# New data on the Miocene stem lagomorph *Eurolagus fontannesi*, and its northernmost record

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We describe new dental material of *Eurolagus fontannesi* from the Late Miocene (Early Vallesian, MN 9) lignite beds of Bełchatów A (central Poland), which is the northernmost occurrence of this lagomorph. This material considerably increases the sample size of this rare genus and species. We review the systematic position of *Eurolagus* and argue that it is not an ochotonid, but represents a terminal taxon of an independently evolved stem lineage of Lagomorpha. The enamel of the molars, here studied for the first time, exhibits a relatively thin decussating external and a radial internal layer, and in general resembles the palaeolagine lagomorphs (*Palaeolagus*) rather than the archaeolagine leporids (*Hypolagus*) or advanced ochotonids (*Ochotona*). The dental wear features of *Eurolagus fontannesi* indicate that the species was a sylvan mixed-feeder. This agrees with the Bełchatów A paleoenvironment, which is best approximated as the kind of mixed mesophytic forest now encountered in the Caucasus, Iran, and India. The extinction of *Eurolagus* was probably related to the noticeable faunal change following the increased cooling of the European climate during the Late Miocene. The first indicator of this event can be observed in Bełchatów A, marked by the immigration of *Microtocricetus* and the absence of *Neocometes*.

Key words: Lagomorpha, *Eurolagus*, microwear, paleoecology, semihypsodonty, Vallesian, Bełchatów, Poland.

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## Introduction

*Eurolagus fontannesi* (Depéret, 1887) was a relatively large semihypsodont lagomorph inhabiting western and central Europe (Fig. 1) during the late Middle to Late Miocene (Tobien 1974; López Martínez 1977, 1989). Its stratigraphic distribution ranges from the Astaracian to the Vallesian, with the taxon first appearing in the Middle Astaracian (MN6) assemblages of Subpiatră 2/1 in the Bihor Mountains, Romania (Hír and Venczel 2005), and Four near La Grive Saint-Alban, Isère, France (Maridet et al. 2000), although according to Sen (in Bernor et al. 2004) *E. fontannesi* might already have appeared during the Late Orleanian/Early Astaracian (MN 5, Rothenstein 1, Germany). The last occurrence of this species is recorded from Late Vallesian (MN 10) deposits in Spain (Trinxera Nord Autopista, Can Jofresa section, Terrassa; Agustí and Gibert 1982) and France (Soblay near Saint-Martin-du-Mont; Ménouret and Mein 2008).

In Poland, this species was first reported from the Sarmatian beds of Opole 1 (= Oppeln; Wegner 1913), which

correlate with MN 7+8 (Kowalski 1990), but the material housed in the collection of the then German University of Wrocław was most probably lost during World War II (Tobien 1974; Wolsan 1989). The scarce lagomorph material from the nearby Opole 2 locality (Kowalski 1967), dated to a similar age (Kowalski 1990), is insufficient to allow an assignment even at the generic level. Therefore, we decided not to include the material from Opole in this paper.

*Eurolagus fontannesi* is only known from sparse dental remains (e.g., Tobien 1974; López Martínez 1989; Pickford et al. 2000; Kälin and Engesser 2001; Hír and Venczel 2005; Hír and Kókay 2010). The only exception is La Grive (France), the type locality, from which over 80 specimens, including maxillae and mandible fragments, have been reported.

In this paper, we provide a description of the second most abundant (except the type locality) material of *Eurolagus fontannesi*, documenting both the northernmost and one of the latest occurrences of this species from level A (MN 9) of the Bełchatów lignite mine in south-central Poland. The enamel structure and dental microwear of *Eurolagus* are

Fig. 1. Spatio-temporal distribution of *Eurolagus fontannesi* (Depéret, 1887) in Europe. Sites: 1, Sant Quirze; 2, Can Mata; 3, St Miquel de Taudell; 4, Can Llobateres; 5, Terrassa; 6, La Grive; 7, Four; 8, Soblay; 9, Anwil; 10, Langenmoosen; 11, Attenfeld; 12, Rothenstein; 13, Hammerschmiede; 14, Giggenhausen; 15, Opole; 16, Rudabánya; 17, Felsötárkany; 18, Subpiatră; 19, Grytsev; 20, Belometchetskaya. Bełchatów marked with a star, the diamond indicates *Eurolagus* aff. *fontannesi* (Pickford et al. 2000), and the square marks "*Amphilagus*" *sarmaticus* (Topachevsky 1987). White circle = MN 5 and 6, gray circle = MN 7+8, and black circle = MN 9 and 10. Data from Fortelius (2010) and references in the text.

studied for the first time, giving some insights into the dietary preferences of this animal. Moreover, we attempt to elucidate the relationships of this poorly understood species. Finally, we also provide a short overview of the Early Vallesian fauna and the sedimentary environment of Bełchatów level A.

*Institutional abbreviations.*—ISEZ, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland; MIIZ, Museum and Institute of Zoology, Polish Academy of Sciences, Warszawa, Poland; ML, Muséum d'Histoire Naturelle (currently Musée des Confluences), Lyon, France; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warszawa, Poland.

*Other abbreviations.*—CMT, mean temperature of the coldest month; HSB, Hunter-Schreger bands; MAP, mean annual precipitation.

# Material and methods

The studied material is housed in the collection of the ISEZ. Measurements were taken to the nearest 0.01 mm using SYLVAC digital caliper. The specimens were examined under a stereoscopic light microscope (Nikon SMZ 800) equipped with a camera lucida, and two electron scanning microscopes: Hitachi S-3400N with a Thermo Noran Company X-ray microanalysis system (at MIIZ), and Philips XL20 with an SE detector and EDX dual-window (JTW/ Open) ECON detector for X-ray energy dispersive analyses (at ZPAL). We used the Hitachi SEM to examine the specimens without coating, using a natural mode (low vacuum) with Backscattered Electron Detector (BSE). It was employed mainly to study the element content and distribution of iron sulphide aggregates. The Philips XL20 SEM was used to study the enamel microstructure and tooth morphol-

ogy. The samples for the enamel study were embedded in epoxy resin and polished and etched with dilute (1%) orthophosphoric acid for ca. 60 seconds (Wood 2000), before being coated with platinum. The study of microwear patterns included counting the pits and scratches on a square surface of 0.09 mm$^2$ at a magnification of ×100, a standard procedure for such studies on rodents (Nelson et al. 2005; Townsend and Croft 2008). The counting was performed twice and microphotographs were used instead of casts. Morphological terminology follows Meng et al. (2005), with some modifications; enamel microstructure terminology was adapted from Martin (1999, 2004).

# Geological setting

The Bełchatów open-pit mine is one of the largest lignite deposits in Europe and is located in central Poland (51°15'N, 19°20'E), within a series of tectonic depressions referred to as the Kleszczów Graben (Stuchlik et al. 1990; Worobiec and Lesiak 1998; Szynkiewicz 2000; Worobiec 2003; Worobiec and Szynkiewicz 2007). A series of Neogene deposits fills the tectonic fault, which is about 40 km long, 2.5 km wide, and 500 m deep, extending in an E-W direction. The bedrock of the basin is formed by Jurassic and Cretaceous rocks, with a centrally located salt dome (Stuchlik et al. 1990; Szynkiewicz 2000).

The Neogene sediment sequence at Bełchatów (Fig. 2) is dated to the Eggenburgian–Pannonian and includes clastic deposits (sand and sandy clays) intercalated with lignite beds (xylite brown coals with or without clays and sapropelic coals), lake marls, and volcanic ash layers (Stuchlik et al. 1990; Szynkiewicz 2000). Within this series, four informal litostratigraphic units, referred to as sedimentary complexes, have been recognized (Czarnecki et al. 1992; Szynkiewicz 2000). These complexes are from lowest to highest: the "below coal sedimentary complex acronymed as PW", the "coaly sedimentary complex or W" which includes the main coal bed, the "coaly-clay sedimentary complex or I-W", and the "sandy-clay sedimentary complex or I-P" (Fig. 2; Szynkiewicz 2000: fig. 1).

Since their discovery in the 1960s, the rich fossil flora and fauna of Bełchatów have been intensively investigated (Jerzmańska and Hałuszczak 1986; Głazek and Szynkiewicz 1987; Stuchlik et al. 1990; Kowalski 1993a, b, 1997a, b; Kowalski and Kubiak 1993; Rzebik-Kowalska 1993, 1994, 1996, 2005; Stworzewicz 1995, 1999a, b; Worobiec 1995, 2003; Van der Made and Kowalski 1996; Garapich and Kälin 1999; Kadolsky and Piechocki 2000; Szynkiewicz 2000; Nadachowski 2001; Rzebik-Kowalska and Kowalski 2001; Garapich 2002; Kowalski and Rzebik-Kowalska 2002; Worobiec and Worobiec 2005; Worobiec and Szynkiewicz 2007). Plant megafossils are known from almost the entire Miocene sequence and indicate a moderately warm and humid sylvan environment with a prevalence of azonal vegetation indicative of swamp or riparian forests, as well as zonal mixed mesophytic

forests for most of the time during which the sedimentary complexes P-W to I-W were formed (Stuchlik et al. 1990; Worobiec and Lesiak 1998; Worobiec 2003; Worobiec and Worobiec 2005; Worobiec and Szynkiewicz 2007). The level of humidity varied during the time of deposition, resulting in a sequence of more and less hygrophilous species, but the overall environmental character was not substantially different from recent counterparts found in south-eastern North America, East Asia, and Transcaucasia. The absolute minimum for winters has been estimated at no lower than -5°C (Szynkiewicz 2000; Kowalski and Rzebik-Kowalska 2002; Worobiec 2003) and probably was above 0°C (the average CMT for Massenhausen, Germany, 48°21'N, 11°39'E, was ~2°C during the early Pannonian; Bruch et al. 2004).

There are three principal faunal levels in the Neogene deposits of Bełchatów. The oldest assemblage (fauna C) is correlated with the Ottangian–Karpatian–Early Badenian and the MN 4/5 mammal zone. This fauna is located within the main coal bed and is overlain by a layer of volcanic ash and tephra track dated to 18.1±1.7 Ma (Burchart et al. 1998). By contrast, faunal level B is of Early Badenian (MN5) origin, lies at the boundary between the "coaly" and "coaly-clay" sedimentary complexes, and is superimposed by tephra dated to 16.5±1.3 Ma (Burchart et al. 1998), while fauna A is of Late Sarmatian–Early Pannonian (MN 7+8/9 or MN 9) origin and was recognized in the middle of the "coaly-clay sedimentary complex" (Szynkiewicz 2000; Nadachowski 2001; Kowalski and Rzebik-Kowalska 2002).

The estimated age of Bełchatów A as MN 9 is strongly supported by the coexistence of two cricetid rodents: *Anomalomys gaudryi*, which persisted in Europe no longer than until MN 9; and *Microtocricetus molassicus*, which is characteristic of the MN 9 zone (Kowalski and Rzebik-Kowalska 2002; Mein 2003).

All of the lagomorph specimens described herein were recovered from the uppermost faunal level, Bełchatów A. Although unidentified remains of Lagomorpha have also been reported from the other two levels (Nadachowski 2001; Kowalski and Rzebik-Kowalska 2002) they were not available to the authors for study.

# Depositional environment and taphonomy

The studied remains were recovered from thin lignite layers intercalated with lacustrine limestones (lake marls) containing a rich freshwater (Kadolsky and Piechocki 2000) and terrestrial malacofauna (Stworzewicz 1995, 1999a, b; Stworzewicz and Sołtys 1996). The depositional conditions can be reconstructed as shallow stagnating water with a thick layer of organic debris accumulated at the bottom, creating an anoxic environment. The pH was, however, rather close to neutral, with a low level of humic acids. The qualitative and quantitative X-ray microanalyses of the teeth, at the occlusal
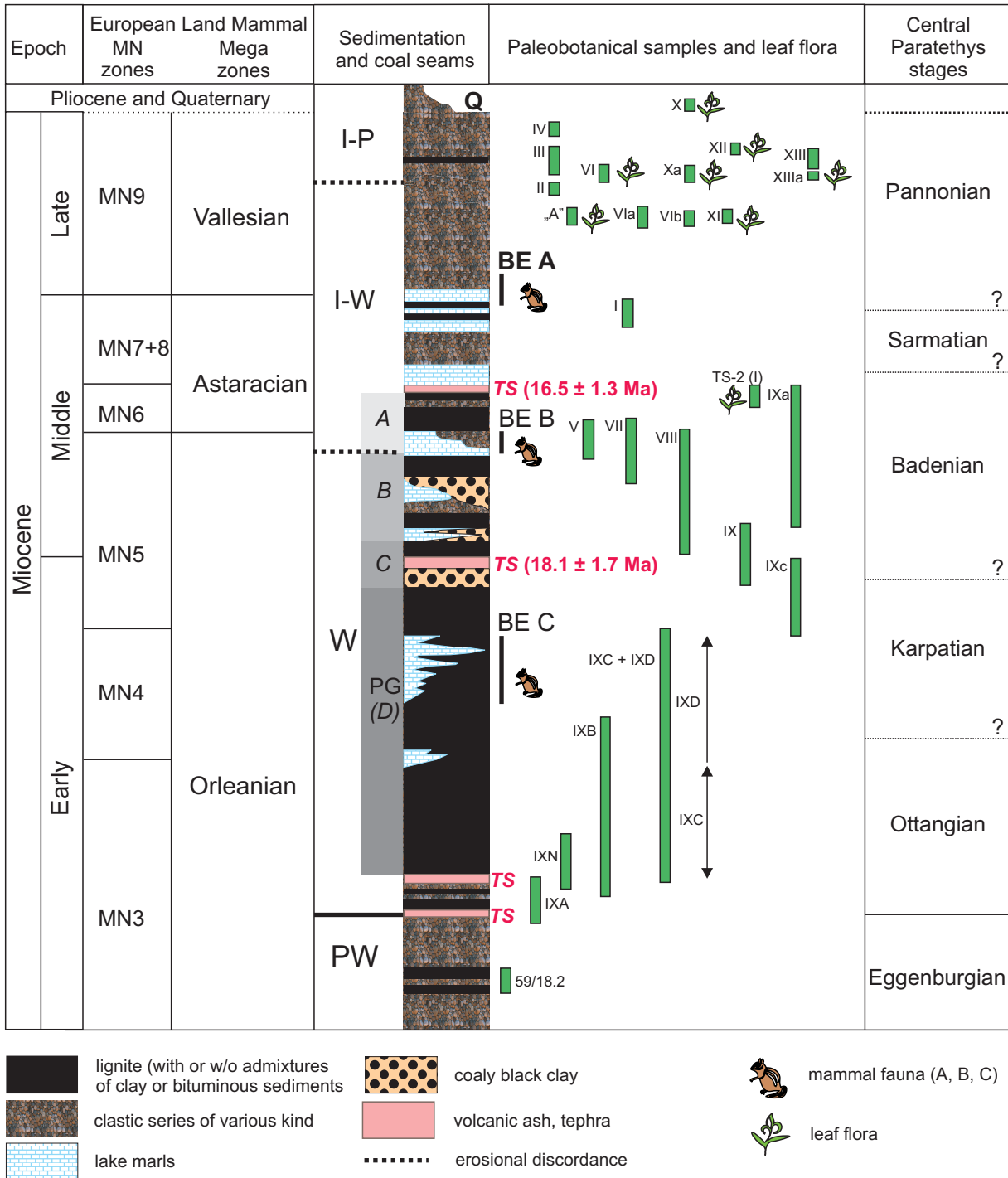
Fig. 2. Generalized lithostratigraphic section of the Neogene deposits of the Bełchatów site, with the position of vertebrate faunas (after Szynkiewicz 2000; Worobiec and Szynkiewicz 2007, modified). I–XIII, paleobotanical profiles, A–D, coal seams, *TS*, tonsteins (track dating).

and sectioned surfaces, show an average Ca/P atomic ratio typical for biogenic hydroxyapatite (i.e., 1.67), with only a slight decrease in the ratio at the external surface (Table 1). Thus, neither considerable wash-out, nor enrichment in Ca, which is normally observed in diagenetically altered samples (Dauphin and Williams 2004), were detected. These conditions are confirmed by the abundance of well-preserved snail shells found in the same beds (Stworzewicz 1993, 1999a, b).

The specimens are rather brittle, and the dentine and cement surfaces are heavily cracked, indicating temporary drying of the poorly consolidated sediment. However, the enamel structure appears not to have been affected or altered by these conditions, allowing the study of microwear patterns in these specimens.

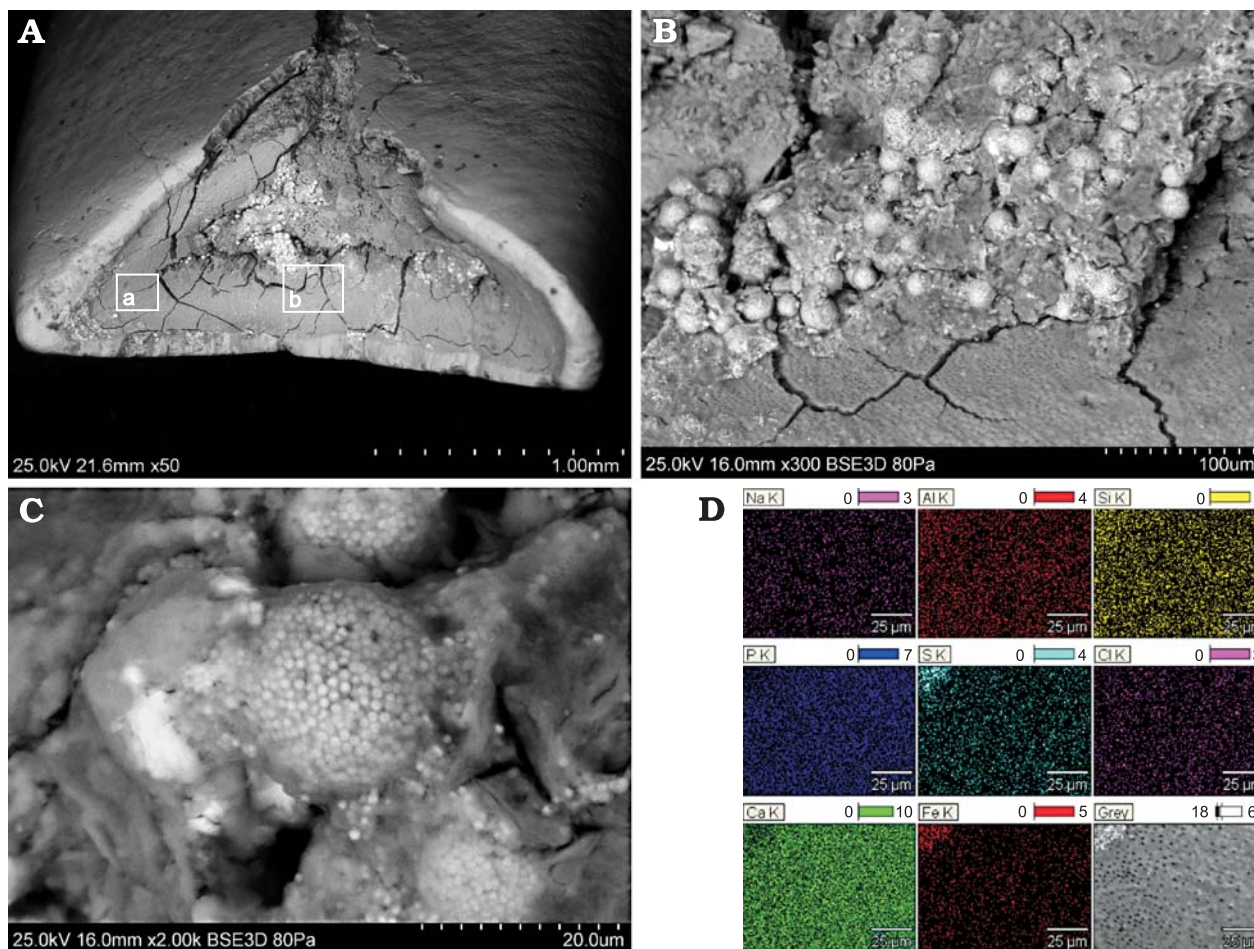The quantitative chemical analysis and element mapping of the molar occlusal surface revealed the presence of

Fig. 3. Mineralization of the lagomorph dental elements from Bełchatów level A. **A–C**. Aggregates of framboidal pyrite at the lower molar occlusal surface. **A**. The trigonid showing regions analyzed for element content, frame a, dentine, frame b, region mapped in D. **B**, **C**. Closeups of A. **D**. Element mapping of a fragment of the dental occlusal surface; note the presence of silicates, iron sulfide, and chlorides.

Na, Al, Si, Fe, S, and Cl (Fig. 3D, Table 1). This array of elements indicates aluminosilicate, iron sulfide, and chloride mineralization. Iron (II) disulfide, in the form of aggregates of framboidal pyrite on the tooth surface (Fig. 3A–C), marks highly reductive (anoxic) deposition conditions and extensive bacterial activity, as may be expected from bog-like deposits (Stachura and Ratajczak 2004). The presence of chlorides was also indirectly supported by the brackish malacofauna reported form Bełchatów levels A and B (Ka-dolsky and Piechocki 2000; Kowalski and Rzebik-Kowalska 2002).

# Systematic paleontology

Order Lagomorpha Brandt, 1855
Family Palaeolagidae Dice, 1929

Table 1. Element content (carbon and oxygen excluded) of the tooth surfaces of *Eurolagus fontannesi* (Depéret, 1887) from Bełchatów A.

| Sample | Element composition [At%] | | | | | | | | Ca/P |
|---|---|---|---|---|---|---|---|---|---|
| | Na | Cl | Al | Si | Fe | S | Ca | P | |
| Dentine (occlusal surface) | 0.91 | 0.27 | 0.88 | 0.71 | 0.36 | 0.27 | 14.90 | 10.89 | 1.37 |
| Dentine (cross section) | 0.34 | 0.05 | – | 1.07 | 0.08 | 0.19 | 11.60 | 6.80 | 1.70 |
| Enamel (cross section) | 0.54 | 0.13 | – | 0.92 | 0.21 | 0.23 | 17.73 | 11.40 | 1.55 |
| Framboidal pyrite area | – | – | 3.96 | 2.57 | 31.80 | 7.70 | 3.48 | 1.55 | not relevant |
| Point 1 | – | – | 0.57 | 0.92 | 5.96 | 3.07 | 0.86 | 0.55 | |
| Point 2 | – | – | 5.60 | 5.86 | 2.33 | 0.41 | 1.18 | 0.68 | |
| Point 3 | – | – | 2.08 | 1.72 | 4.63 | 1.72 | 0.90 | 0.67 | |
| Point 4 | – | – | 3.49 | 2.60 | 5.41 | 0.51 | 1.53 | 0.79 | |
| Point 5 | | | 2.19 | 1.61 | 4.02 | 0.99 | 0.97 | 0.59 | |

## Genus *Eurolagus* López Martínez, 1977

*Type species*: *Eurolagus fontannesi* (Depéret, 1887), by monotypy; La Grive Saint-Alban (Isère, France), Astaracian.

*Diagnosis.*—Large semihypsodont lagomorph, smaller than *Megalagus* and larger than *Amphilagus antiquus*, *Desmatolagus*, most species of *Gobiolagus*, *Gripholagomys*, *Mytonolagus*, *Piezodus*, and *Titanomys*, and all species of *Palaeolagus,* except the larger *P. intermedius*. More strongly hypsodont than most of the primitive stem lagomorphs, with a tooth crown height comparable to that of *Megalagus* and advanced *Mytonolagus* (*M. wyomingensis*), slightly lower than that of *Amphilagus*, and markedly lower than that of the semihypsodont species of *Palaeolagus*. Curvature of the upper teeth is definitely larger than in *Palaeolagus*, less than in the rootless *Titanomys calmensis*, and similar to that in *Amphilagus*, *Desmatolagus*, *Megalagus*, *Mytonolagus*, *Titanomys visenoviensis*, and *Piezodus branssatensis*. A trilobate P2 distinguishes *Eurolagus* from the basically bilobate tooth of *Palaeolagus*. P3 is not molarized, unlike that of *Palaeolagus*; the lingual lobe of P3 is longer than in *Amphilagus*, *Desmatolagus*, *Gobiolagus*, and most of *Mytonolagus*, and more compressed anterodistally than in those genera and in *Megalagus*. P4 molarized unlike that of *Gobiolagus* and *Lushilagus*. Persistency of the enamel pattern on the upper cheek teeth separates *Eurolagus* from *Lushilagus*, *Shamolagus*, and *Gobiolagus*, in all of which the hypostriae are weak and the occlusal pattern wears relatively quickly. The hypostria is deeper than in *Desmatolagus*, and comparable to that of *Mytonolagus* and *Megalagus*; it is relatively shallow on P3 and P4 (shallower than in *Palaeolagus*) and cuts across one-third of the occlusal surface on M1 and M2. Hypostrial lakes are absent in *Eurolagus*, unlike in *Palaeolagus*, *Megalagus*, *Mytonolagus*, *Gripholagomys*, and *Desmatolagus*. The p3 is single-rooted, unlike the double-rooted tooth of *Mytonolagus*, *Megalagus*, and *Strenulagus*. The crown of p3 is bilobate and compact, with a short and relatively large trigonid, and a slightly concave anterolingual side in younger individuals, resembling in outline and proportions the p3 of *Amphilagus antiquus*, *Megalagus*, and *Gripholagomys* at most wear stages. This tooth further differs from that of *Desmatolagus*, which has a smaller trigonid, *Mytonolagus*, which has an enlarged trigonid, and *Gobiolagus*, *Lushilagus*, and *Shamolagus*, which have a trilobate p3. The lingual reentrant of p3 is much less persistent than in *Titanomys*, *Palaeolagus*, and some species of *Mytonolagus*. Together with the absence of an isolated anteroconid, this distinguishes *Eurolagus* from *Piezodus*. Differs from all genera (apart from *Mytonolagus*) in having more persistent reentrants on the buccal instead of the lingual side of the talonids of the lower cheek teeth. The m2 has fused roots as in *Amphilagus* and *Palaeolagus*, unlike the condition in *Megalagus* and *Mytonolagus*. The m3 is reduced in comparison to that in *Lushilagus*, *Shamolagus*, and *Gobiolagus* and marked by two conids, unlike the m3 in *Amphilagus*, *Titanomys*, and *Piezodus* (m3 with single conid). Both conids become fused late during ontogeny as in *Desmatolagus,* but unlike the condition

Table 2. Dental measurements (in mm) of *Eurolagus fontannesi* (Depéret, 1887) from Bełchatów A. Abbreviations: W, width; L, length; CrH, height of the tooth crown. Estimated values are italicized.

| Tooth | Specimen # | W | L | CrH |
|---|---|---|---|---|
| P2 | MF/5065 | 2.30 | 1.41 | – |
| | MF/5066 | 2.64 | 1.39 | 2.1 |
| | MF/5067 | 2.48 | 1.25 | – |
| | MF/5068 | 2.50 | 1.10 | – |
| | MF/5069 | 2.21 | 1.40 | – |
| P3 | MF/5070 | – | *2.00* | 5.88 |
| | MF/5071 | 3.67 | 2.24 | – |
| | MF/5075 | 3.95 | 2.12 | 5.13 |
| P4 | MF/5074 | 3.12 | 2.08 | 5.62 |
| M1 | MF/5076 | 4.35 | 2.36 | 6.96 |
| | MF/5101/b | 4.22 | 2.30 | 6.94 |
| M2 | MF/5078 | 3.40 | 2.36 | – |
| | MF/5079 | 3.30 | 2.09 | 3.34 |
| | MF/5081 | 3.24 | 1.96 | 4.60 |
| p3 | MF/5082 | 2.67 | 2.33 | – |
| | MF/5083 | 2.23 | 2.01 | – |
| m1 or m2 | MF/5084 | 2.80 | 2.72 | *6.00* |
| | MF/5086 | 2.87 | 2.50 | 6.00 |
| m3 | MF/5087 | 1.55 | 1.50 | 2.77 |
| Isolated trigonids | MF/5089–95, MF/5099 | (8) 2.65±0.37 | (6) 1.17±0.10 | – |
| Isolated talonids | MF/5097–98, MF/5096 | (3) 2.16 | (3) 1.28 | – |

seen in *Megalagus* and *Palaeolagus*. *Eurolagus* further differs from *Gobiolagus*, *Lushilagus*, *Mytonolagus*, and *Shamolagus* in having no trace of an additional lobe on m3.

## *Eurolagus fontannesi* (Depéret, 1887)

Figs. 4–9.

*Holotype*: ML LGr 169, maxilla with P4 and M2. Figured in Depéret 1887: pl. 13: figs. 19–19b.

*Material.*—P2 (MF/5065, MF/5066, MF/5067, MF/5068, MF/5069); P3 (MF/5070, MF/5071, MF/5072 juv., MF/5075); P4 (MF/5074, MF/5101/a, MF/5077); M1 (MF/5076, MF/5101/b, MF/5080); M2 (MF/5078, MF/5079, MF/5081, MF/5073 juv., MF/5088); p3 (MF/5082, MF/5083); m1 or m2 (MF/5084, MF/5085, MF/5086); m3 (MF/5087); trigonids of lower premolars or molars (MF/5089–95, MF/5099); talonids of lower premolars or molars (MF/5096–98); other tooth fragments (MF/5101).

*Diagnosis.*—As for the genus.

## Description

The studied material consists of isolated teeth representing all loci except the incisors (dI2/di2) and M3 (Table 2).

*P2.*—Five specimens at different stages of wear are represented in the Bełchatów sample. The tooth is oval, trilobate, and compressed anterodistally. Generally, the morphology of P2 is very conservative in Lagomorpha, and the same
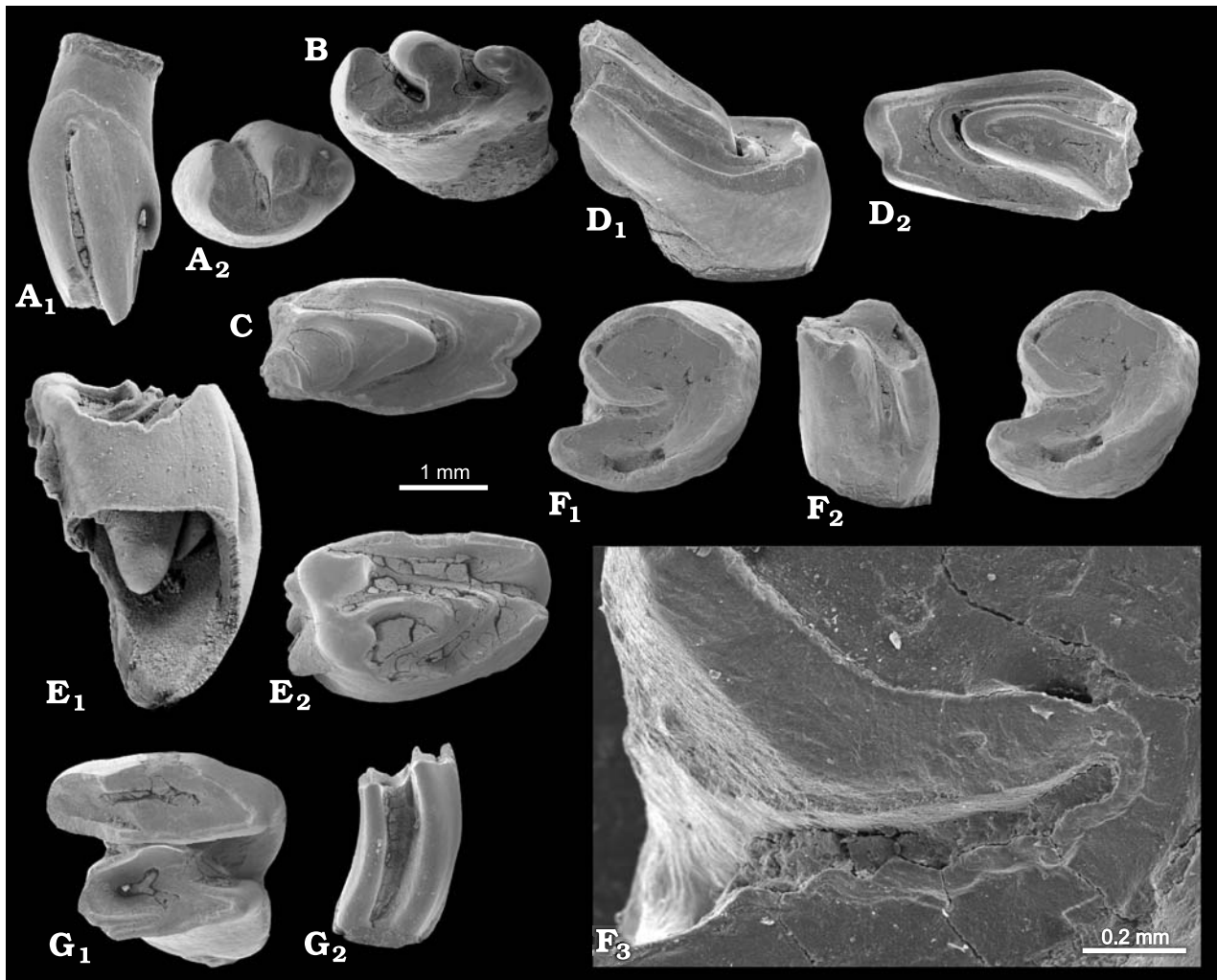
Fig. 4. The Miocene stem lagomorph *Eurolagus fontannesi* (Depéret, 1887) from Bełchatów A, Poland. **A**. P2 (MF/5065), in anterior ($A_1$) and occlusal ($A_2$) views. **B**. P2 (MF/5066) in occlusal view. **C**. P3 (MF/5075) in occlusal view. **D**. P3 senile form (MF/5071) in anterior ($D_1$) and occlusal ($D_2$) views. **E**. M2 (MF/5078), in distal ($E_1$) and occlusal ($E_2$) views; note the depth of the internal dorsoventral crescent in distal view. **F**. p3 (MF/5082) in occlusal (stereopair $F_1$) and buccal ($F_2$) views, and magnified view of the buccal reentrant area ($F_3$) showing gentle crenulation of the distal wall and cement filling. **G**. ?m2 (MF/5084) in occlusal ($G_1$) and buccal ($G_2$) views.

trilobate pattern is shared by most species known from the Eocene to the Miocene, with the teeth differing only in their level of hypsodonty (Dawson 1958; Tobien 1974, 1975; Topachevsky 1987; Meng et al. 2005; Fostowicz-Frelik and Tabrum 2009).

The lobes are separated by two anterior reentrants, of which the buccal one is less persistent (Figs. 4A, B, 5A, B). The lingual lobe is the largest, convex lingually, and in juvenile specimens sometimes gently flattened or concave buccally. The central lobe is more symmetrical; in juvenile specimens, it is elongated, tear-shaped, and connected to the posterior base of the tooth through a narrow isthmus. The latter broadens during ontogeny, and in older specimens nearly equals the width of the lobe at mid-length (Fig. 5A$_2$). Both lobes have a thickened enamel layer, the lingual lobe mainly on the lingual side and the central lobe along the anterior wall. The buccal lobe appears last during ontogeny. It forms a small separate cusp, initially placed much more dorsally on

the tooth shaft than the other two cusps (Figs. 4A, 5A$_2$). As wear progresses, this cusp eventually becomes nearly equal in dorsoventral dimension to the other two cusps (Fig. 5A$_1$). At this stage, it is connected to the central lobe by a long, low ridge (Fig. 5A$_2$). While the occlusal surface of the buccal lobe is generally round, it sometimes develops a shallow buccal groove in older specimens (Fig. 5B). The enamel layer of the buccal lobe is sometimes thickened along the anterior and buccal surfaces. The P2 has a single root (Figs. 4A$_1$, 5A$_1$), and a moderately high crown broadening near the base. The latter is of uneven height, being highest on the lingual side, at the base of the lingual reentrant, and lowest on the buccal side dorsal to the buccal lobe.

*P3.*—The P3 is represented by two strongly damaged and two worn teeth (Fig. 4C, D), one (MF/5071) classified as a senile stage (sensu Tobien 1974). The early ontogenetic stages of this locus can therefore not be ascertained. In both specimens, the lingual lobe is markedly long, surrounding
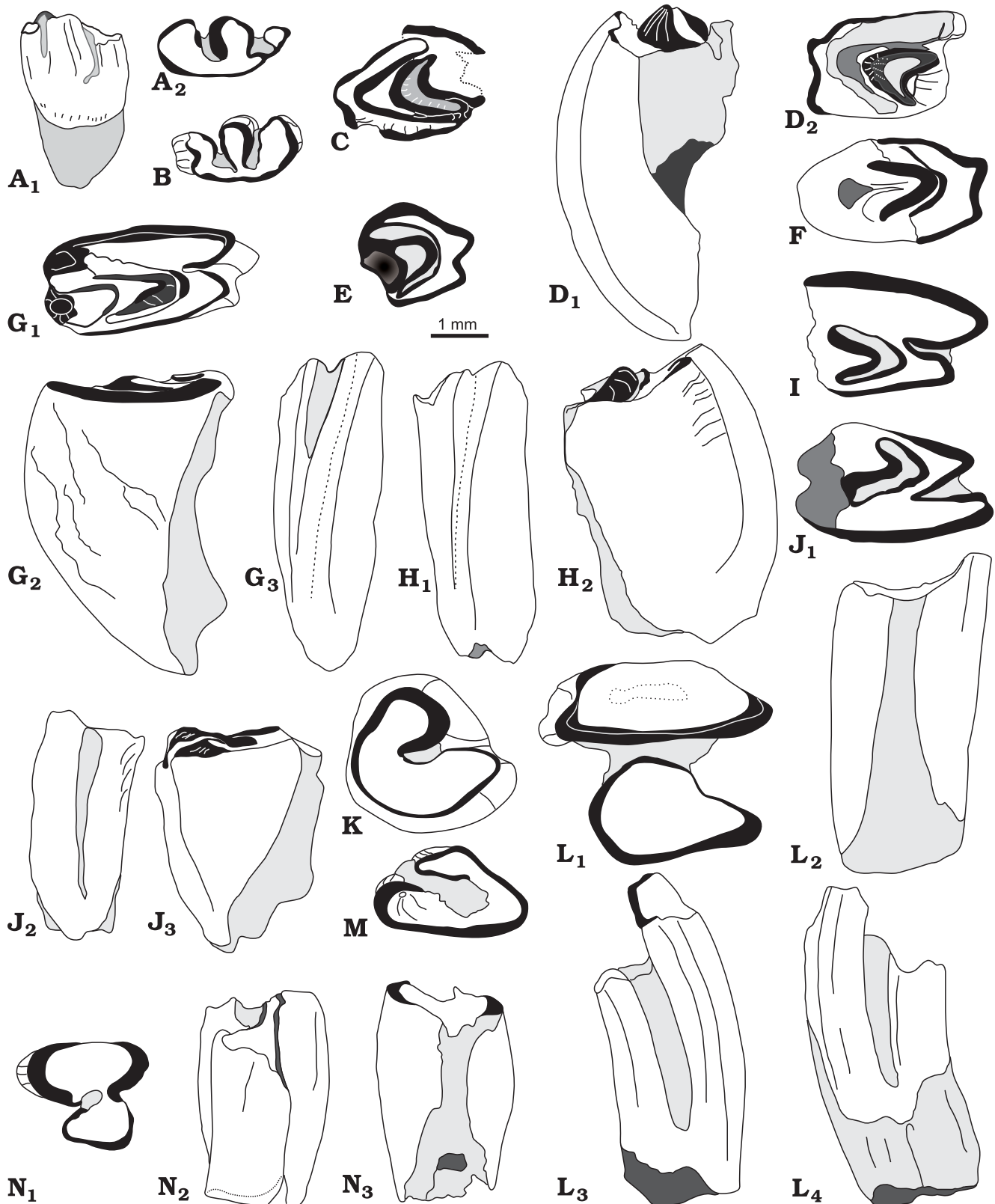
Fig. 5. The Miocene stem lagomorph *Eurolagus fontannesi* (Depéret, 1887) from Bełchatów A, Poland. **A**. P2 (MF/5067) in anterior (A$_1$) and occlusal (A$_2$) views. **B**. P2 (MF/5068) in occlusal view. **C**. Fragment of juvenile P3 (MF/5072). **D**. P4 (MF/5074) in distal (D$_1$) and occlusal (D$_2$) views. **E**. Juvenile P4 (MF/5101/a) in occlusal view. **F**. Fragment of P3 (MF/5070) in occlusal view. **G**. M1 (MF/5101/b) in occlusal (G$_1$), anterior (G$_2$), and lingual (G$_3$) views. **H**. M1 (MF/5076) in lingual (H$_1$) and distal (H$_2$) views. **I**. M2 (MF/5079) in occlusal view. **J**. M2 (MF/5081) in occlusal (J$_1$), lingual (J$_2$), and distal (J$_3$) views. **K**. p3 (MF/5083) in occlusal view. **L**. m2 (MF/5086) in occlusal (L$_1$), anterior (L$_2$), buccal (L$_3$), and lingual (L$_4$) views; note the enamel hiatus in anterior view. **M**. Separated trigonid of juvenile lower molar (MF/5089) in occlusal view. **N**. m3 (MF/5087) in occlusal (N$_1$), distal (N$_2$), and anterior (N$_3$) views.
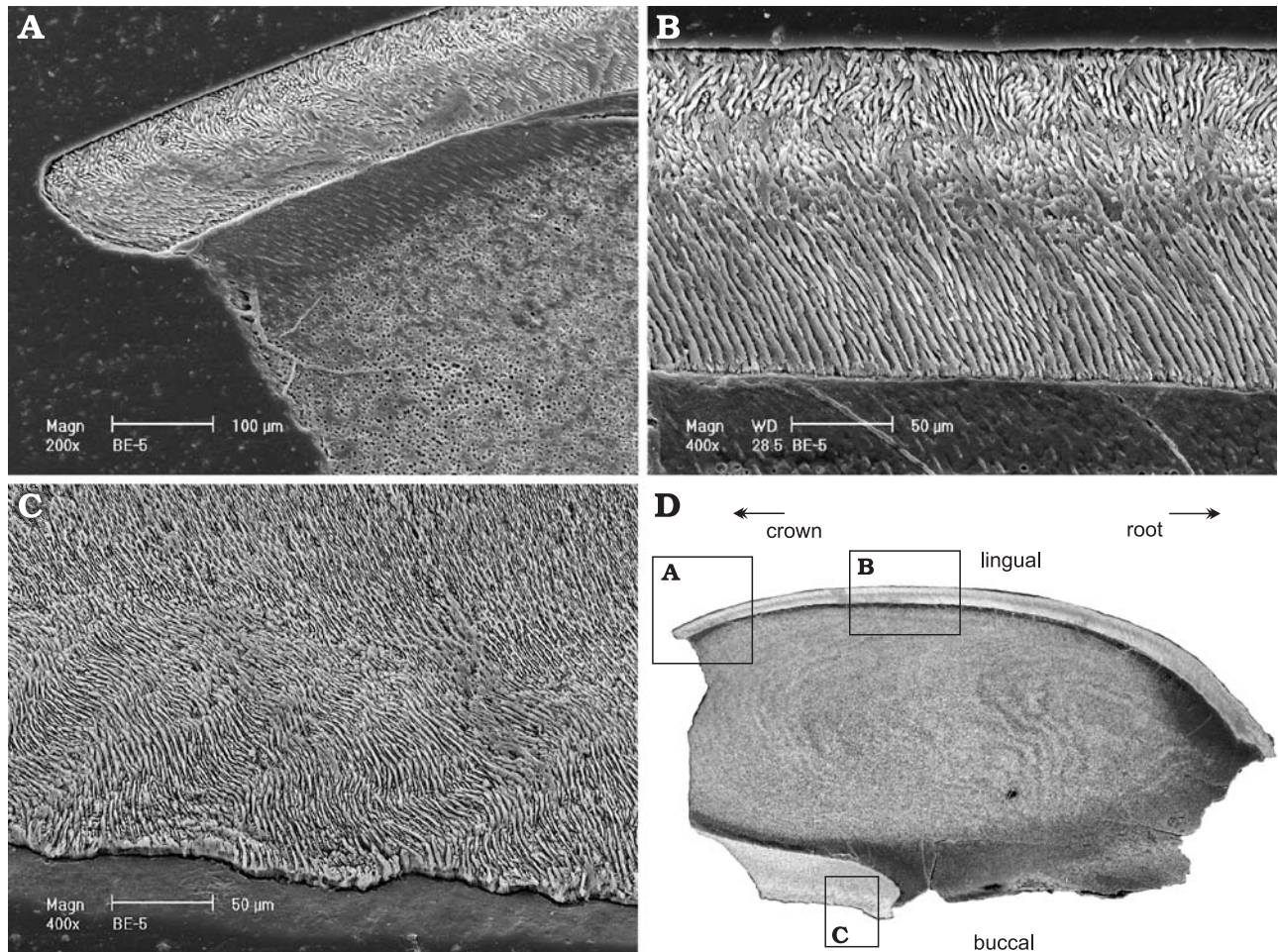
Fig. 6. Longitudinal section of P4 of the Miocene stem lagomorph *Eurolagus fontannesi* (Depéret, 1887) from Bełchatów A, Poland (MF/5077). **A**. Enamel structure of the lingual cutting edge, with radial (internal) and decussating (external) layers exhibiting Hunter-Schreger bands. **B**. Lingual enamel structure, magnified. **C**. Enamel structure of the crescent area (tangential section of the enamel lamella). **D**. Explanatory image of the studied specimen.

the central lobe almost completely. At this stage of wear, it is more extended buccally than in *Amphilagus antiquus* (Tobien 1974), the P3 of *Eurolagus fontannesi* from La Grive (Tobien 1974), and the strongly worn teeth of "*Amphilagus*" *sarmaticus* (Topachevsky 1987: fig. 9), a contemporaneous species from Ukraine (listed as *Eurolagus sarmaticus* in Nesin and Nadachowski 2001). The crescentic valley is open (Fig. 4C, D) and there is no anterobuccal connection between the lingual and central lobes, contrary to the condition observed in some specimens of *E. fontannesi* from La Grive (see Tobien 1974: fig. 36). In the less worn specimen (MF/ 5075, Fig. 4C), the central lobe resembles an irregular triangle with a convex buccal margin featuring a shallow buccal basin. In the senile specimen (Fig. 4D), the central lobe is larger and oval, and the buccal valley is completely missing. The remnants of the buccal lobe are obliterated in MF/5075 and absent in MF/5071 (Fig. 4D). The hypostria is very shallow, cutting across ca. 10% or less of the occlusal surface. The occlusal surface of the senile specimen displays a morphology typical of semihypsodont teeth; there is marked slope relief, with an elevated, less worn buccal side and a depressed lingual part (Fig. 4D$_1$).

*P4*.—The P4 is only represented by fragments, some of them juvenile (Figs. 5D, E, 6). The best-preserved specimen, MF/5074, has a very shallow but still persistent hypostria, which extends almost to the base of the crown, and a clearly visible crescent-like central lobe. The lingual lobe is connected to the buccal side of the tooth, virtually closing the crescentic valley, even though the valley shallows rapidly buccally toward the anterior buccal cusp (Fig. 5D$_2$). The buccal side of the tooth is missing and the internal structure of the crescent can be observed. Its dorsoventral dimension equals ca. two-thirds of the total height of the tooth. The two arms of the crescent are marked throughout all of its height, resulting in this structure retaining its crescent-like shape at the occlusal surface until late during ontogeny. This feature seems to characterize the European lineages of the semihypsodont lagomorphs and differentiates them from the North American stem lagomorphs, such as *Mytonolagus* or *Palaeolagus*, in which the occlusal shape of the crescent rather quickly turns into a rounded islet (Dawson 1958, Fostowicz-Frelik and Tabrum 2009).

The other specimens tentatively classified as P4 share a characteristic shallow hypostria and a generally centrally

placed central lobe with an eminent and thickly enameled lingual margin, forming the buccal part of the crescent structure late during ontogeny.

*M1* and *M2*.—These teeth are similar in structure, differing mainly in size (M2 is smaller), lobe structure and position of the crescent. The hypostriae are visibly deeper than on P4 (cutting across ca. 35% of the occlusal surface) and filled partly with cement (Figs. $4E_2$, 5I, $J_1$). In M2, the hypostria is directed slightly anteriorly (Fig. 5I, $J_1$). The anteroposterior length of the anteroloph is larger than that of the posteroloph in M2 (Fig. 5I, $J_1$), whereas this asymmetry is only weakly expressed in M1 (Fig. $5G_1$). Nevertheless, the crescent is placed mainly within area of the posteroloph. In the ontogenetically younger specimens, such as MF/5078 (Fig. $4E_2$), two buccal cusps and the buccal basin are well-preserved, as are the remains of two buccal roots.

*p3*.—There are two p3s (left and right) in our sample (Figs. 4F, 5K). One (MF/5083) is from a slightly younger individual than the other, but both represent adult specimens. Their outline is rounded, with a deep external reentrant (hypoflexid; López Martínez 1977), crossing about half of the total width of the tooth. While the slender talonid remains wider than the trigonid throughout ontogeny, the trigonid becomes more rounded and enlarges with wear, as seen in the ontogenetically older specimen. Unlike in "*Amphilagus*" *ulmensis* and *Piezodus*, there are no additional anteroconids or cingula at the anterior margin of the trigonid (López Martínez 1974; Tobien 1974).

The enamel layer surrounding the tooth is generally thick, being thickest in the region of the trigonid and thinnest on the talonid side of the reentrant, which is also crenulated (Fig. $4F_3$). The anterolingual side of the trigonid is gently concave in both specimens. Specimen MF/5082 resembles the specimens of *Eurolagus fontannesi* from La Grive in having a shallow concavity on the lingual margin (Fig. $4F_1$; Tobien 1974: figs. 39, 43, 45; López Martínez 1989: fig. 50). However, this concavity is much less marked than in "*Amphilagus*" *sarmaticus*, and there is no pronounced buttress situated anterior to the concavity as found in both the latter species (Topachevsky 1987: figs. 4–7) and *Titanomys visenoviensis* (Tobien 1974: figs. 54, 68).

*p4*, *m1*, and *m2*.—The lower molariform teeth all have a similar structure and differ mainly in the degree of curvature of the trigonid and talonid, as is typical for lagomorphs. The later increases anteroposteriorly, with p4 being almost straight, m1 being slightly curved distally, and m2 being strongly bent distally (Figs. 4D, 5L). The material referred to the lower cheek teeth consists mostly of isolated trigonids and talonids (Figs. 7E, 8A), although one m1 (MF/5085) and two complete m2 (Figs. 4G, 5L) are present. The trigonid is not completely surrounded by enamel and shows an enamel-free hiatus in the central part of its anterior wall (Fig. $5L_2$).

In younger individuals, there is an additional fold on the talonid (hypoconulid sensu López Martínez 1989 or "additional talonid" sensu Sych 1977), which disappears during on-

togeny. In juvenile specimens, it forms a separate, small, and anteroposteriorly compressed conid, which later connects to the talonid halfway along its width. This results in the formation of two posterior (lingual and buccal) reentrants of the talonid, which then finally close. As a rule, in *Eurolagus fontannesi*, the lingual one closes first (Fig. 8A) (Tobien 1974; López Martínez 1989), although specimen MF/ 5084 shows the opposite sequence (Fig. $4G_1$). Thus, this character is variable for *Eurolagus* at least in the case of m2. Nevertheless, the longer persistence of the buccal posterior reentrant of the talonid is a very rare feature among the Lagomorpha and distinguishes *E. fontannesi* from all the late Oligocene and Miocene European species, including *Amphilagus*, *Titanomys*, and the *Piezodus–Prolagus* lineages (Tobien 1974, 1975; Topachevsky 1987; Angelone 2009), as well as the majority of Asian semihypsodont lagomorphs, such as *Desmatolagus* or *Gobiolagus* (Erbajeva 1988; Lopatin 1998; Meng et al. 2005), and the North American *Palaeolagus* (Dawson 1958). The only lagomorphs retaining buccal reentrants longer than the lingual ones are representatives of *Mytonolagus petersoni* Burke, 1934 from Utah and specimens assigned to *Mytonolagus* near *petersoni* (sensu Dawson 1970) from the Badwater area in Wyoming (USA).

The lower cheek teeth of *Eurolagus fontannesi* are rooted, with m2 having fused roots with a single pulp cavity. The crown is significantly heightened, with the trigonid and talonid connected by cement for most of the crown height. Because the connection between the trigonid and talonid is located near the base of the crown (Fig. $5L_3$, $L_4$), the formation of the lingual enamel bridge does not occur until the senile stage.

*m3*.—The m3 is the smallest of the lower teeth, although it is not reduced to just one conid as seen in *Amphilagus*, *Titanomys*, and other genera usually assigned to Ochotonidae (sensu Tobien 1974; López Martínez 1977, 1989). Instead, it is marked by two conids joined by a very thin central isthmus (Fig. 5N). The trigonid is large, wide and oval, whereas the talonid is more triangular. The enamel layer is thickened particularly along the buccal and lingual sides of the trigonid, and there is an enamel hiatus in the anterior wall of the trigonid (Fig. $5N_3$). A bilobate structure of the m3 as observed in *Eurolagus fontannesi* has not been reported for any ochotonid species, but is typical for all leporids and stem groups such as "Palaeolaginae" and "Mytonolaginae" (Wood 1940; Dawson 1958, Fostowicz-Frelik and Tabrum 2009), as well as *Procaprolagus* and *Agispelagus* (Gureev 1960), and was also found in Desmatologinae (Tobien 1974; McKenna 1982; Lopatin 1998).

*Enamel microstructure*.—Previous work on the enamel structure of lagomorphs focused on their incisors (see Koenigswald 1995; Martin 2004), with their premolars and molars, especially those of their primitive semihypsodont representatives, generally not attracting much attention (but see Mazza and Zafonte (1987) for *Prolagus* and Koenigswald (1996) for some extant taxa). For the purpose of this study, we sectioned
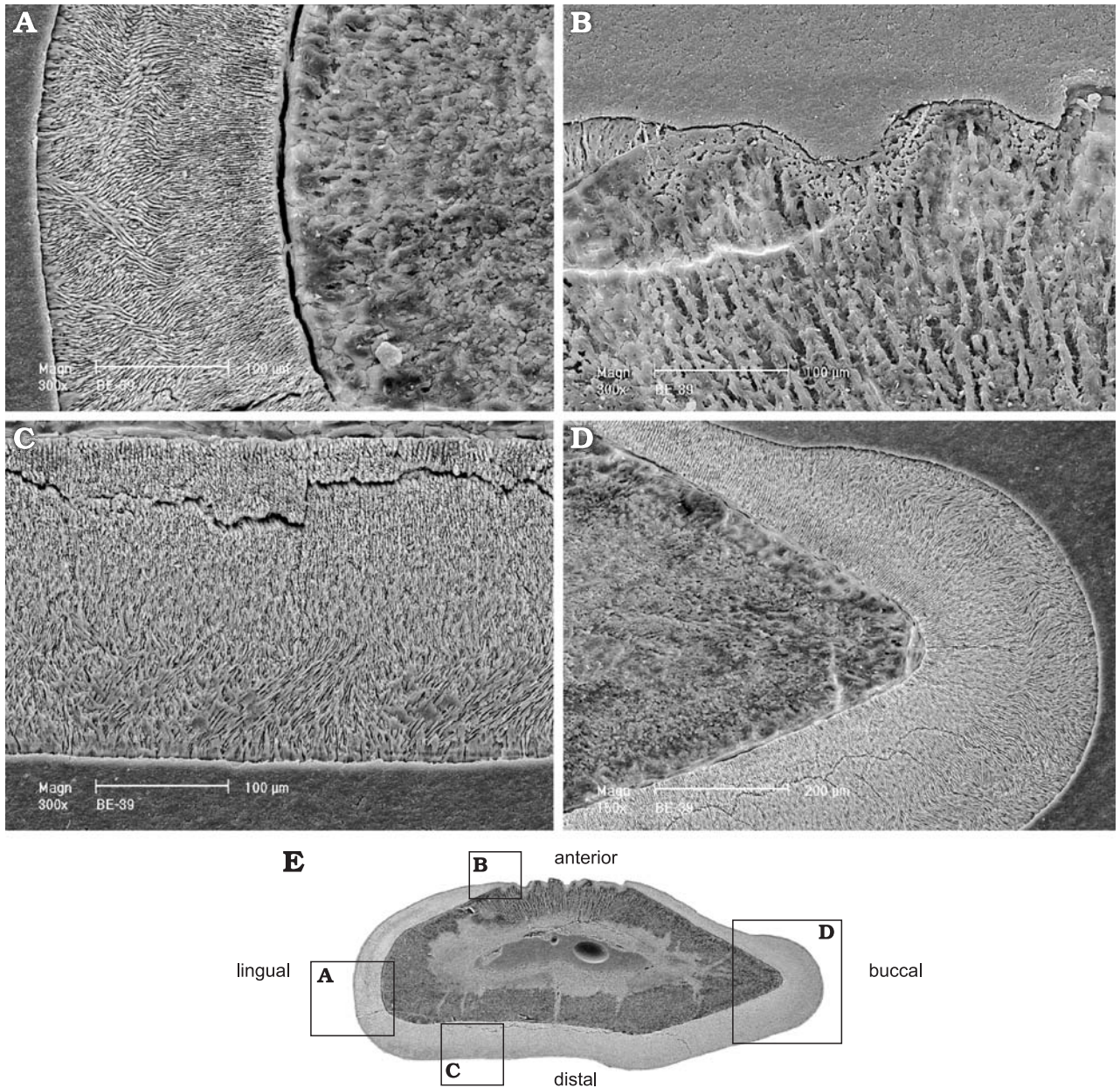
Fig. 7. Cross-section of the lower molar trigonid of the Miocene stem lagomorph *Eurolagus fontannesi* (Depéret, 1887) from Bełchatów A, Poland (MF/5099). **A**. Lingual enamel layer with radial (internal) and decussating (external) layers. **B**. Crenulated anterior side without enamel (hiatus). **C**. Distal enamel layer (main cutting edge), showing thick radial (internal) and decussating (external) layers. **D**. Structure of the buccal tip of trigonid. **E**. Explanatory image of the specimen.

the upper (Fig. 6) and lower (Figs. 7, 8) cheek teeth of *Eurolagus fontannesi* and studied the enamel structure in vertical (longitudinal sensu Koenigswald 1995) and transverse sections; the longitudinal section of P4 gave an insight into the tangential view as well, as a part of the crescent was cut along this plane (Fig. 6C).

The enamel shows some variability in thickness (Table 3) and level of complexity owing to its position at the occlusal surface of the tooth and the biomechanical requirements resulting from the orthogonal shearing and transverse grinding movements characteristic for lagomorphs (Meng et al. 2003). In the upper molarized teeth, the thickest and most complex enamel is found along the anterior margin of the anteroloph

and in the central part of the crescent (Figs. 5, 6). In the lower molarized dentition, this type of enamel is located on the distal, buccal, and lingual margins of the trigonid (Fig. 7, Table 3) and along the talonid rim, except for the anterobuccal margin and the internal areas of the folds (Fig. 8). The anterior part of the trigonid displays a hiatus, which completely lacks enamel (Fig. 7B, E).

The enamel of the cheek teeth is mainly two-layered (internal and external layers), with either a strongly or weakly pronounced transition. The internal layer is composed of radial enamel showing a noticeable degree of inclination towards the external surface, which varies from 45° in the upper premolars (Fig. 6A, B) to almost 90° in the lower molars
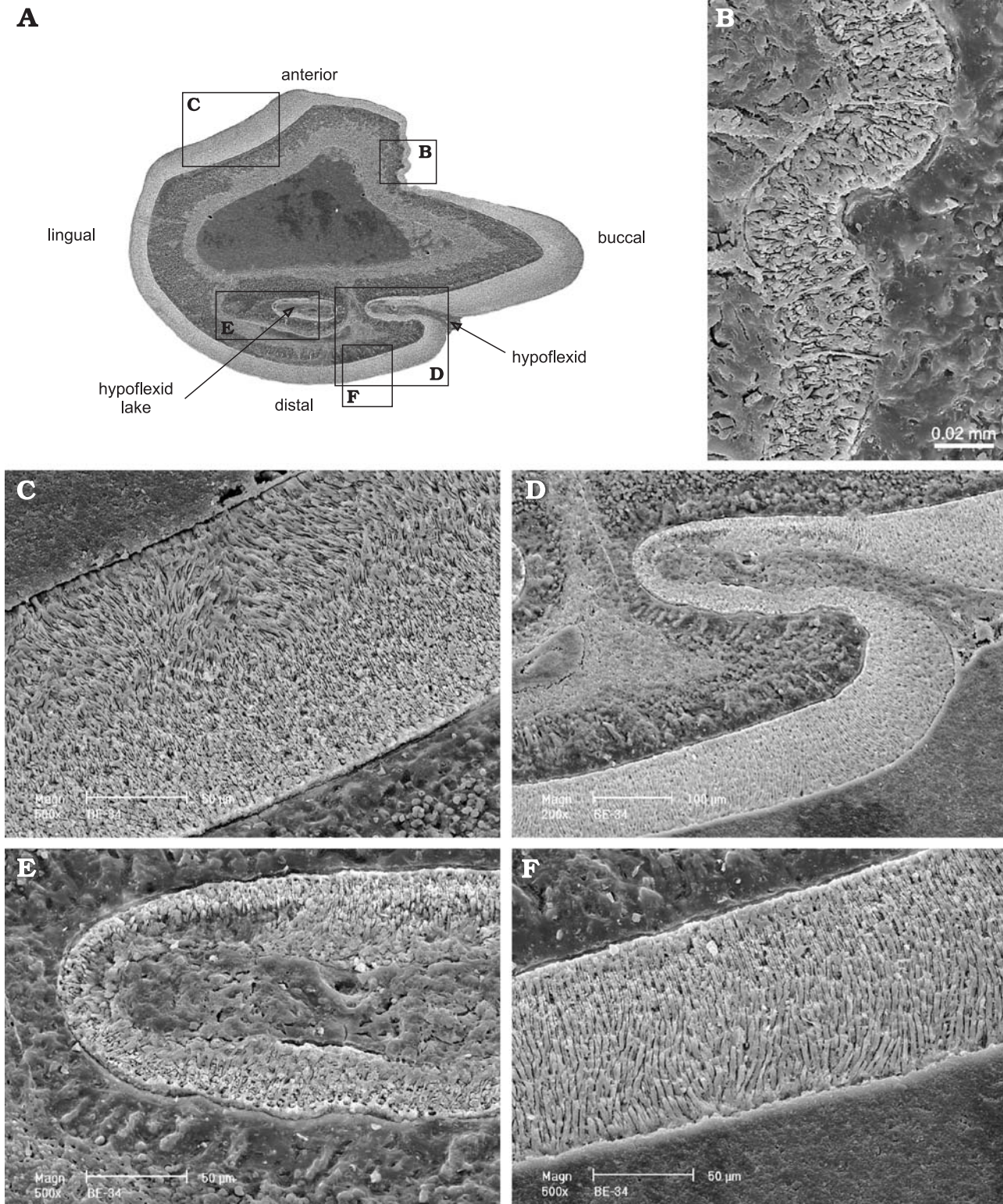
Fig. 8. Cross-section of the lower molar talonid of the Miocene stem lagomorph *Eurolagus fontannesi* (Depéret, 1887) from Bełchatów A, Poland (MF/5098). **A**. Explanatory image of the studied specimen. **B**. Buccal margin showing thin crenulated enamel. **C**. Anterolingual margin with radial (internal) and irregular decussating (external) enamel layers. **D–F**. Hypoflexid region, showing thin, poorly differentiated enamel.

(Figs. 7C, 8C). The angle of the inclination is frequently not constant within the layer, and increases towards the outer surface, changing the direction of the prisms from tangential (internally) to radial sensu stricto (externally), i.e., perpendicular to the enamel-dentine junction (Martin 1999). The interprismatic matrix is parallel to the prisms, thus expressing a condition primitive for Glires (Martin 1999; Meng et al. 2003).

Table 3. Thickness of the structural layers of enamel (in μm) and percentage of Hunter-Schreger bands (HSB) within the enamel layer in the teeth of *Eurolagus fontannesi* (Depéret, 1887) from Bełchatów A. Abbreviations: PLEX, prismless external layer; RA, radial enamel layer.

| Tooth | Orientation (layer) | Total | RA | HSB | PLEX | % of HSB |
|-------|--------------------|-------|-----|-----|------|----------|
| Upper premolar (P4, MF/5077) | lingual | 133 | 71 | 46 | 15 | 35 |
| Lower molar – trigonid (MF/5099) | lingual | 183 | 91 | 92 | 10 | 50 |
| | buccal | 260 | 148 | 103 | 12 | 40 |
| | distal | 243 | 136 | 107 | 12 | 44 |
| Lower molar – talonid (MF/5098) | antero-lingual | 131 | 71 | 50 | 8 | 38 |
| | buccal | 213 | 109 | 87 | 10 | 41 |
| | distal | 94 | 43 | 44 | 5 | 47 |
| | hypoconulid folds | 34 | – | – | – | – |

The external zone is formed by decussating bundles of prisms forming Hunter-Schreger bands (HSB). In *Eurolagus*, the HSB bands, consisting of 4–6 prisms, are best expressed in longitudinal section (Fig. 6A, B), whereas in cross-sections the margins of the decussating bundles and the general pattern are obscured (Figs. 7A, C, D, 8C). The decussating external enamel occupies 35–50% of the total enamel layer (Table 3), and is least developed along the talonid. While the antero-lingual (Fig. 8C) and the most pronounced buccal parts of the talonid clearly show the decussating external layer of enamel, the prisms in the external layer along its distal edge only display a slight degree of lateral undulation, indicating very weakly developed HSB (Fig. 8F). In addition, an even more simplified enamel structure is present in the internal parts of the folds (Figs. 8B, D, E).

The most external segment of the enamel, varying from 5 to 15 μm in thickness (Table 3), forms prismless enamel (PLEX), as commonly observed in Glires (Martin 1999, 2004).
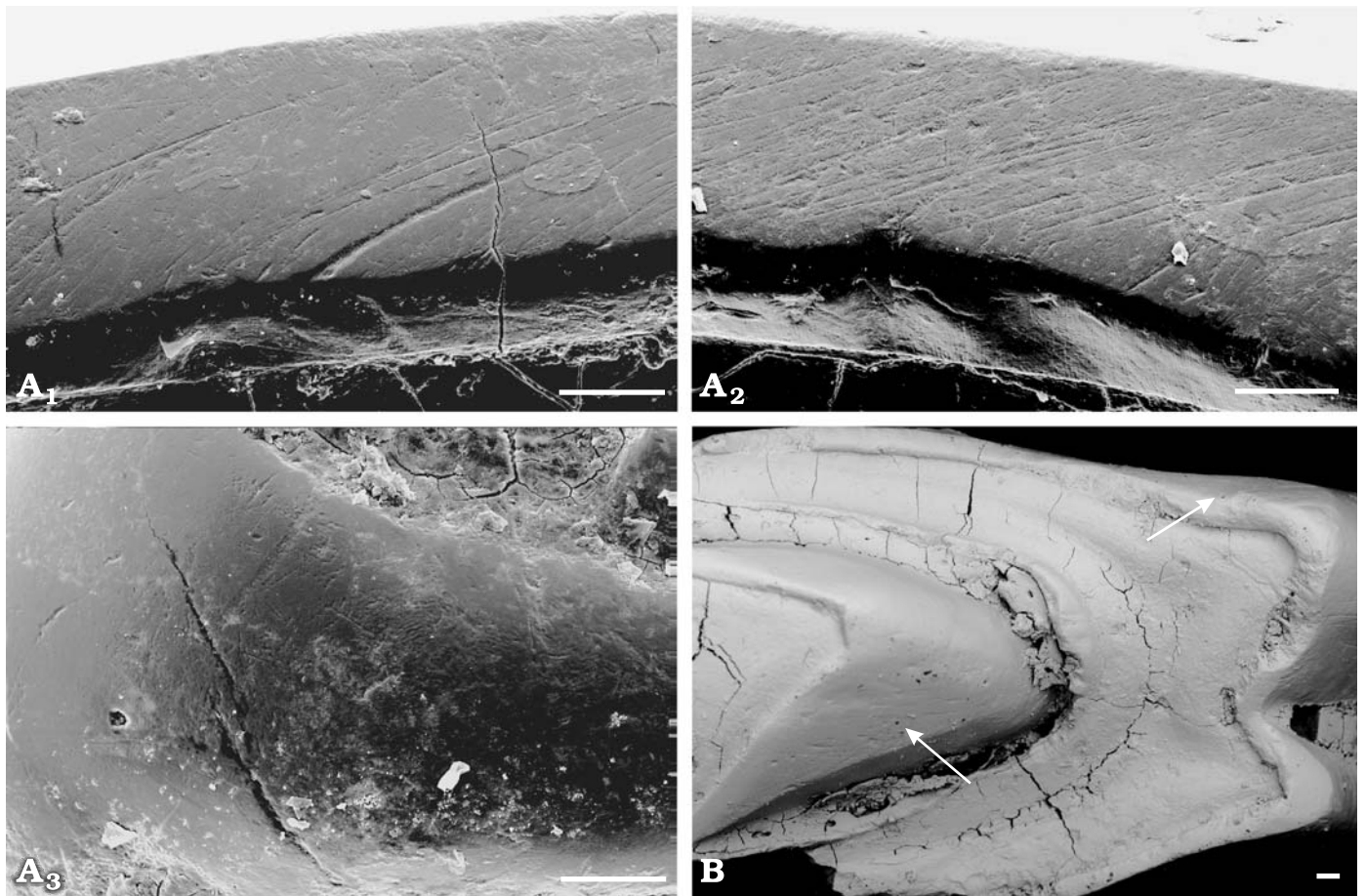


Fig. 9. Microwear structures of the premolars and molars of the Miocene stem lagomorph *Eurolagus fontannesi* (Depéret, 1887) from Bełchatów A, Poland. **A**. Occlusal enamel surface of the anteroloph of M1 (MF/5101/b). Anterior shearing surface ($A_1$, $A_2$) and buccal cusp ($A_3$). **B**. Occlusal enamel surface of P3 (MF/5075); note the scratches on the crescent and the anterior shearing surface (arrows). Scale bar 100 μm.

*Dental microwear*.—Tooth microwear was only observed in some of the best preserved upper premolars and molars (Fig. 9). Fine scratches and small pits dominate the microwear pattern, and are most strongly developed on the main enamel shearing blades, the anterior enamel layer of the anteroloph, and on the distal surface of the crescent (Fig. 9A$_1$, A$_2$, B). By contrast, the dentine seems to be unaffected, and the buccal cusps show only very fine microwear consisting mainly of small pits and cross-scratches (Fig. 9A$_3$). The upper M1 (MF/5101/b; Figs. 5G, 9A) was chosen for a more detailed study. However, the results should be treated as preliminary, as microwear has not been studied in lagomorphs previously, thus the comparisons are limited to rodents and ungulates.

The striae on the grinding surfaces are generally shallow and delicate compared to those found in most ungulates (Solounias and Semprebon 2002) and some rodent groups, such as Caviidae or Muridae (Townsend and Croft 2008; Gomes Rodrigues et al. 2009).

The main shearing blade shows an average of 34 pits and 20 scratches per 0.09 mm$^2$. There is a great predominance of small pits (19–40) over large pits (2–3), and fine scratches (13–20) over coarse scratches (0–4) or cross-scratches (0–4). The scratches are parallel or subparallel and inclined 20–30° in a buccolingual direction, indicating the main chewing movements. The two gouges present on the main shearing blade may be artifacts caused by transport and sedimentation, and thus their presence needs to be treated with caution. Towards the lingual edge of the shearing blade, the fine parallel scratches become less noticeable and occur less frequently (5–9 per 0.09 mm$^2$), whereas the cross-scratches are more common (8–9 per 0.09 mm$^2$). The count of small pits increases in the lingual area (up to 70 per 0.09 mm$^2$ along the edge), but the count of large pits remains low (1–2 per 0.09 mm$^2$) and no gouges are present. The microwear on the buccal cusps consists mainly of small pits (56 per 0.09 mm$^2$) and cross-scratches (14 per 0.09 mm$^2$); the number of large pits is similar to that on the main shearing blade (4 per 0.09 mm$^2$) and no gouges were observed (Fig. 9A$_3$).

*Discussion*.—*Eurolagus fontannesi* has previously been placed within *Lagodus*, *Titanomys*, or *Amphilagus* (Depéret 1887, 1892; Major 1899 and Wegner 1913; Gureev 1964 and Tobien 1974, respectively). López Martínez (1977) placed *Amphilagus fontannesi* in a new genus, *Eurolagus* on the basis of two sets of characters: first, the relative primitive features found in *Eurolagus* in comparison with *Amphilagus antiquus*, such as the less developed hypsodonty and bilobate m3; and secondly, the development of an occlusal pattern on p3 indicating a *Titanomys*-like stage with two symmetrically placed reentrants (lingual and buccal) present in juvenile specimens (López Martínez 1977, 1989). Moreover, there is no trace of the minute separate anteroconid characteristic of "*Amphilagus*" *ulmensis* and *Piezodus*. These characters clearly differentiate *Eurolagus* from *Amphilagus* and *Piezodus*, as well as from *Titanomys* (besides the basic p3 pattern in juveniles). *A. antiquus* displays only a single buccal (ex-

ternal) reentrant during ontogeny. This difference in the development of the p3 reflects the formation of an enamel lake present in both genera in subadult and young adult specimens. According to López Martínez (1977), the enamel lake in *Eurolagus* was formed as a result of the closure of the lingual reentrant, as can also be observed in many North American taxa—including *Mytonolagus*, *Palaeolagus*, and *Chadrolagus* (Dawson 1958; Gawne 1978; Fostowicz-Frelik and Tabrum 2009), as well as the European *Titanomys* (Tobien 1974). By contrast, the enamel lake in *Amphilagus antiquus* was formed from the internalmost part of the buccal reentrant, cut off buccally by a dentine bridge (López Martínez 1977, 1989: fig. 50). Furthermore, *Eurolagus* differs from most other lagomorphs in the formation of the posterior reentrants of the talonid on p4–m2 (Wood 1940; Dawson 1958; Gureev 1960; López Martínez 1989; Lopatin 1998; Meng et al. 2005; Angelone 2009; Fostowicz-Frelik and Tabrum 2009).

Despite the overall morphological similarity of the cheek teeth of *Eurolagus* and *Amphilagus*, the presence of the bilobate m3 casts doubt upon the assignment of *Eurolagus fontannesi* to the Ochotonidae. This character is recognized as typical of the Leporidae (unlike the Ochotonidae, which have a single column m3), and outside this group is found only in the Desmatolaginae (McKenna 1982), which, although they share some typically ochotonid characters (e.g., the premolar foramen), also display a leporid type of incisor enamel (Martin 2004) and have been suggested to form a clade separate from the ochotonids (Lopatin 1998).

Tobien (1974) proposed *Eurolagus fontannesi* as the final link in the *Amphilagus antiquus*–"*Amphilagus*" *ulmensis* lineage. By contrast, López Martínez (1977) linked the latter to the *Piezodus* lineage and instead suggested *E. fontannesi* to be a representative of a primitive lineage of Asian descent, which arrived in Europe a few million years after "*Amphilagus*" *ulmensis* had disappeared. However, López Martínez (1977) still placed *Eurolagus* within the Ochotonidae. The Asian origin of *Eurolagus* is to some extent supported by the presence of some scarce findings attributed to "*Amphilagus*" cf. *fontannesi* from the Late Oligocene and/or Early Miocene of Kazakhstan, the Baikal region (Russia), and Japan (Erbajeva 1988; Tomida and Goda 1993; Erbajeva and Filipov 1997; Erbajeva and Tyutkova 1997; McKenna and Bell 1997), as well as specimens from the Middle Miocene of the Caucasus area reported as *Eurolagus* aff. *fontannesi* (Pickford et al. 2000). Some of these findings stratigraphically precede the earliest European records of *Eurolagus* from Subpiatră (Hír and Venczel 2005), as well as the material from Rothenstein 1 (Sen in Bernor et al. 2004). Remains of a large lagomorph from Sandelzhausen (MN 5, Germany), although regarded as "*Amphilagus*" sp. by Angelone (2009) on the basis of stratigraphy, also resemble *Eurolagus* in size and morphology.

We consider *Eurolagus fontannesi* to be a stem lagomorph (sensu Asher et al. 2005; see López Martínez 2008 for the contents of this group), which most probably origi-

nated independently from "Amphilaginae" and Ochotonidae, and follow López Martínez (1977) in proposing that it represents a lineage descended from some immediate Asian ancestors, probably more closely related to Desmatolaginae. Until a comprehensive phylogenetic analysis is conducted, we thus place *Eurolagus* in Palaeolagidae Dice, 1929, along with other stem lagomorph taxa.

*Stratigraphic and geographic range.*—Late Middle to Late Miocene of western and central Europe (Fig. 1)

# Paleobiological implications

Very little is known about the paleobiology of the primitive European Oligocene to Miocene semihypsodont lagomorphs. For the purpose of our study, we find it useful to use the term "Amphilaginae" (or amphilagins) as an eco-morphological grade not referring to phylogenetic relationships and origins, which are still not fully resolved, but to a particular dental morphology (i.e., semihypsodont dentition, marked tooth curvature, and well-distinguishable buccal roots) indicating feeding specialization.

Using the extant ochotonids (i.e., *Ochotona*) as a proxy can be misleading, as they are restricted to steppe and mountain habitats today and in paleocommunities are frequently regarded as bioindicators of dry, open environments (e.g., Fostowicz-Frelik and Frelik 2010; Fostowicz-Frelik et al. 2010).

The paleoenvironmental characteristics of the localities from which amphilagins have been recovered indicate moist sylvan environments, often in the vicinity of river systems or lakes (Maridet et al. 2000; Reichenbacher and Prieto 2006; Tütken et al. 2006; Alba et al. 2009; Mörs and Kalthof 2010). Since this type of environment was also reconstructed for most of the Bełchatów deposition period (Stuchlik et al. 1990; Worobiec 1995; Szynkiewicz 2000; Kowalski and Rzebik-Kowalska 2002), and since broad-leaf evergreen, mixed deciduous, and mixed mesophytic forests dominated in central and central-western Europe (Agustí and Antón 2002; Kovar-Eder 2003; Böhme et al. 2007; Utescher et al. 2007), as well as the eastern part of the Iberian Peninsula (Jiménez-Moreno et al. 2010) during the Miocene, we can assume this kind of habitat to be typical for amphilagins. Generally, reconstructions of the terrestrial climate of central Europe during the Late Miocene are characterized by a high precipitation rate (average MAP~1000 mm) unaffected by Late Miocene cooling (Mosbrugger et al. 2005; Van Dam 2006), which also implies a rich xyloflora.

Interestingly, *Eurolagus fontannesi* has not been reported from the Calatayud-Daroca and Teruel, inner basins located in NE Spain, which on the basis of their mammal species composition (e.g., Agustí 1990; Van Dam et al. 2001; Casanovas-Vilar and Agustí 2007) are regarded as drier and more open environments than the coastal Vallès-Penedès basin, where *E. fontannesi* is present. This
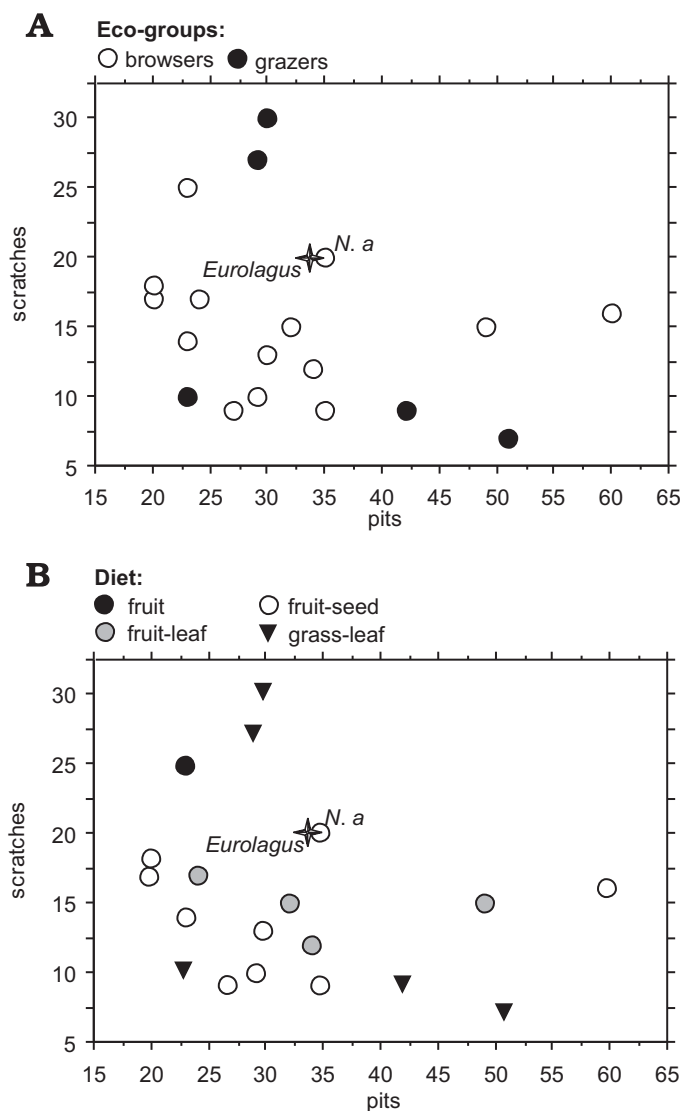
Fig. 10. Plotted microwear data for *Eurolagus fontannesi*, modern squirrels and caviids. **A**. According to the eco-group classification, *Eurolagus fontannesi* is a typical browser, whereas the diet type (**B**) plot suggests a fruit-seed or fruit-leaf based diet for this species. Note the position of *Notocitellus annulatus* (*N. a.*), a tropical ground squirrel. Comparative data after Nelson et al. (2005) and Townsend and Croft (2008).

suggests that this species indeed preferred forested landscapes.

The mammalian fauna of Bełchatów A lacks species indicating large open areas. On the contrary, there is a great abundance of forest forms known to inhabit or climb trees (arboreal and scansorial forms), such as *Blackia*, *Forsythia*, and *Miopetaurista*, all representatives of flying squirrels (Petauristinae = Pteromyini), Eomyidae (e.g., *Keramidomys* and *Eomyops*), and a diversity of similarly adapted Gliridae (Nadachowski 2001; Kowalski and Rzebik-Kowalska 2002). Their presence, and in particular the presence of *Glirulus lissiensis*, which was a gliding form with a patagium (Mein and Romaggi 1991), certainly points to a forested environment (Van Dam and Weltje 1999; Casanovas-Vilar and Agustí 2007). Remains of Castoridae, known only from level

A (Kowalski and Rzebik-Kowalska 2002), imply open water in the vicinity, whereas the relatively depauperate fauna of this level (as compared to the older levels B and C) lacks tropical elements such as hairy hedgehogs (Galericinae), fruit bats (Pteropidae), the giant squirrel (*Ratufa*), and *Neocometes*—a representative of spiny dormice (Placanthomyinae). These changes have been interpreted in terms of noticeable cooling (Kowalski and Rzebik-Kowalska 2002) and, together with the simultaneous occurrence of the first sigmodont cricetid *Microtocricetus*, likely signal the beginning of the significant change in climate known as the Vallesian Crisis (Agustí et al. 1999; Agustí and Antón 2002) or, more accurately, the Vallesian Faunal Change, given its diachronous character across Europe (Koufos 2006). However, in general, the environmental conditions during the deposition of Bełchatów level A are still considered to be a stage of the Early Vallesian Optimum, as characterized by Agustí and Antón (2002).

From an environmental standpoint, we can narrow the dietary preferences of *Eurolagus fontannesi* to leafs, grass, and fruits, and test the preliminary dental microwear data against results known for a few rodent and ungulate groups (Solounias and Semprebon 2002; Meng et al. 2003; Nelson et al. 2005; Gomes Rodrigues et al. 2009). Such a comparison, based on the ratio of the average number of pits versus scratches, places *Eurolagus fontannesi* in the morphospace of a typical browser close to fruit-leaf and fruit-seed groups in the Townsend and Croft (2008) classification for the living Caviidae (Fig. 10A), or that of a seasonal-regional mixed-feeder according to the Solounias and Semprebon (2002) classification of ungulates. The relatively high number of fine scratches and very low number of coarse scratches points to a diet dominated by delicate vegetation, such as C3 grass-like plants frequently found in sylvan environments, and soft fruits with edible pericarps or arils. A similar pattern of microwear has been observed in *Tragelaphus scriptus*, which inhabits rainforests, as well as *Cervus canadensis* and *Cavia*, although the latter two taxa display a higher number of scratches in general (Solounias and Semprebon 2002; Townsend and Croft 2008). Compared to modern squirrels, the most similar pits-to-scratches ratio is expressed in *Notocitellus* (= *Spermophilus*) *annulatus* (Fig. 10), which inhabits the tropical deciduous forests of Mexico, and feeds on fruits, nuts, and insects; however, this species shows a much coarser type of microwear (Nelson et al. 2005).

*Eurolagus fontannesi* from Bełchatów A displays a relatively high number of small puncture pits, which are probably related to the small size of the animal forcing it to feed near the ground, where soil particles can be an important abrasive factor (Nelson et al. 2005), as well as the presence of grass seeds in the diet, which are responsible for such a microwear pattern in *Cavia* (Townsend and Croft 2008). In conclusion, we can assume that *Eurolagus fontannesi* was a sylvan species with a browsing type of behavior whose diet consisted mainly of soft grass and foliage, as well as fruits and fine seeds.
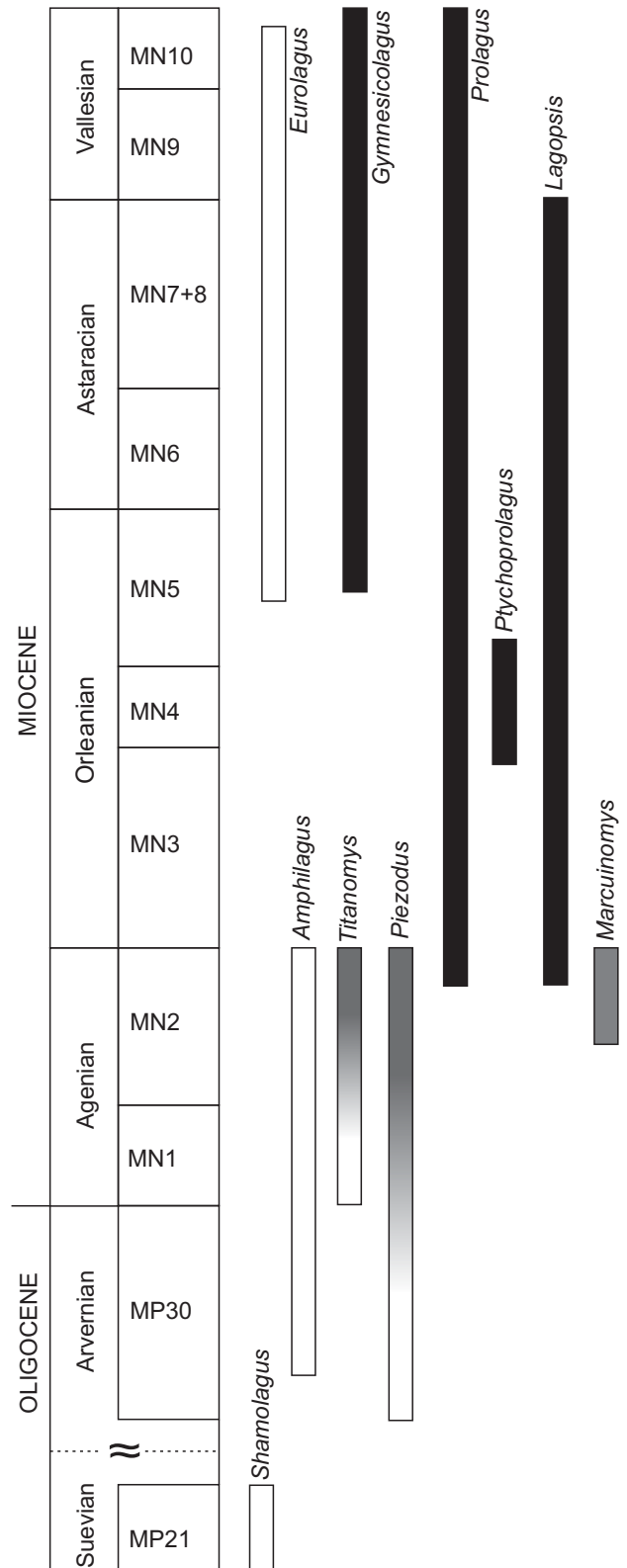


Fig. 11. Dental morphology and heterochrony of hypsodonty in European lagomorphs from the Oligocene to the early Late Miocene. White, semi-hypsodont dentition with buccal roots present; gray, primitive hypsodonty, no roots on the upper teeth but tooth curvature strongly marked; black, hypsodont dentition, upper teeth gently curved. Data on *Shamolagus* from Heissig and Schmidt-Kittler (1975) and on *Gymnesicolagus* from Mein and Adrover (1982).

# Conclusions

The Middle to Late Miocene with its events of cooling and drying, and spreading of open landscapes, first around 14 Ma and later during the Late Vallesian (ca. 9.6 Ma) marks the beginning of a great faunal turnover and paleoenvironmental change across Europe (Agustí et al. 1999; Agustí and Antón 2002). At this time, a modern climatic regime began to establish itself and a modern faunal distribution started to take shape.

The lagomorph fauna was no exception and underwent extensive change. The Late Miocene witnessed the last faunal relicts possessing a primitive array of morphologies, such as a semihypsodont dentition with well-developed buccal roots, coexisting with more advanced, fully hypsodont lineages (Boon-Kristkoitz and Kristkoiz 1999; Fig. 11). Hypsodonty is a strongly heterochronic character in lagomorphs, with both fully hypsodont and semihypsodont species occurring in the latest Eocene of North America (Fostowicz-Frelik 2009). In Europe, the earliest lagomorphs expressing a fully developed, albeit primitive, type of hypsodonty are known from the Early Miocene (Tobien 1974), appearing first in the form of the advanced representatives of the *Titanomys* (*T. calmensis*), *Piezodus* (*P. tomerdingensis*), and *Marcuinomys* lineages. Although their upper cheek teeth lack buccal roots, they are still strongly curved, resulting in a specific wear pattern preserving buccal structures until a late ontogenetic stage. The modern type of full hypsodonty, with the upper cheek teeth showing markedly weaker curvature, appeared almost concurrently in *Lagopsis* and *Prolagus* (Tobien 1974, 1975; López Martínez 1989; McKenna and Bell 1997). Simultaneously, *Amphilagus* (Late Oligocene to Early Miocene) and *Eurolagus* (Middle to early Late Miocene), which still retained a primitive (semihypsodont) tooth morphology, were widespread in Europe (Fig. 11). It is noteworthy that *Eurolagus* is the last European semihypsodont lagomorph, with the last occurrence of this species falling into the MN 10 zone.

The rich floral and faunal remains from Bełchatów A offer a unique insight into the Central European paleobiocenosis of the early Late Miocene, and provide us with the best clues for studying the habitat preferences of the declining *Eurolagus fontannesi* in its northernmost outpost.

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