

Revision of the type material of the Pliocene species *Prolagus bilobus* Heller, 1936 (Mammalia, Lagomorpha), with comments on the taxonomic validity of *P. osmolskae* Fostowicz-Frelik, 2010

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The taxonomy of the Pliocene *Prolagus* in central Europe is still poorly understood. The proven record is limited there just onto *P. bilobus* from Gundersheim localities (Germany) and *P. osmolskae* from Raciszyn 1 (Poland). Unfortunately, the taxonomy of *P. bilobus* has until now remained unclear. Apart from the original description, no studies have provided data based on direct observation of the type material. Only minor attention has also been paid to a detailed analysis of additional material from the Gundersheim localities. Therefore, we are providing the first revision of the type material of *P. bilobus* accompanied by a synoptic survey of the type locality. Based on previously undescribed material of *P. bilobus*, we clarify the morphologic variability and dimensional range of *P. bilobus*, and question the validity of *P. osmolskae*. A direct revision of the both species evidenced that the only available specimen – the holotype – of *P. osmolskae* clearly falls within the recorded size and morphological range of the very large *P. bilobus*. And thus *P. osmolskae* Fostowicz-Frelik, 2010 is regarded here as a junior subjective synonym of *P. bilobus* Heller, 1936. • Key words: Lagomorpha, Prolagidae, *Prolagus bilobus*, *Prolagus osmolskae*, Pliocene, Central Europe.

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Taxonomy and phylogeny of *Prolagus* Pomel, 1853 from the Pliocene of central Europe are still poorly understood especially if compared with the Mediterranean region. The main reason is that the genus is relatively rare in the Pliocene of transalpine Europe. It is much more frequently recorded in the Mediterranean region, which seems to have been particularly attractive. The proven Pliocene record of *Prolagus* from central Europe is limited to three localities: Gundersheim (fissure 4 and Findling), Germany (*P. bilobus* Heller, 1936) and Raciszyn 1, Poland (*P. osmolskae* Fostowicz-Frelik, 2010). Its record from Wölfersheim, Germany (cf. Tobien 1977 without description) cannot be confirmed, as the material is unavailable.

Unfortunately, until now, the taxonomy of *Prolagus bilobus* has remained unclear. Apart from the original description, no studies have provided data based on direct observation of the type material. Only minor attention has also been paid to a detailed analysis of additional material from the Gundersheim localities (cf. Fejfar *et al.* 2006).

Therefore, we are providing a revision of the type material of *P. bilobus* accompanied by a nomenclature survey of the different sites at Gundersheim. Based on previously undescribed material of *P. bilobus*, we clarify the morphologic variability and dimensional range of *P. bilobus*, and question the validity of *P. osmolskae* as described by Fostowicz-Frelik (2010).

Material and methods

The nomenclature and metrics used here follow López Martínez & Thaler (1975) and Angelone & Sesé (2009). All drawings and measurements were made using a binocular microscope with a camera lucida and ocular micrometer. For consistency, only adult specimens (recognized by their prismatic tooth shape) were used. Abbreviations used in the text and tables are as follows: Ht – holotype, L – length, Lt – lectotype, Ltrig – trigonid length, N – number

of specimens, OR – observed range, Plt – paralectotype, W – width, Wtl – third lobe width of m2, Wtal – talonid width, Wtrig – trigonid width, X – mean. Capital and lower-case letters, P/p (premolar) and M/m (molar), refer to upper and lower cheek-teeth, respectively. The material of *Prolagus* from Gundersheim localities is housed in the SMF, from Raciszyn 1 in the ZPAL. The geographical distance between the two localities is about 750 km.

Comparisons were made with continental European species dating to MN 13–17 and including *P. savagei* Berzi, 1970; *P. depereti* López Martínez in López Martínez & Thaler, 1975; *P. ibericus* López Martínez in López Martínez & Thaler, 1975; *P. michauxi* López Martínez in López Martínez & Thaler, 1975; *P. sorbinii* Masini, 1989; *P. caucasicus* Averianov & Tesakov, 1998; *P. italicus* Angelone, 2008. All nomenclatural acts presented here conform to the mandatory provisions of the International Code of Zoological Nomenclature (ICZN 1999).

Institutional abbreviations. – SMF – Senckenberg Museum, Frankfurt am Main, Germany; ZPAL – Institute of Paleobiology, Polish Academy of Sciences, Warszawa, Poland.

Results

Type material of *Prolagus bilobus*

Table 1, Figure 1A, C–F

Name-bearing type. – The nominal taxon was established by Heller (1936) based on the material from Gundersheim (see below). The name-bearing type is indicated in his original description as: “...several upper teeth, a fragment of right mandible with m1–m2 and one isolated, unfortunately damaged, right p4” [translated from German] (Heller 1936, p. 139). Heller did not designate the holotype (*contra* Fostowicz-Frelik 2010, p. 610). All the original material of *Prolagus* published by Heller (1936) is deposited in the SMF, including original labels contained in boxes with the specimens. It is worth to remark, though, that there are inaccuracies in tooth position assignments of the type series in Heller (1936); the material consists of a partly broken left p3 (cut in the bottom part; Heller 1936, fig. 3), a right fragment of mandible with p4–m2, and three fragments of lower molariform teeth, *i.e.*, right talonid of p4, right talonid of p4 or m1 and right trigonid of p4 or m1.

The first valid designation of a lectotype (see Articles 74.3 and 74.5 of ICZN 1999) was done by López Martínez & Thaler (1975). Following Article 74.4 (ICZN 1999) the figured specimen in Heller (1936, fig. 3), SMF 1996/136, is thus the sole name-bearing type of *Prolagus bilobus*. The later designation of a lectotype provided by Tesakov & Averianov (2002) must be regarded as invalid.

Size and morphology. – The lectotype is a prismatic p3 of an adult individual. On the occlusal surface the anterior and lingual parts of the tooth are broken (anteroconid, metaconid and entoconid are lacking). All tooth morphostructures are well observable in its bottom transverse section and do not show any major morphological differences from those in more apical parts of the tooth. The L × W of p3 measured on the tooth shaft is 2.70 × 2.55 mm. The triangular anteroconid is large (of similar size as the metaconid), linguallly elongated, with very shallow posterior and labial indentations, and its central axis is shifted towards the lingual side of the tooth. The metaconid is smooth, quadrangular, connected with the thick entoconid by a relatively wide metaisthmus. The mesoflexid is bent posteriorly. There is no enamel hiatus on the entoconid. On the lingual side the anteroconid and the entoconid are almost vertically aligned, whereas the metaconid protrudes slightly from this line. The crochet is well developed and bent buccally. The centroflexid enamel border is gently folded, and its lateral lobe is longer than the lingual one. The protoisthmus is long and thin, longer and thinner than the metaisthmus. The protoconid is transversally enlarged in its central part and its connection with the thick and relatively short protoculid is characterized by a spur.

On the poorly-preserved mandible fragment (paralectotype SMF 1994/895) the posterior mental foramen lies under the m1: the anterior mental foramen is not preserved. The height of the mandibular body, measured buccally at the level of p4/m1, is 10.8 mm. On p4–m2, the trigonids lack enamel hiatus in the anterior part and the talonids bear a well-developed anterior isthmus.

Localities of Gundersheim

The problem. – Since Heller’s publication (1936) of the fauna from the quarries near Gundersheim (District Alzey-Worms, Rheinland-Pfalz, Germany), the exact location, age and name of each locality have been the subject of confusion and discussion. There are three abandoned quarries from which the fossil fauna was collected (Tobien 1980; Fejfar & Čermák pers. obs., June 2006): Gewerkschaftsbruch (N 49°41′ 05″, E 8°10′ 53″), Rosengartenbruch (N 49°41′ 02″, E 8°10′ 57″) and Kesselsteinbruch (N 49°41′ 11″, E 8°11′ 29″). All these quarries are *ca* 1200–1800 m SW from the midpoint of the Gundersheim village (N 49°41′ 46″, E 8°12′ 09″, the coordinates given by Fostowicz-Frelik (2010, p. 610) for the “type” locality). Most of the fauna from this area was collected by F. Heller and W. Weiler in 1933 (Weiler 1935, Heller 1936) from Rosengartenbruch and Gewerkschaftsbruch. Although F. Heller kept separate the material he collected from different places/fissures of quarries (see Sindowski 1937), he, unfortunately, published all the specimens as one faunal

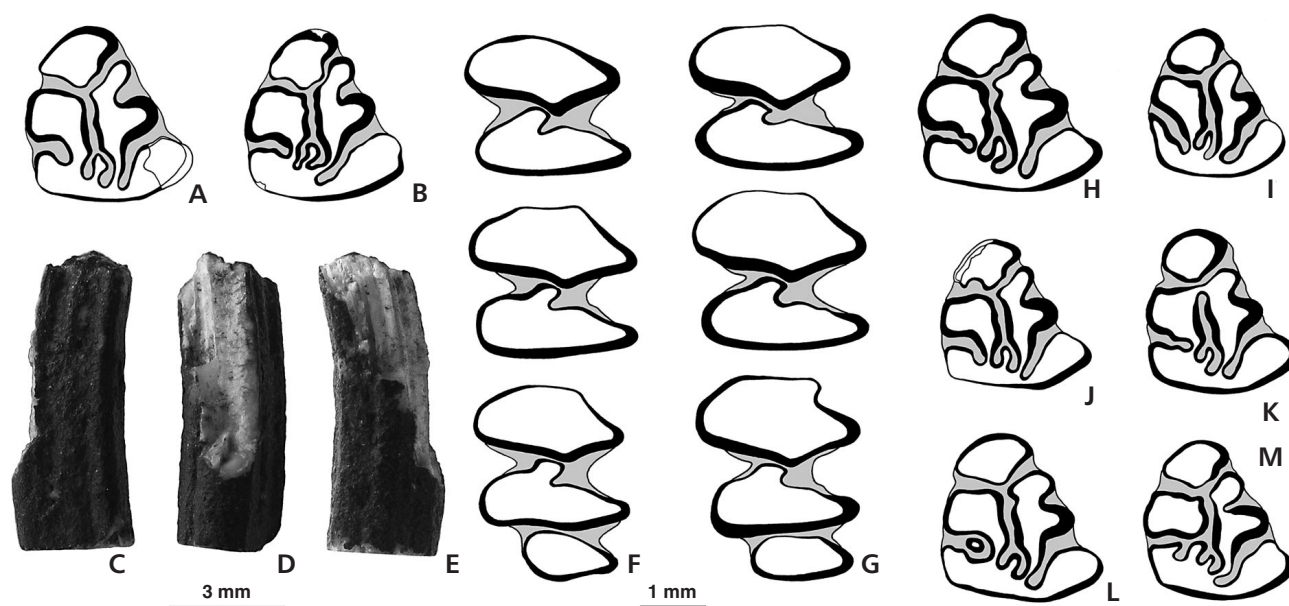


Figure 1. Pliocene *Prolagus* of central Europe. • A, C–E – lectotype of *Prolagus bilobus* Heller, 1936, left p3; A – transverse section, C – buccal view, D – anterior view, E – lingual view. • B, G – holotype of *P. osmolskae* Fostowicz-Frelik, 2010; B – occlusal view of right p3, G – occlusal view of right p4–m2. • F – paralectotype of *P. bilobus*, occlusal view of right p4–m2. • H–M – p3s of *P. bilobus* from Gundersheim-Findling, occlusal views (all figured as right specimens; I, J and L are reversed). Scale bars: 3 mm for photos (grey), 1 mm for drawings (white).

assemblage with only sporadic notes concerning their original provenance.

Localities and age. – Until the 1960s, all the fauna was generally considered as one faunal complex/assemblage and called simply Gundersheim (e.g., Kretzoi 1956). Later, Kretzoi (1962) divided the rodents from Gundersheim into two faunal units, an older one correlated with the Csarnotian (*sensu* Kretzoi 1962; *ca* MN 15b), and a younger one correlated with the Late Villányian (*sensu* Kretzoi 1962; *ca* MN 17). This view was subsequently broadly accepted (see Tobien 1980, for details). Tobien (1980) used numbers to distinguish the different faunal sub-samples of Heller's original collections from Gundersheim. He called the older faunal complex (*sensu* Kretzoi 1962) as Gundersheim-1 (however this locality was sometimes referred to MN 16a, e.g., in Fejfar & Heinrich 1981) and the younger one as Gundersheim-2. Tobien (1980) also numbered, parallel to the numbering of the faunas and independently to them, specific karst fissures discovered and studied by him (since the 1950s) in the quarries of Gundersheim. He numbered 22 fissures of which five yielded identifiable faunal remains (fissures Nos. 1, 4, 5, 7 and 11). Among them No. 4 was especially interesting (MN 15b, Fejfar *et al.* 2006) due to several finds of *Trilophomys*. Tobien (1980) assumed that the major part of Heller's "Csarnotian" elements most likely originated from this fissure.

Another Gundersheim fauna was discovered in 1976 and originated from an isolated block of fossiliferous sediment. Fejfar & Heinrich (1987) called this locality

Gundersheim-Findling. Later, after the arrangement with H. Tobien, Fejfar & Storch (1990) used the name Gundersheim-4 for this locality. The faunal assemblage from this block was correlated with the Late Ruscinian (MN 15b). The last paper about Gundersheim (Fejfar *et al.* 2006) described the Ruscinian fauna of fissure No. 4 (*sensu* Tobien 1980). But, the locality was once again called as Gundersheim-4 (= "Spalte Nr. 4 aus dem Gundersheimer Rosengartenbruch" *sensu* Dahlmann & Storch 1996, p. 181, = "undescribed material formerly in the possession of H. Tobien" *sensu* Fejfar 2001, p. 190). Thus, to avoid a potential misunderstanding, we propose to use the names 'Gundersheim-fissure 4' for the karst fissure No. 4 (*sensu* Tobien 1980, material described in Fejfar *et al.* 2006), and 'Gundersheim-Findling' for the isolated block discovered in 1976 (Fejfar & Storch 1990).

Pliocene Lagomorpha of Gundersheim. – According to Tobien (1974), Heller's original material of *P. bilobus* comes from the older faunal assemblages, i.e., Gundersheim-1 *sensu* Tobien (1980). This is strongly supported by other phenotypically comparable finds of *Prolagus* limited exclusively to the undoubtedly Late Ruscinian (MN 15b) sites Gundersheim-fissure 4 and Gundersheim-Findling. Gundersheim-Findling yielded also the leporid *Pliopentalagus dietrichi* (Fejfar, 1961), which is typical for MN 15. Moreover, there is no record of *Prolagus* in the MN 17 of central Europe (Germany, Poland, the Czech Republic, Slovakia, Hungary – except from Kisláng, which is a taphonomic mixture, *cf.* Mayhew 2012); this makes less

probable that *P. bilobus* comes from the MN 17 locality Gundersheim-2 (*sensu* Tobien 1980).

Taxonomic validity of *Prolagus osmolskae*

The criteria provided by Fostowicz-Frelik (2010) for the discrimination of *P. osmolskae* from *P. bilobus* are (1) the indentation of the posterior margin of p3 anteroconid (see Diagnosis, p. 609); (2) the size of the p3 of *P. osmolskae* being much larger than *P. bilobus* (see Discussion, p. 610). Both remarks are not correct, as we will discuss in the following sections (see also Fig. 1A, B, Table 1).

Size. – The lectotype (p3) of *P. bilobus* is slightly larger ($L \times W = 2.70 \times 2.55$ mm) than the holotype of *P. osmolskae* ($L \times W = 2.61 \times 2.42$ mm). Fostowicz-Frelik (2010, p. 610) underestimated the size of the lectotype of *P. bilobus* (2.20×2.52 mm) and also stated that “... additional material of *P. bilobus* from the same locality [*i.e.* Gundersheim-fissure 4] (Fejfar *et al.* 2006) includes a p3 of definitely smaller size”. As shown above, there is no direct evidence that Gundersheim-fissure 4 is the same as the original type locality of *P. bilobus*. At any rate, the size of *Prolagus* specimens from both Gundersheim localities is very variable. A direct observation of material from Gundersheim-fissure 4 published by Fejfar *et al.* (2006) proved the presence of very large specimens. For example P3 SMF 2005/3 ($L = 2.31$ mm) falls even over the dimensional range (L : OR = 1.94–2.21 mm, $N = 7$) of adult P3 specimens from Gundersheim-Findling. The measurements of p3 of *P. osmolskae* also fall in the observed range [$OR L \times W = (2.28–2.77$ mm) $\times (2.11–2.57$ mm), $X = 2.52 \times 2.30$ mm, $N = 6$] of comparative adult p3s from the equally relevant locality Gundersheim-Findling.

Morphology. – The name-bearing specimens of *P. bilobus* and *P. osmolskae* share on the p3 a: (1) large triangular anteroconid (of similar size as metaconid), which is indented posteriorly and buccally and whose central axis is shifted towards the lingual side of the tooth; (2) enamel folded around the centroflekid; (3) very well-developed and buccally bent crochet; (4) quadrangular metaconid; (5) well-developed protoconid and protoconulid; (6) long and thin protoisthmus; and (7) thick entoconid lacking enamel hiatus. In addition, the specimens from Gundersheim (Fig. 1H–M) show a tendency to plication of the p3 enamel pattern and to variability in the presence of standard additional lophids or enamel islets (note specimens with closed centroflekid, Fig. 1K; mesoflekid with enamel islet, Fig. 1L; or isolated metaconid, Fig. 1M). Considering the morphology of mandible, apart from the same position of the posterior

mental foramen (under the m1), no other observation can be made within the type series.

Conclusions and summary

The data above establish that *P. bilobus* is not “noticeably smaller” (Fostowicz-Frelik 2010, p. 610) than *P. osmolskae*. The confusing measurements of the lectotype of *P. bilobus* in Fostowicz-Frelik (2010), were most likely taken at the broken occlusal part of the tooth ($L \times W \sim 2.20 \times 2.50$ as measured by SC). This resulted in a misleading taxonomical consideration of the specimen from Raciszyn 1. Thus, considering the size and morphological variability of *Prolagus* from Gundersheim, the almost identical p3 size and morphology of the lectotype of *P. bilobus* and holotype of *P. osmolskae*, and the age and geographical distance (without any major barrier) of the type localities under study, it is proposed to consider *Prolagus osmolskae* Fostowicz-Frelik, 2010 as a junior subjective synonym of *P. bilobus* Heller, 1936. In conclusion, the above can be summarized as shown in the following chapter.

Systematic palaeontology

Order Lagomorpha Brandt, 1855
Family Prolagidae Gureev, 1960

Genus *Prolagus* Pomel, 1853

Prolagus bilobus Heller, 1936

Table 1, Figure 1

Synonym. – *Prolagus osmolskae* Fostowicz-Frelik, 2010, p. 609, fig. 1 (original description).

Lectotype. – SMF 1996/136, left p3, illustrated in Heller (1936, fig. 3).

Paralectotypes. – SMF 1994/895, right mandible fragment with p4–m2; SMF 1994/896, right talonid of p4; SMF 1994/897, right talonid of p4 or m1; SMF 1996/137, right trigonid of p4 or m1.

Type locality and age. – Gundersheim (probably Gundersheim-1 *sensu* Tobien 1980; MN 15b–16a), Rheinland-Pfalz, Germany; the exact age uncertain (within the possible age range, taking into account phenotypically comparable finds of *Prolagus* from other localities of Gundersheim, a referral to MN 15b seems to be most likely).

Referred material. – ZPAL M.10, right mandible body with complete dentition (Raciszyn 1, MN 15b); SMF

Table 1. Tooth measurements of type material of Pliocene *Prolagus* of central Europe (* = tooth fragment of uncertain determination, p4 or m1).

Species		p3		p4				m1				m2			
Specimen No.	Type	L	W	L	Ltrig	Wtrig	Wtal	L	Ltrig	Wtrig	Wtal	L	Wtrig	Wtal	Wtl
<i>Prolagus bilobus</i>															
SMF 1996/136	Lt	2.70	2.55												
SMF 1994/895	Plt			2.20	1.27	2.40	2.36	2.32	1.27	2.50	2.44	2.93	2.28	2.24	1.43
SMF 1994/896	Plt						2.31								
SMF 1994/897	Plt						1.76*								
SMF 1996/137	Plt				1.12*	2.25*									
<i>Prolagus osmolskae</i>															
ZPAL M.10	Ht	2.61	2.42	2.25	1.36	2.36	2.40	2.48	1.42	2.59	2.47	3.10	2.41	2.11	1.45

2005/3, left P3 (Gundersheim-fissure 4, MN 15b); SMF 1985/77–83, 3 left and 4 right P3s; SMF 1985/159–164, 3 left and 3 right p3s (Gundersheim-Findling, MN 15b).

Emended diagnosis. – Very large p3 (largest one among the continental European MN 13–17 species) with lingually shifted, large, triangular, posteriorly and buccally indented anteroconid; crenulated centroflexid, long and buccally bent crochet; metaconid of similar size as anteroconid; thick entoconid lacking enamel hiatus. Lower third premolar differs from that in: (1) *P. depereti*, *P. ibericus*, *P. italicus*, *P. savagei* in having a larger crochet; (2) *P. caucasicus* in having a quadrangular metaconid; and (3) *P. michauxi*, *P. sorbinii* in having a triangular indented anteroconid, which is vertically aligned with the entoconid.

Stratigraphic and geographic distribution. – Early/Late Pliocene (MN 15b/?16a); localities Gundersheim-1, Gundersheim-fissure 4, Gundersheim-Findling, possibly Wölfersheim (all in Germany) and Raciszyn 1 (Poland); central Europe.

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