossils from Gratkorn are stored at the Universalmuseum Joanneum in Graz (Geology&Palaeontology, abbreviated as UMJGP).

The dental nomenclature and the measurements follow Angelone and Sesé (2009) implemented from López Martínez (1989) and Angelone (2007). The width of the hypoconulid (Whyp) of the m2 is added. Measurements (mm) were taken digitally with a Leica M165FC binocular microscope, using a Leica DFC480 camera.

Systematic palaeontology

Order Lagomorpha Brandt, 1855
Family Ochotonidae Thomas, 1897

Remarks: Hoffman and Smith (2005) in Wilson and Reeder (2005) database of extant mammal taxonomy accept the existence of the family Prolagidae, erected as a subfamily by Gureev (1964) and elevated to the family rank by Erbajeva (1988; see also Erbajeva et al. 2011). However, the assignment of *Prolagus* to the (sub)family Prolagid(n)ae is not widely followed in the literature, especially in western and central Europe.

Bendukidze et al. (2009: 347) refrain from using this subdivision, arguing that the use of the phylogenetic approach may be too dependent on the influence of new findings, and thus may lead to instability of the nomenclature. Dawson (2008: 295) states that this further subdivision contributed “neither to phylogenetic nor to palaeobiogeographical understanding of the order”.

López-Martínez (2012: 124) argues that the distinction between Prolagidae and Ochotonidae “is found in the lack of a m3, replaced by a trilobed m2. This change is gradual, and well documented in the succession *Piezodus* and *Prolagus* observed between the late Oligocene and the earliest Miocene. Other cranial and dental characteristics indicate a close relationship of the lineage *Piezodus*-*Prolagus* and other Ochotonidae”. Consequently, she assigns the genus *Prolagus* to the family Ochotonidae.

Here, we recognise that (1) the descendants of *Piezodus*, the genera *Prolagus* and *Ptychoprolagus*, are indeed very peculiar and show features that distinguish them from the rest of the ochotonids; and (2) *Prolagus* has a long, independent, complex evolution and is very diverse. However, in our opinion, including *Prolagus* and *Ptychoprolagus* or not (according to us, there is no reason that these have to be two separated genera) in a separate family or subfamily does not have a consequence in the “practical” applications of taxonomy (e.g. biochronology). Thus, to avoid complication of the taxonomy, we prefer to follow the western and central European nomenclatorial “custom”, also followed by most of the revisions dealing with *Prolagus*, and place *Prolagus* in the family Ochotonidae.

Genus *Prolagus* Pomel, 1853
Prolagus oeningensis (König, 1825)

Figures 1, 2a–m, 3a.

2011 *Prolagus oeningensis*. Gross et al., table 1

2012 *Prolagus oeningensis*. Prieto et al., pp. 113–115

Type locality: Öhningen (Germany), Middle Miocene.

Geographical and temporal distribution: *P. oeningensis* is a common element of the Early Miocene to the Middle Miocene and probably of the earliest Late Miocene fossil assemblages of the Iberian Peninsula, central Europe, eastern Europe and westernmost Asia (Angelone and Sesé 2009 and references therein).

Material and measurements: 2 left lower jaws with p3–m2 (UMJGP 204000, 204001) presented by Prieto et al. (2012) and additional material as detailed in Table 1 and Fig. 1.

Description of additional material

P2: the mesial hyperloph is absent; the protocone is slightly higher than the other cones, followed by lagicone and postcone; para- and mesoflexus are deep; the lagicone has a bottleneck distal end; the paraflexus is enlarged, almost bifurcated at its distal end.

P3: mesial hypercone less protruding lingually than distal one; mesial hyperloph without enamel hiatus; lagicone/lagiloph connection marked by a concavity; the lagiloph reaches the labial edge of the tooth; quadrangular postcone.

P4: thin mesial hypercone; V-shaped and then U-shaped hypoflexus proceeding from the lingual to the labial side, entering for about 50 % of the tooth width (AA); very long, not oblique parafossette, covering the mesofossette.

M1–2: very long hypoflexus; J-shaped fossettes, very large on M1, smaller on M2.

d3: very worn specimens, the three lobes are connected; relatively deep centroflexid; no accessory cusps.

p3: diamond-shaped anteroconid, in rather central position, smaller than the quadrangular metaconid; proto- and metaisthmus very long; U-shaped, straight to low inclined mesoflexus; developed entoconid without enamel hiatus; quite large crochet, in central position, inclined towards the labial side, with bottleneck end; very small protocone; rather long, developed protoconulid.

Remarks: *Prolagus* from Gratkorn was classified as *P. oeningensis* by Prieto et al. (2012), and we confirm here this taxonomic assignment (cf. the overall morphology of p3 with central, diamond-shaped anteroconid, smaller than metaconid, the well-developed crochet; P2 without mesial hyperloph and with flexa of equal depth; M1 with large, J-shaped fossettes).

However, the additional material allows us to remark a high occurrence in *Prolagus* from Gratkorn of the morphological characters: (1) p3 with bottleneck crochet; and (2) P2 with distally enlarged (bifurcated) paraflexus. Such

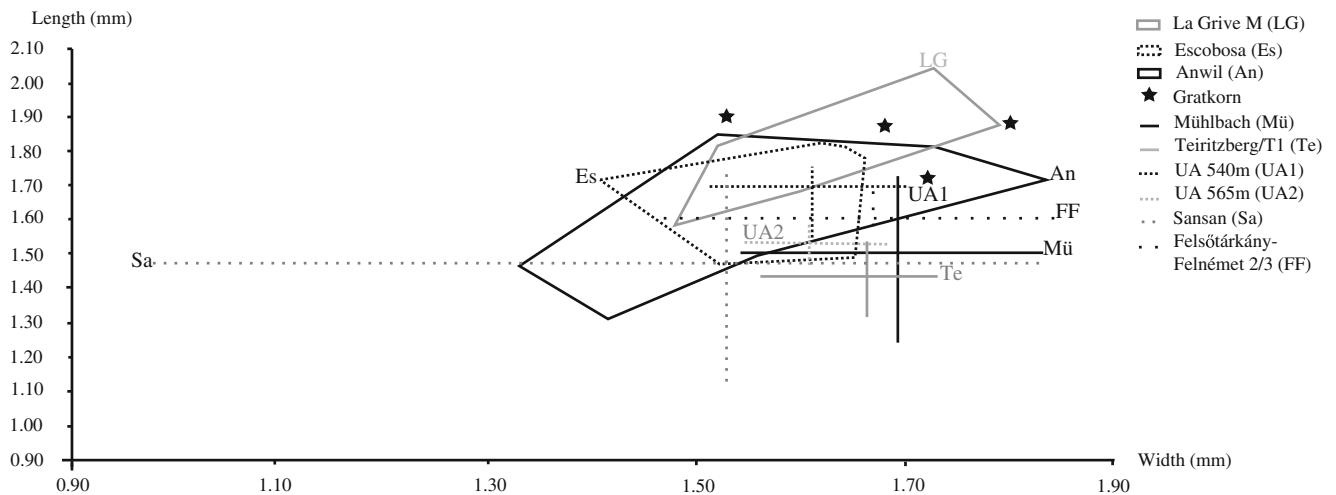


Fig. 1 Size (in mm) of *Prolagus oeningensis* (König, 1825) p3 from Gratkorn compared with those of late Middle Miocene selected European populations and with those of Austrian populations of the same species. Data of Escobosa are from Angelone and Sesé (2009), La Grive M from Angelone (unpublished data) and Prieto et al. (2012), Anwil from

Engesser (1972), Teiritzberg/T1 from Boon-Kristkoiz (1998), Mühlbach from Boon-Kristkoiz (2003), Sansan from López-Martínez (2012), Untereichen-Altenstadt from Prieto et al. (2009), Felsőtárkány-Felnémet 2/3 from Hír (2004)

characters are very frequent in the remains from Gratkorn, but can also be observed, though not common, in large populations of *P. oeningensis*; thus they do not justify taxonomic splittings.

From a dimensional point of view, the size of p3 of *Prolagus oeningensis* from Gratkorn is comparable with the coeval populations of La Grive in France and Escobosa in Spain (C. Angelone, personal database).

Genus *Eurolagus* López Martínez, 1977

Remarks: The genus *Eurolagus* has been considered since its erection as an ochotonid (López Martínez 1977, 1989; Angelone 2009a). De Bruijn in Bendukidze et al. (2009: 347) follows Martin (2004) including *Eurolagus* in the family Leporidae Fischer de Waldheim, 1817 together with *Amphilagus* and *Desmatolagus*, considering the three taxa as belonging to the same genus. Fostowicz-Frelik et al. (2012) assign *Eurolagus* to the family Palaeolagidae Dice, 1929. López Martínez (2008) considers *Eurolagus* and other European primitive lagomorphs (sensu Angelone 2009a: rooted teeth, simple p3 and hypoconulid on lower teeth) as stem lagomorphs, except for *Amphilagus* from the earliest Miocene, which is considered as an ochotonid. The reason for this choice is not explained in the text.

We follow here Angelone (2009a) in considering *Eurolagus* as an ochotonid.

cf. *Eurolagus fontannesii* (Depéret, 1887)
Figure 3b–g

2011 *Eurolagus* sp. Gross et al., table 1

Type locality: La Grive (France), Middle Miocene.

Geographical and temporal distribution: The monospecific genus *Eurolagus* was thought to be a marker of European and Anatolian MN7/8 (López Martínez 1989; Angelone 2008, 2009a and references therein). Recently, Fostowicz-Frelik et al. (2012) reconsidered the temporal distribution of *Eurolagus* (MN5–MN10). However, they included without discussion forms clearly different from *Eurolagus* (e.g. “*Amphilagus*” sp. from the MN5 of Sandelzhausen; Angelone 2009a). Based on the NOW database, Fostowicz-Frelik et al. (2012, fig. 1, p. 2) include in the genus *Eurolagus* doubtful or wrong reports (as *Eurolagus* from Can Llobateres, for a long time excluded from lists; C. Angelone, personal observation 2013). Reports of *Eurolagus fontannesii* (often indicated as *Amphilagus fontannesii*) out of Europe tend to be incorrect (e.g. Erbajeva and Filippov 1997) and, moreover, most of them are not figured. It is evident that the spatio-temporal distribution of *Eurolagus* needs a serious revision.

Material and measurements: see Table 1.

Description

All teeth are rooted.

P2: protocone and lagicone are well developed, whereas the postcone is much reduced; probably with wear, a kind of mesial hyperloph will appear; an additional, small cusp is visible under the precone.

P3: the mesial hypercone is more protruding than the distal one; the mesial hyperloph is thin and covers the lagicone; the



Fig. 2 *Prolagus oeningensis* (König, 1825) and Ochotonidae indet. From Gratkorn. **a–m** *P. oeningensis*. **n, o** Ochotonidae indet. **a** right d3 (UMJGP 210982); **b** right p3 (UMJGP 210983); **c** left p3 (UMJGP 210986); **d** right m2 (UMJGP 210994); **e** right P2 (UMJGP 210984); **f** right P3 (UMJGP 204705/3); **g** left P3 (UMJGP 210987); **h** right left P3 (UMJGP 210990); **i**

right P4 (UMJGP 210988); **j** right P4 (UMJGP 210985); **k** left upper jaw fragment with damaged P4–M2 (UMJGP 204746/2); **l** left M1 (UMJGP 210976); **m** juvenile right ?M2 (UMJGP 210977); **n** right ?M2 (UMJGP 211002); **o** left ?M2 (UMJGP 211003)

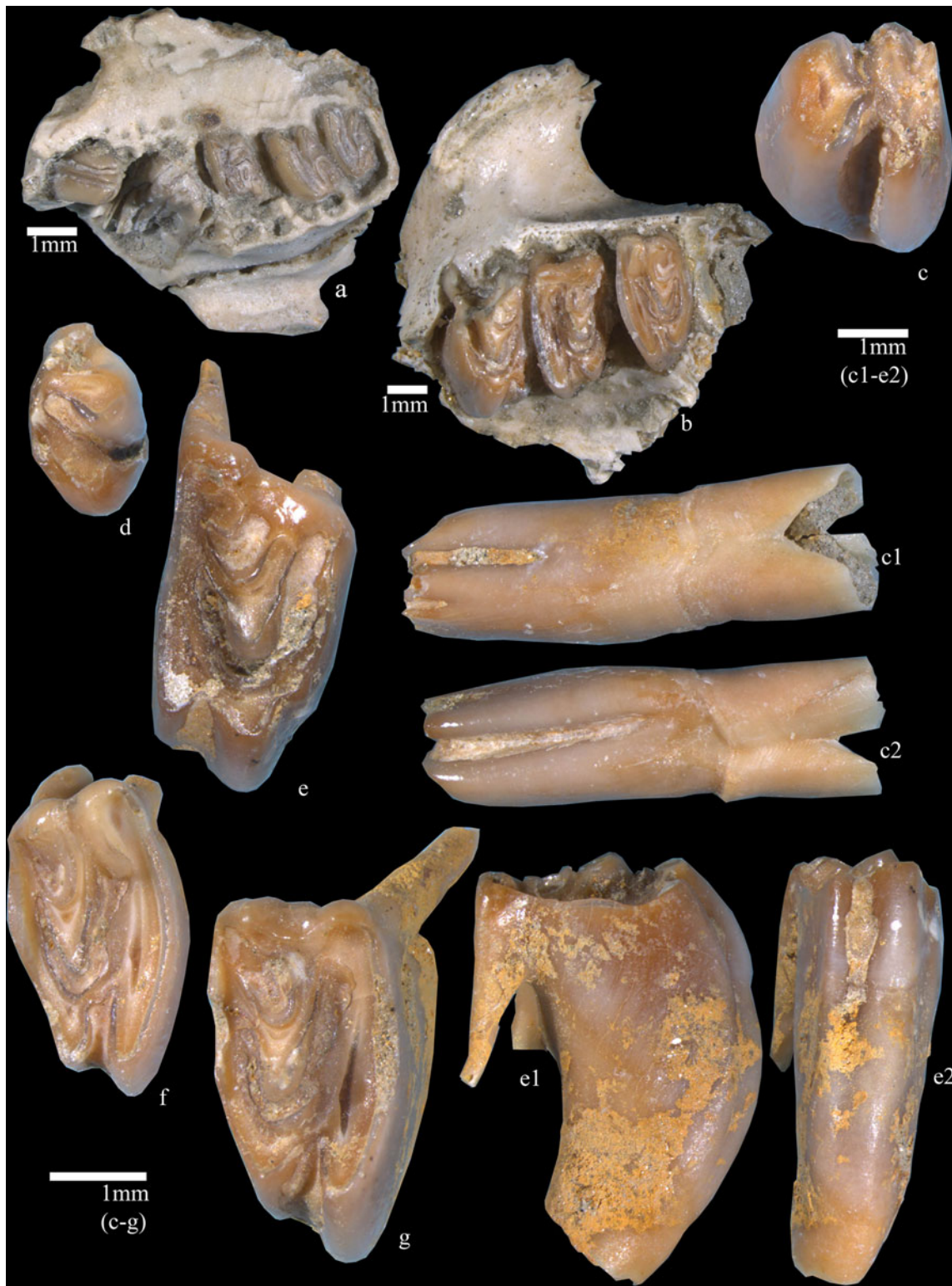


Fig. 3 *Prolagus oeningensis* (König, 1825) and cf. *Eurolagus fontannesi* (Dépéret, 1887) from Gratkom. **a** *P. oeningensis*; **b–g** cf. *E. fontannesi*. **a** right maxillary fragment with P2–M2 (UMJGP 204002/2); **b** left maxillary fragment with P3–M1 (UMJGP 204002/1); **c** left p3 (UMJGP 204023/1); **c1** labial view; **c2** lingual view; **d** right P2 (UMJGP 210999); **d1** posterior view; **d2** lingual view; **e** right P3 (UMJGP 210998); **e1** posterior view; **e2** lingual view; **f** right M1 (UMJGP 211000); **g** right P4 (UMJGP 211001)

lagiloph is well developed but does not reach the labial edge of the tooth; the flexa are closed; the postcone is bilobed.

P4–M1: the mesial hypercone is more protruding than the distal one; the flexa are closed; in M1, the hypoflexus is bifurcated.

Table 1 Material and measurements of the ochotonid remains from Gratkorn

Reference no.	Species	Specimens		L	TH or Ltrig	W or Wtrig	AA or Wtal	PH or Whyp	Figure
210975	<i>Prolagus oeningensis</i>	P4	Left	1.23	0.84	2.32	1.11	0.97	Not figured
210976	<i>Prolagus oeningensis</i>	M1	Left	1.24	0.55	2.32	0.47	1.71	Fig. 2l
204054	<i>Prolagus oeningensis</i>	LJ fragm. with p4 or m1	Left	1.44	0.74	1.64	1.45		Not figured
204705/3	<i>Prolagus oeningensis</i>	P3	Right	1.65		ca. 2.52	ca. 1.89		Fig. 2f
294746/1	<i>Prolagus oeningensis</i>	LJ fragm. with p4- fragm.m3	Right	*	*	*	*		Not figured
204746/2	<i>Prolagus oeningensis</i>	UJ fragm. With P4-M2	Left	P4 1.31 M1 ca 1.29 M2 ca 1.2	0.78 0.74 0.61	2.19 1.84 *	0.28 0.44 *	1.76 1.39 *	Fig. 2k
210977	<i>Prolagus oeningensis</i>	?M2	Right	0.86	0.42	1.45	0.46	0.96	Fig. 2m
210978	<i>Prolagus oeningensis</i>	P2	Left	0.95		1.71			Not figured
210979	<i>Prolagus oeningensis</i>	fragm. Lower (pre)molar	Right?	*					Not figured
210980	<i>Prolagus oeningensis</i>	P3	Right	ca. 1.37		ca. 1.47	*		Not figured
210981	<i>Prolagus oeningensis</i>	p4 or m1	Left	1.52	0.85	1.67	1.53		Not figured
210982	<i>Prolagus oeningensis</i>	d3	Right	1.66		1.49			Fig. 2a
210983	<i>Prolagus oeningensis</i>	p3	Right	1.90		1.53			Fig. 2b
210984	<i>Prolagus oeningensis</i>	P2	Right	0.88		1.78			Fig. 2e
210985	<i>Prolagus oeningensis</i>	P4	Right	1.21	0.76	2.49	2.17	0.69	Fig. 2j
210986	<i>Prolagus oeningensis</i>	p3	Left	*		1.38			Fig. 2c
210987	<i>Prolagus oeningensis</i>	P3	Left	1.73		2.53	1.98		Fig. 2g
210988	<i>Prolagus oeningensis</i>	P4	Right	1.35	0.77	3.12	2.74	1.12	Fig. 2i
210989	<i>Prolagus oeningensis</i>	p3	Right	1.72		1.72			Not figured
210990	<i>Prolagus oeningensis</i>	P3	Right	1.69		3.05	2.14		Fig. 2h
210991	<i>Prolagus oeningensis</i>	P3	Left	1.55		2.62	1.92		Not figured
210992	<i>Prolagus oeningensis</i>	M1	Right	1.29	0.68	2.08	1.99	1.62	Not figured
210993	<i>Prolagus oeningensis</i>	m2	Right	1.96	0.81	1.46	1.47	1.09	Fig. 2d
210994	<i>Prolagus oeningensis</i>	m2	Left	2.06	1.32	1.38	1.39	1.03	Not figured
210995	<i>Prolagus oeningensis</i>	P4	Left	1.25	0.71	2.62	2.30	1.75	Not figured
210788	<i>Prolagus oeningensis</i>	Lj with p3-m2	Left	*	Teeth in sediment				Not figured
210996	<i>Prolagus oeningensis</i>	P3	Left	*					Not figured
204002/2	<i>Prolagus oeningensis</i>	UJ fragm. with juvenil P2-M2	Right	P2 0.52 P3 * P4 0.96 M1 0.96 M2 0.86	ca 0.68 ca 0.53 ca 0.50	1.15 1.46 1.70 1.65	1.35 1.68 1.54	ca 0.41 ca 1.22 ca 1.14	
204000	<i>Prolagus oeningensis</i>	LJ fragm. with p3-m2	Left	p3 1.68 p4 1.53 m1 1.53 m2 2.19		1.88 1.90 1.79 ca.1.35	0.65 1.73	ca. 1.48 ca. 1.13	See Prieto et al. 2012
204001	<i>Prolagus oeningensis</i>	LJ fragm. with p3-m1	Left	p3 1.80 p4 1.51 m1 1.68	1.88 0.80 0.80	1.66 1.74	ca. 1.60 1.65		See Prieto et al. 2012
210997	cf. <i>Eurolagus fontannesii</i>	UJ fragm. with P3-M1	Left	P3 2.01 P4 2.11	3.04 1.17	2.27 3.47	* 2.20	0.78	Fig. 3b

Table 1 (continued)

Reference no.	Species	Specimens	L	TH or Ltrig	W or Wtrig	AA or Wtal	PH or Whyp	Figure	
			M1	2.02	1.13	3.33	2.40	0.74	
204023/1	cf. <i>Eurolagus fontannesi</i>	p3	Left	1.83	0.77	1.72	1.32	Fig. 3c	
210998	cf. <i>Eurolagus fontannesi</i>	P3	Right	2.09		3.30	2.98	Fig. 3e	
210999	cf. <i>Eurolagus fontannesi</i>	P2	Right	1.15		1.90		Fig. 3d	
211000	cf. <i>Eurolagus fontannesi</i>	M1	Right	1.88	0.72	3.25	3.03	0.83	Fig. 3f
211001	cf. <i>Eurolagus fontannesi</i>	P4	Right	2.31	0.88	3.26	2.94	0.66	Fig. 3g
211002	Ochotonidae indet.	? M2	Right	1.98	0.90	3.04	2.27		Fig. 2n
211003	Ochotonidae indet.	? M2	Left	*	*	*	*		Fig. 2o

* Damaged specimens

p3: hourglass-shaped; trigonid and talonid are connected by a narrow and centrally-positioned bridge; the talonid bears a lingually directed hypoconulid; in lateral view, we can observe that the hypoconulid disappears first, followed by the other lingual flexus; the hypoflexus remains until very advanced stages of wear.

Remarks: several morphological characters of the primitive lagomorph from Gratkorn fit those of *Eurolagus fontannesi*. The observation of the occlusal surface of p3 and of its flexa in lateral view, indicate that, with wear, the p3 would have followed the ontogenetic pattern illustrated by López Martínez (1989: 189, fig. 50A). Also, the reduced postcone in P2 (even if not as reduced as in western and central European species) is a particular feature of *Eurolagus*, as well as a long mesial hyperloph and a developed lagiloph in P3.

Unlike other European rooted lagomorphs, *E. fontannesi* has lower molariforms with labially pointing hypoconulids. Unfortunately, this discriminant feature is not observable on the Gratkorn specimens as these tooth positions have not been recovered. Other features of the specimens from Gratkorn deviate from the general features of *E. fontannesi*: (1) an additional cusp under the precone of P2; (2) the possible mesial hyperloph in P2, absent in other known populations; and (3) the small size, smaller but compatible with that of *Eurolagus* from the Vallès-Penedès, but sensibly smaller than the average of central European populations (see Angelone 2009a and references therein).

As it fits, but not completely, the characters of *E. fontannesi*, we classify the Gratkorn rooted ochotonid as cf. *E. fontannesi*.

Ochotonidae indet.

Material and measurements: see Table 1.

Description

Upper molariform teeth: these specimens are apparently two M2, very large, very robust, with hypercones of the same

length and equally protruding (evident in the specimen Fig. 2n, but hardly visible on Fig. 2o), very deep hypoflexus and no fossettes.

Remarks: The appearance of these two teeth is that of an advanced ochotonid: ever growing, no fossettes, deep hypoflexus. Their size is 50–60 % larger than that of *Prolagus* from the same assemblage. Also, their morphology is very different compared to *Prolagus*, the most evident difference being their significant robustness. Their ascription to *Lagopsis* (a genus that has never been recorded in Austria and in general further eastwards than Germany) has to be excluded, because the M2 of *Lagopsis* is more elongate and smaller in size. For these reasons, we leave these two teeth in open nomenclature as Ochotonidae indet.

Discussion and conclusions

Lagomorphs are traditionally less studied than other small mammal taxa in Austria, but intensive work is ongoing to correct this lack of knowledge. The new ochotonid data from Gratkorn add new details to the palaeobiodiversity of Austrian late Middle Miocene. Moreover, the lagomorph assemblage from Gratkorn is the most diverse in the country, with three different ochotonids forms recorded in it.

At present, the Austrian lagomorph record can be summarised as follows (Table 2):

- (1) *P. vasconensis* is recorded from the Eggenburgian followed by *Prolagus* sp. in the Ottnangian;
- (2) *P. oeningensis* ranges from the Karpatian to the Pannonian F (sensu Papp 1951); the locality Gratkorn records the earliest report of a rooted ochotonid in Austria and a unique record of a quite large-sized, unknown ochotonid. *P. oeningensis* is a very common and relatively abundant element of European Middle Miocene assemblages.
- (3) In the MN10 fossil sites of Richardhof-Wald and Schernham bei Haag occur two undescribed species of *Prolagus* (C. Angelone, personal data, observations

Table 2 Miocene lagomorph record from Austria; abbreviations in “Materials and methods”

Locality	Basin	Dating	<i>Prolagus vasconensis</i>	<i>Prolagus oeningensis</i>	<i>Prolagus crusafonti</i>	<i>Prolagus</i> sp.	primitive, rooted Ochotonid ^a	Ochotonidae indet. Large form	References
Kohlfisch	Fissure filling (Styrian)	MN 11, Pannonian H		x					Bachmayer and Wilson 1970; López-Martínez 1989
Schemham	NAFB	Pannonian, G			x		indet.		C. Angelone (pers. data)
Richardhof-Wald	Vienna	Pannonian, G			x				C. Angelone (pers. data)
Götzendorf	Vienna	Pannonian, F		x					Bachmayer and Wilson 1984; Rögl et al. 1993
Gaweinstal	Vienna	Early Pannonian (?), C(?)	x				x (3)		Harzhauser et al. 2011
Atzelsdorf	Vienna	Early Pannonian, C					x (2)		Angelone 2009b
Bullendorf	Vienna	Earliest Pannonian, A/B					?		Daxner-Höck et al. 1990; Angelone 2009b
Graukorn	Styrian	earliest late Sarmatian	x				x (1)	x	Gross et al. 2011; Prieto et al. 2012, this paper
Mühlbach	NAFB	Early Badenian	x						Boon-Kristkoiz 2003
Teiritzberg/T1	Korneuburg	Karpatian	x						Boon-Kristkoiz 1998
Oberdorf	Styrian	Ottmangian				x			Daxner-Höck 1998
Maigen	NAFB	Eggenburgian	x						Mein 1989

^a cf. *Eurolagus fontannesi*: 1; *Amphilagus* sp.: 2; *Amphilagus fontannesi*: 3

NHMW 2007). *P. crusafonti* is recorded in the MN11 fissure infilling of Kohfidisch (López Martínez 1989, but originally classified as *P. oeningensis* by Bachmayer and Wilson 1970). As for primitive, rooted ochotonids, Austria represents one of the last strongholds of the group, together with other central European countries (e.g. Germany, Poland, Hungary; Bernor et al. 2004; Prieto 2007; Angelone 2009b; Fostowicz-Frelik et al. 2012; J. Prieto, personal data; we excluded Spain from the list as the report of a rooted lagomorph from Can Jofresa, MN10, Agustí and Gibert 1982, is likely to be wrong; C. Angelone, personal data).

The ochotonids from Gratkorn in the framework of central European late Middle Miocene conspecific populations

P. oeningensis is a common and relatively abundant element of European Middle Miocene assemblages. As noticed by Prieto et al. (2012), the remains from Gratkorn do not differ morphologically and dimensionally from coeval European populations to such an extent as to be specifically or subspecifically separated. However, the Gratkorn assemblage shows more primitive characters with respect to western and central western European populations of *P. oeningensis*.

According to some authors (López Martínez 1977, 1989; Angelone 2008) *Eurolagus* is a MN7/8 marker, whereas others (Fostowicz-Frelik et al. 2012) include in the genus all rooted European lagomorphs from MN5 to MN10. We do not follow here the second working hypothesis. *Eurolagus* is not very common in late Middle Miocene assemblages. The late Middle Miocene distribution of *Eurolagus* covers Europe from the Vallès-Penedès Basin (López Martínez 1989) to Hungary (Ehik 1926; Hír 2004) and probably Serbia (Vračević; Marković and Milivojević 2010, not figured). However, such a distribution is not “continuous” but is represented by scattered reports. Thus, *Eurolagus fontannesi* from Gratkorn represents a useful additional record in this framework as it fills the geographical gap in Central Europe, especially for future taxonomic works, in order to study possible variations in the *Eurolagus* populations.

Ochotonidae indet. has, to our knowledge, nothing equivalent in Europe, thus it is not possible to provide a useful comparison.

Acknowledgements The authors express their gratitude to the community of Gratkorn for financial support during the excavations in 2008, and to the Wietersdorfer and Peggauer Zementwerke AG (especially Josef Plank). Norbert Winkler (Joanneum) meticulously prepared some specimens. The excavations of the Universalmuseum Joanneum were partly financed by the Land Steiermark/Wissenschaftsreferat. We are grateful to the reviewers K. Hordijk and Ş. Şen whose comments contributed to improve the manuscript. For the study of NHMW material, Chiara Angelone received support from the SYNTHESYS Project (AT-TAF-3508), financed by the European

Community Research Infrastructure Action under the FP6 “Structuring the European Research Area” Programme and from the Spanish Ministerio de Economía y Competitividad (CGL2011-28681). We thank from all our earth Bérénice and Leonie for their omnipresence during the writing, revising, and editing of this paper.

References

- Agustí J, Gibert J (1982) Roedores e insectívoros (Mammalia) del Mioceno Superior de Can Jofresa y Can Perellada (Vallès-Penedès, Cataluña). *Pal I Evol* 17:29–41
- Angelone C (2007) Messinian *Prolagus* (Ochotonidae, Lagomorpha, Mammalia) of Italy. *Geobios* 40:407–421
- Angelone C (2008) *Prolagus italicus* n. sp. (Ochotonidae, Lagomorpha), a new Pliocene species of the peninsular Italy. *Geobios* 41:445–453
- Angelone C (2009a) Lagomorphs from the Miocene of Sandelzhausen (southern Germany). *Palaeontol Z* 83:67–75
- Angelone C (2009b) The early Vallesian vertebrates of Atzelsdorf (Late Miocene, Austria) 6. Lagomorpha. *Ann Naturhist Mus Wien* 111A: 515–518
- Angelone C, Sesé C (2009) New characters for species determination within the genus *Prolagus* (Ochotonidae, Lagomorpha, Mammalia). *J Paleontol* 83:80–88
- Bachmayer F, Wilson RW (1970) Die Fauna der altploziänen Höhlen- und Spaltenfüllungen bei Kohfidisch, Burgenland (Österreich). Small mammals (Insectivora, Chiroptera, Lagomorpha, Rodentia) from the Kohfidisch Fissures of Burgenland, Austria. *Ann Naturhist Mus Wien* A 74:533–587
- Bachmayer F, Wilson RW (1984) Die Kleinsäugerfauna von Götzendorf, Niederösterreich. *Sitzber Österr Akad Wiss math-Naturwiss KI* 193(6–10):303–319
- Bendukidze OG, Bruijn H, van den Hoek Ostende LW (2009) A revision of Late Oligocene associations of small mammals from the Aral Formation (Kazakhstan) in the National Museum of Georgia, Tbilisi. *Palaeodiversity* 2:343–377
- Bernor RL, Kordos L, Rook L, Agustí J, Andrews P, Armour-Chelu M, Begun DR, Cameron DW, Damuth J, Daxner-Höck G, De Bonis L, Fejfar O, Fessaha N, Fortelius M, Franzen J, Gasparik M, Gentry A, Heissig K, Heryak N, Kaiser T, Koufos GD, Krolopp E, Janossy D, Llenas M, Mészáros L, Müller P, Renne P, Roček Z, Şen Ş, Scott R, Szynklar Z, Topal G, Ungar PS, Utescher T, Van Dam JA, Werdelin L, Ziegler R (2004) Recent advances on multi-disciplinary research at Rudabanya, late Miocene (MN9), Hungary: a compendium. *Palaeontogr Ital* 89:3–36
- Boon-Kristkoiz E (1998) Säugetiere (Mammalia) aus dem Karpat des Komeuburger Beckens 2. Lagomorpha. *Beitr Paläontol* 23:363–366
- Boon-Kristkoiz E (2003) *Prolagus oeningensis* (Lagomorpha, Mammalia) from the Middle Miocene of Mühlbach am Manhartsberg, Lower Austria. *Ann Naturhist Mus Wien* 104A:293–296
- Dawson MR (2008) Lagomorpha. In: Janis CM, Gunnell GF, Uhen MD (eds) Evolution of Tertiary mammals of North America. Volume 2: Small mammals, xenarthrans, and marine mammals. Cambridge University Press, New York, pp 293–310
- Daxner-Höck G (1998) Wirbeltiere aus dem Unter-Miozän des Lignit-Tagebaues Oberdorf (Weststeirisches Becken, Österreich) 7. Rodentia 2 und Lagomorpha (Mammalia). *Ann Naturhist Mus Wien* 99A:139–162
- Daxner-Höck G, de Bruijn H, Foussekis D (1990) Bericht 1989 über das Projekt “Kleinsäuger” der begleitenden Grundlagenforschung. *Jb Geol Bundes-Anstalt* 133:508–510
- Ehik J (1926) The right interpretation of the cheek teeth tubercles of *Titanomys*. *Ann Mus Nation Hung* 22:178–186

- Engesser B (1972) Die obermiozäne Säugerfauna von Anwil (Baselland). Tätigkeitsber Naturforsch Ges Baselland 28:37–363
- Erbajeva MA (1988) Cenozoic pikas (Taxonomy, Systematics, Phylogeny). Nauka, Moscow [in Russian]
- Erbajeva MA, Filippov AG (1997) Miocene small mammalian faunas of the Baikalian region. Mem Trav Eco prat Haut Etu, Montpellier 21: 249–259
- Erbajeva MA, Mead JI, Alexeeva NV, Angelone C, Swift S (2011) Taxonomic diversity of Late Cenozoic Asian and North American ochotonids (an overview). Palaeontol Elect 14:9p
- Fostowicz-Freluk Ł, Nadachowski A, Kowalewska-Groszkowska M (2012) New data on the Miocene stem lagomorph *Eurolagus fontannesi*, and its northernmost record. Acta Palaeontol Pol 57:1–20
- Gross M, Böhme M, Prieto J (2011) Gratkorn: A benchmark locality for the continental Sarmatian s. str. of the Central Paratethys. Int J Earth Sci 100:1895–1913
- Gureev AA (1964) Fauna SSSR. Mlekopitayushchie. Zaitseobraznye, III 10:49. [in Russian]
- Harzhauser M, Daxner-Höck G, Göhlich UB, Nagel D (2011) Complex faunal mixing in the early Pannonianpalaeo-danube Delta (Late Miocene, Gaweinstal, Lower Austria). Ann Naturhist Mus Wien 113A:167–208
- Hír J (2004) Late Astaracian (late Sarmatian) Lagomorphs and rodents from Felsőtárkány-Felnémet (Northern Hungary). Beitr Palaeontol 30:155–173
- Hoffmann RS, Smith AT (2005) Order Lagomorpha. In: Wilson DE, Reeder DM (eds) Mammal species of the world: A taxonomic and geographic reference. The Johns Hopkins University Press, Baltimore, pp 185–211
- López Martínez N (1977) Nuevos Lagomorfos (Mammalia) del Neógeno y Cuaternario Español. Trab Neog-Cuat 8:7–45
- López Martínez N (1989) Revisión sistemática y biostratigráfica de los Lagomorpha (Mammalia) del Terciario y Cuaternario de España. Mem Mus Paleontol Univ Zaragoza 3:1–342
- López Martínez N (2008) The Lagomorph fossil record and the origin of the European rabbit. In: Alves PC, Ferrand N, Hackländer K (eds) Lagomorph biology: evolution, ecology, and conservation. Springer, Berlin, pp 27–46
- López Martínez N (2012) Les Lagomorpha de Sansan, in: Peigné S, Şen Ş (eds.), Mammifères de Sansan. Mem Mus Natl Hist Nat, 119-144
- Marković Z, Milivojević M (2010) The Neogene small mammals from Serbia - Collection methods and results. Bul Nat Hist Mus 2010:105–114
- Martin T (2004) Evolution of incisor enamel microstructure in Lagomorpha. J Vertebr Paleontol 24:411–426
- Mein P (1989) Die Kleinsäugerfauna des Untermiozäns (Eggenburgien) von Maigen, Niederösterreich. Ann Naturhist Mus Wien 90A:49–58
- Papp A (1951) Das Pannon des Wiener Beckens. Mitt Geol Ges Wien 39–41:99–193
- Prieto J (2007) Kleinsäuger-Biostratigraphie und Paläoökologie des höheren Mittelmiozäns (MN 8) Bayerns: Spaltenfüllungen der Fränkischen Alb und Lokalitäten der Oberen Süßwassermolasse im Vergleich. PhD thesis, LMU, Munich
- Prieto J, Böhme M, Maurer H, Heissig K, Abdul Aziz H (2009) Biostratigraphy and sedimentology of the Fluvatile Untere Serie (Early and Middle Miocene) in the central part of the North Alpine Foreland Basin: implications for palaeoenvironment and climate. Int J Earth Sci 98:1767–1791
- Prieto J, Böhme M, Gross M (2010) The cricetid rodents from Gratkorn (Austria, Styria): a benchmark locality for the continental Sarmatian sensu stricto (late Middle Miocene) in the Central Paratethys. Geol Carpathica 61:419–436
- Prieto J, Angelone C, Gross M, Böhme M (2012) The pika *Prolagus* (Ochotonidae, Lagomorpha, Mammalia) in the late Middle Miocene fauna from Gratkorn (Styrian Basin, Austria). N Jb Geol Paläont, Abh 263:111–118
- Rögl F, Zapfe HBRL, Brzobohaty RL, Daxner-Höck G, Draxler I, Fejfar O, Gaudant J, Herrmann P, Rabeder GSO, Zetter R (1993) Die Primatenfundstelle Götzendorf an der Leitha (Obermiozän des Wiener Beckens, Niederösterreich). Jb Geol Bdanstalt 136: 503–526
- Wilson DE, Reeder DM (ed) (2005) Mammal species of the world. A taxonomic and geographic reference, 3rd edn, Johns Hopkins University Press, Baltimore