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Article

The pika *Prolagus* (Ochotonidae, Lagomorpha, Mammalia) in the late Middle Miocene fauna from Gratkorn (Styrian Basin, Austria)

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With 4 figures

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Abstract: Although the importance of pikas (Ochotonidae, Lagomorpha, Mammalia) in biostratigraphic and palaeoecologic purposes comes more and more to light, this family continues to be understudied in Austria and Central Europe in general. Two mandibles of the widespread and long-living genus *Prolagus* have been recently excavated from the new fossil locality Gratkorn. They are ascribed to *Prolagus oeningensis*, and represent the youngest occurrence of the genus in the Styrian Basin at around 12-12.2 Ma (Late Sarmatian s. str., late Middle Miocene). This discovery completes our knowledge on ochotonid evolution in the peri-Paratethyan area leading to hypothesize differences in the evolutionary history of *P. oeningensis* in central-eastern and Western Europe.

Key words: *Prolagus oeningensis*, Ochotonidae, Late Sarmatian s. str., small mammals.

1. Introduction

Late Middle to earliest Late Miocene vertebrate faunas are rare in the (Central-) Paratethyan area, and thus the vertebrate evolution and faunal interchanges during this time range are poorly known. In this context the recently excavated fossil site at the clay pit St. Stefan near Gratkorn (Gross et al. 2007; Gross 2008) is of primary importance due to its age (Late Sarmatian s. str.), its faunal and floral content, and the excellent preservation of the remains (Harzhauser et al. 2008; Gross et al. 2009, 2011; Daxner-Höck 2010; Prieto et al. 2010a, b), allowing to reconstruct the continental environment of the north-western part of the Styrian Basin at around 12-12.2 Ma.

Beside fishes, amphibians, reptiles, birds, insectivores, chiropterans and rodents, the small vertebrate fauna comprises pikas (family Ochotonidae, Lagomorpha), whose geographic distribution is now restricted to central Asia and North America. In this paper we present the *Prolagus* remains from Gratkorn in their biostratigraphic context, in order to improve the knowledge of Austrian ochotonids, as this taxon is important for biostratigraphic and palaeobiogeographic studies.

2. Geological setting and correlation

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 in the Gratkorn Basin, a satellite basin of the Styrian Basin. The specimens presented herein were excavated from a vertebrate-bearing paleosoil exposed in the lowermost part of the pit. The several findings of the fossil legume *Podocarpium podocarpum* in the pelites above the vertebrate horizon (Meller & Gross 2006) gave first indications for a dating older than Late Miocene. In addition, the terrestrial gastropod fauna correlate to the Late Sarmatian s. str. (Harzhauser et al. 2008),

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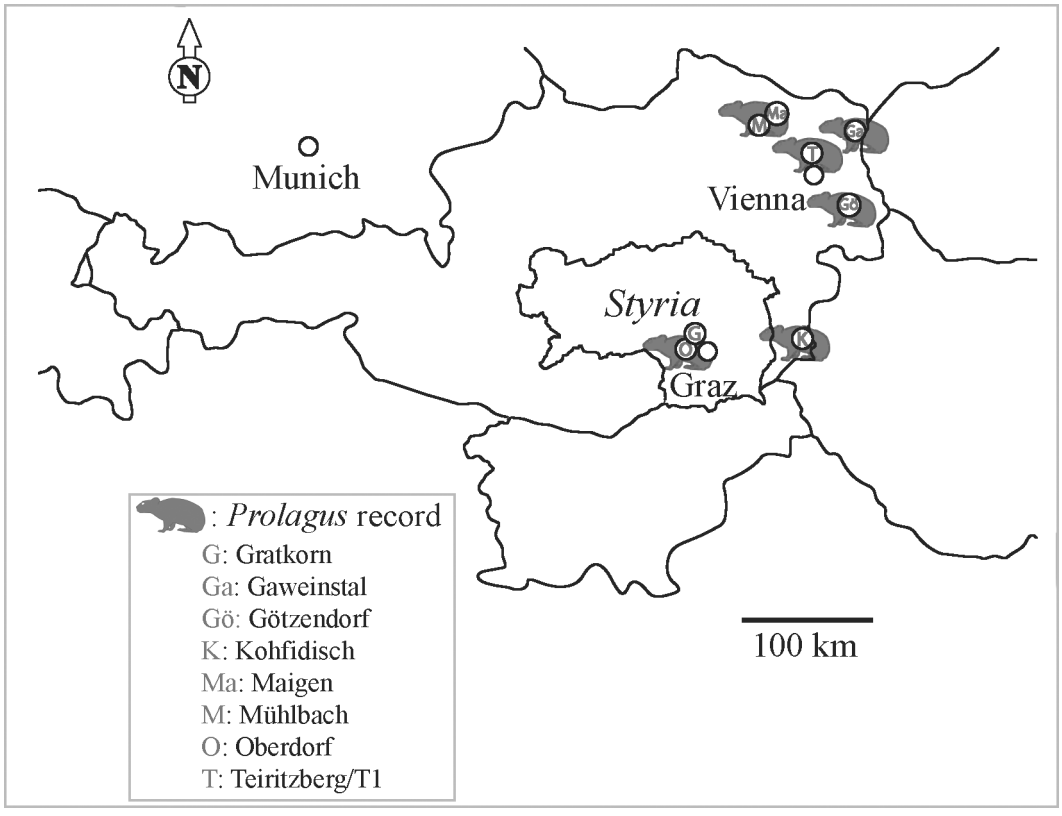

Fig. 1. Fossil record of the genus *Prolagus* Pomel, 1853 in the Miocene of Austria.

shortly postdating the so-called Carinthian Phase. Finally, Gross et al. (2011) proposed that the locality was formed around the Early/Late Sarmatian boundary, at an age of about 12.2-12.0 Ma on the basis of integrated stratigraphic data.

3. Overview of the evolutionary history of *Prolagus*

Prolagus is a remarkably long-lived genus with a quite high species diversity recorded over more than 22 Ma, since the Early Miocene (MN2, Mèbre 698, Switzerland; Engesser et al. 1993). Archaeological proofs (Vigne 1987; Wilkens 2005) and testimonies of the historians (Polybius) indicate that *Prolagus* survived in Corsica and Sardinia till the classic epoch. The fascinating hypothesis of the survival of *Prolagus* at least till the 18th century in the islands of Tavolara and S. Pietro (respectively located in front of the North-Eastern and the South-Western Sardinian coast), arisen from a misinterpretation of the writings of the naturalist F. Cetti (1777), has recently been definitively discarded (Wilkens 2005). Fossil remains of *Prolagus* are very frequent and abundant in Neogene European fossil sites and in Pleistocene-Holocene fossiliferous localities of Corsica and Sardinia (López Martínez 2001; Prieto 2007; Angelone et al. 2008).

The high specific diversity, the long stratigraphic record, and the abundance in the fossil record makes *Prolagus* a powerful biochronological tool at local and larger scales (Angelone 2008b and references therein). Moreover, *Prolagus* has been demonstrated to be important also for palaeogeographical purposes (Angelone 2007). Such considerations led to enhance systematic studies at the specific and intra-specific level (Angelone 2008c, 2009; Angelone et al. 2008; Angelone & Sesé 2009).

4. The *Prolagus* record in Austria

The Austrian Miocene fossil record is dominated by large mammal localities, at least for the Styrian Basin (e.g., Mottl 1970). The lagomorphs are traditionally less studied than other small mammal taxa in Austria, and the pikas are only described from few localities (Fig. 1):

Prolagus is recorded from the Early Miocene of Maigen (*P. vasconensis*, Mein 1989) and Oberdorf (*Prolagus* sp., Daxner-Höck 1998). *P. oeningensis* is found in Teiritzberg/T1 and Mühlbach (Boon-Kristkoiz 1998, 2003). An age of 16.5-16.7 Ma (Late Karpatian) is proposed for Teiritzberg T1 (Harzhauser et al. 2002; Daxner-Höck 2003); Mühlbach, due to the presence of *Cricetodon meini*, is clearly younger, shortly antedating the German Ries impact event (Daxner-Höck et al. 2004) in the early Badenian (Abdul Aziz et al. 2008, 2010).

Prolagus is also present in the Austrian Late Miocene: Harzhauser et al. (2011) describe *P. oeningensis* in Lower Austria at Gaweinstal (Lower Pannonian). Bachmayer & Wilson (1984) report *P. oeningensis* in Götzendorf (Pannonian, zone F sensu Papp 1951). *P. crusafonti* (originally described as *P.* cf. *oeningensis* by Bachmayer & Wilson 1970) is recorded in the fissure fill of Kohfidisch (López Martínez 1989, zone G).

5. Material and method

The fossils from Gratkorn are stored in the collection of the Universalmuseum Joanneum in Graz (Geologie & Paläontologie, abbreviated UMJGP).

The dental nomenclature, the measurements and the abbreviations follow Angelone & Sesé (2009, implemented from Angelone 2007 and López Martínez 1989). The width of the hypoconulid (Whyp) of the m2 is added. The abbreviations are: L: length, W: width, Wtrig: trigonid width, Wtal: talonid width, Ltrig: trigonid length. NHMW: Naturhistorisches Museum Wien. Measurements (mm) were taken with an ocular micrometer.

6. Systematic palaeontology

Order Lagomorpha Brandt, 1855
Family Ochotonidae Thomas, 1897
Genus *Prolagus* Pomel, 1853

Prolagus oeningensis (König, 1825)
Figs. 2-4

Emended diagnosis (translated from Spanish): small-sized *Prolagus* species, lower teeth wider than *P. vasconiensis*. p3 bearing a *crochet* in more than 80% of the population specimens and appears to be wider than longer. m1 retains a mesial *hiatus*. Upper molars have long lagilophs separated from the large lagicones by a notch. Enamel *hiatus* present at least in the 95% of the P3 of the population. Fossettes in upper molars are enlarged to form a J (López Martínez 1974).

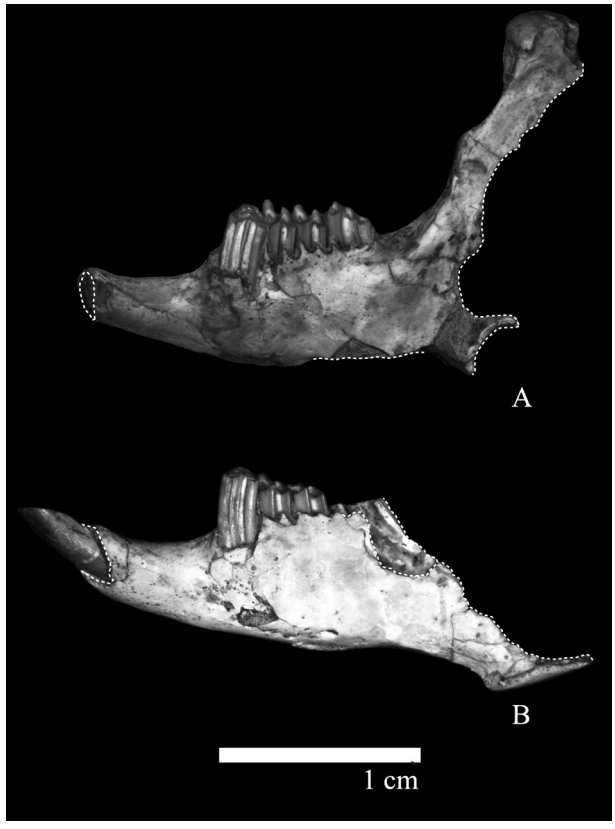

Fig. 2. *Prolagus oeningensis* (König, 1825) from Gratkorn. Left mandibles (A: UMJGP 204.000; B: UMJGP 204.001).

Type locality: Öhningen (Germany), Middle Miocene.

Geographical and temporal distribution: *P. oeningensis* has been identified in more than 150 localities in the Iberian Peninsula, Central Europe (France, Switzerland, Germany, Austria, Hungary), Eastern Europe (Romania) and Asia (Turkey) since MN4 to earliest MN9 (Angelone & Sesé 2009 and references therein).

Material and measurements: 2 left mandibles (UMJGP 204.000 and 204.001).
UMJGP 204.000: **p3**: L: 1.68, W: 1.88; **p4**: L: 1.53, Ltrig: 0.9, Wtrig: 1.9, Wtal:.0,65; **m1**: L:1.53, Ltrig: 0.93, Wtrig: 1.79, Wtal: 1.73; **m2**: L:2.19, Ltrig: ~0.95, Wtrig: ~1.35, Wtal: ~1.48, Whyp: ~1.13.
UMJGP 204.001: **p3**: L: 1.80, W: 1.88; **p4**: L: 1.51, Ltrig: 0.8, Wtrig: 1.66, Wtal: ~1.6; **m1**: L:1.68, Ltrig: 0.8, Wtrig: 1.74, Wtal: 1.65.

Description: Specimen UMJGP 204.000 (Figs. 2A, 3B): The mandible is partly inglobed by sediment, thus only its labial side is observable; p3-m2 are preserved *in situ*; the posterior part of the ramus ascendens is missing, but the apophyse of the coronoide process is still present; the anterior mental foramen lies under the anterior part of p3, sur-

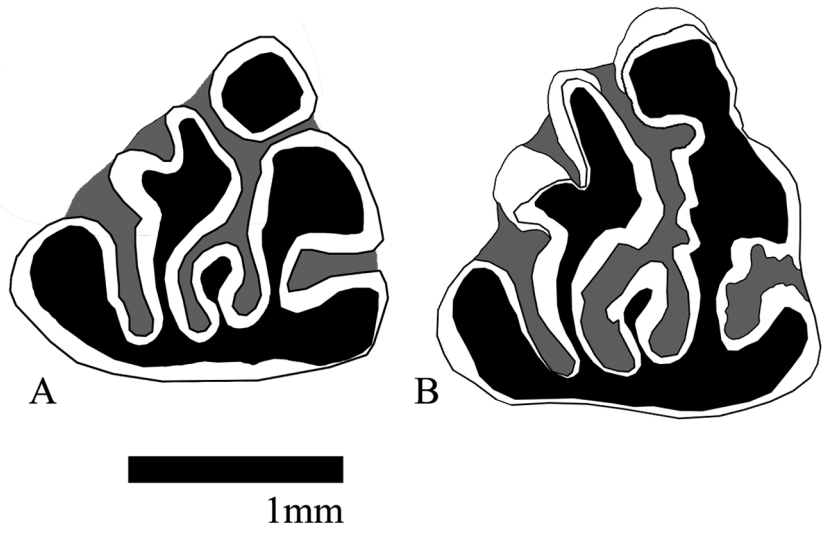

Fig. 3. *Prolagus oeningensis* (König, 1825) from Gratkorn. Drawings of the p3 (A: UMJGP 204.001; B: UMJGP 204.000). Specimen A belongs to the mandible UMJGP 204.001 (Fig. 2B), specimen B belongs to mandible UMJGP 204.000 (Fig. 2A).

rounded by several small accessory foramina; the posterior mental foramen is not observable. In the p3 the anteroconid, rhomboidal and lying in a central position, is connected to the metaconid, that shows a wavy enamel band; meta- and protoisthmus both very long; metaisthmus wider than protoisthmus; entoconid without enamel hiatus; crochet well developed, curved and in central position; small protoconid; long and wide protoconulid. Anterior isthmus on talonids of p4-m2 developed; trigonid of m1 with enamel hiatus in its anterior part; m2 anteriorly damaged.

Specimen UMJGP 204.001 (Figs. 2B, 3A): The incisor and p3-m1 are preserved *in situ*; the ramus ascendens is completely missing with the exception of a part of the apophyse of the angular process; besides the anterior mental foramen surrounded by accessory foramina, a large, oval posterior mental foramen, lying under the posterior part of m1, is observable. In the p3 the rhomboidal anteroconid lies in an almost central position; the anteroconid is smaller than the quadrangular metaconid; the entoconid lacks enamel hiatus; the crochet is well developed, curved and lying in a central position; meta- and protoisthmus are very long and of equal thickness; protoconid and protoconulid are both small. The talonids of p4 and m1 bear a quite developed anterior isthmus (almost as long as talonid); the trigonid of m1 without enamel hiatus in its anterior part.

7. Discussion and conclusions

7.1. Taxonomic attribution and comparison to coeval European populations

The p3 morphology and the mandible characters of *Prolagus* from Gratkorn are compatible with the attribution to the species *P. oeningensis*. In particular, the size of anteroconid smaller than metaconid, a very developed crochet in a central position and the lack of entoconid enamel hiatus are typical of *P. oeningensis* (López Martínez 1988). A protoconulid variable in size (notice the difference between the two available p3) is common in *P. oeningensis* populations. The anteroconid-metaconid connection is quite an unusual feature but it has been observed (even if quite seldom) in *P. oeningensis* (e.g.: Nebelbergweg, Kälin 1993: fig. 89d, also figured in Kälin & Engesser 2001: fig. 44a; some Spanish localities, Hordijk 2010; La Grive M, Angelone, pers. obs. collection of Naturhistorisches Museum Wien) and in other species of *Prolagus*.

With respect to Spanish populations of latest Middle Miocene (Late Aragonian, zone G3) (see López Martínez 1989; Angelone & Sesé 2009; Casanovas-Vilar et al. 2010; Hordijk 2010, pl. 3.5 n.5-13), *P. oeningensis* from Gratkorn shows less advanced p3 antoconid. In general, the p3 of those Spanish populations show a flattened oval to diamond-shaped, larger anteroconid (even if still smaller than the metaconid), often lying in a more lingual position with respect to the axis of the tooth. Such advanced p3 features of Spanish late Middle Miocene population of *P. oeningensis*, together with other advanced characters observed in other tooth positions (e.g.: P2 with incipient hypoflexus; Casanovas-Vilar et al. 2010) are interpreted as evolutionary trends toward *P. crusafonti* (López

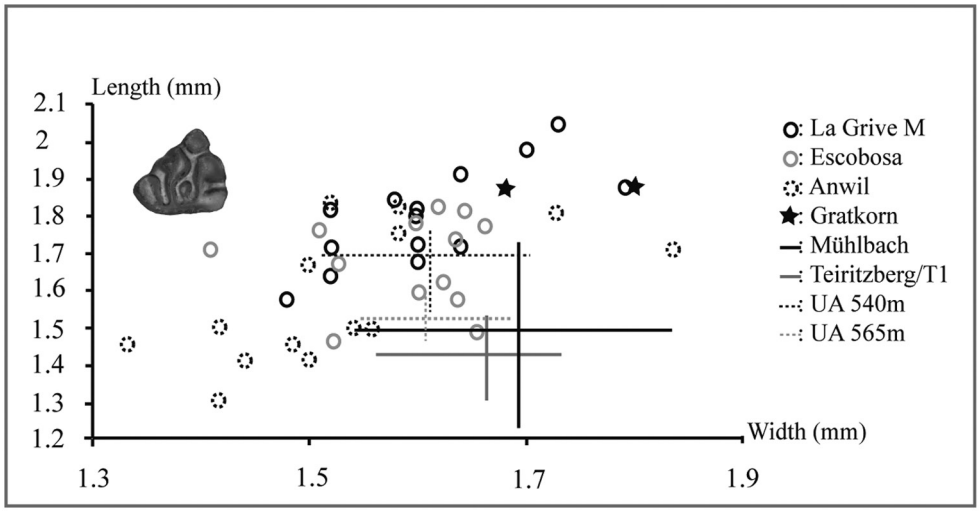

Fig. 4: The dimensions (mm) of p3 of *Prolagus oeningensis* (König, 1825) from Gratkorn are compared with those of late Middle Miocene selected European populations and with those of Austrian populations of the same species. Data of Escobosa are from Angelone & Sesé (2009), La Grive M from Angelone (unpublished data), Anwil from Engesser (1972), Teiritzberg/T1 from Boon-Kristkoiz (1998), Mühlbach from Boon-Kristkoiz (2003), Untereichen-Altenstadt (UA) from Prieto et al. (2009).

Martínez 1989). López Martínez (1989: 131) observed in the Middle-Late Miocene succession of the Vallès-Penedès (NE Spain) the continuous variation of morphological characters that lead from *P. oeningensis* to *P. crusafonti*. Such morphological variation was accompanied by a progressive size decrease.

P. oeningensis from Gratkorn seems to share more morphological similarities with central European late Middle Miocene populations. In particular it was compared with those of La Grive M (France) and Anwil (Switzerland, 13.2 Ma after Kälin & Kempf 2002). The p3 anteroconid of these two populations is more modified than in Gratkorn specimen(s), but lies in a central position. Moreover in the p3 of the population of Anwil, contrary to Gratkorn and La Grive M, the *crochet* is often reduced (~70% of specimens). In Anwil meta- and/or protoisthmus may be absent and additional labial lophs may be present (15-20% of specimens), but the number of specimens from Gratkorn does not allow frequency comparisons. The measurements of *Prolagus* from Gratkorn fall in the uppermost range of the variability of late Middle Miocene central-western European populations of *P. oeningensis* (Escobosa, La Grive M, Anwil). It must be also remarked that the Gratkorn specimens are the largest among Austrian populations of this species (Fig. 4). However, the scantiness of the specimens available from Gratkorn and the great age difference between Gratkorn and the other Austrian localities with *P. oeningensis* (Teiritzberg T1 and Mühlbach), does not allow further considerations, as for example, to verify if *P. oeningensis* from Austria shows the same dimensional tendency to size decrease as in NE Spain (see above).

7.2. Evolutionary remarks

The less advanced appearance of the p3 of *P. oeningensis* from Gratkorn, compared to coeval central-western and western European populations (anteroconid of rounded rhomboidal shape, lying in a central position) is evident. The primitive appearance of *P. oeningensis* from Gratkorn is already anacronistic and absent from Late Middle Miocene populations of central-western and Western Europe. This gives weight to consideration based on such a scanty sample as that from Gratkorn.

In Late Middle Miocene populations of central-western and Western Europe the anteroconid has already shifted lingually. Moreover the anteroconid shape shows a gradient of modification from primitive (rounded rhomboidal) to advanced (flattened oval to diamond-shaped) from East to the West.

As working hypothesis to be demonstrated on the basis of additional Eastern European material, we hypothesize that the evolution of *P. oeningensis* may have followed different pathways in central-eastern Europe.

7.3. Environmental remarks and general conclusions

The differences observed in the evolution of *P. oeningensis* could have been the result of differences in the environmental conditions along Europe. *Prolagus* is a rare element in the Gratkorn fauna, especially when compared with the high number of *Schizogalerix voesendorfensis* (Rabeder, 1973) recovered (Prieto et al. 2010a). This is surprising because pikas and gymnures are believed to be hunted by birds of prey, and can both represent a large segment of the fossil material (e.g., Prieto 2007). As size selection can be excluded since the two species belong to almost the same size range, the reasons for this rarity might be related to the palaeoenvironment of the locality. On the other hand, the extremely quick accumulation of the remains and absence of important secondary disturbances in the small mammal-enriched uppermost part of the palaeosoils lead to spatial heterogeneity in the fossil accumulation (Gross et al. 2011). For instance, few specimens of the gliding squirrel *Albanensia albanensis* (Major, 1893) were discovered in the early years of the excavation campaigns (Daxner-Höck 2010). These remains, including skulls and post cranial material, were concentrated, but no more evidence of this species was found since then in the surrounding sediments. Considering these facts, it can not be excluded that taphonomical biases are responsible for the rarity of *Prolagus*.

However, preliminary studies of Eastern European assemblages bearing *P. oeningensis* (Angelone, unpublished data) seem to point out that *Prolagus* is not as abundant as in Western Europe.

The general rarity of the genus at the end of the Middle Miocene gives thus more importance to the remains from Gratkorn. These are the youngest occurrence of the species in the Styrian Basin (~12-12.2 Ma), and complete our knowledge about ochotonid palaeodistribution in the Miocene of Austria and more generally of Central Europe.

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