Gliridae (Rodentia) from the Villafranchian site of Węże 2 in southern Poland

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A fossil assemblage of dormice (Rodentia: Gliridae) was uncovered at the (Lower?) Villafranchian site of Węże 2 in southern Poland. Based on morphometric criteria, the diagnostic M1 and m1 specimens are assignable to *Glis minor* and *Glis sackdillingensis*, two species which differ only in the dimensions of their cheek teeth. The presence of dormice at Węże 2 implies that the fossil assemblage of this site represents an at least partly wooded environment. The enamel structure in the glirids from Węże 2 is formed predominantly by radial enamel. A thin layer of lamellar enamel, occurring close to the enamel-dentine junction, may be present. Such a type of enamel structure is typical of the Myomorpha, the clade of rodents encompassing the Muroidea (the mouse-like rodents) and Gliridae.

Key words: Villafranchian, rodents, dormice, Węże, karst.

INTRODUCTION

This paper describes the fossil assemblage of dormice (Rodentia: Gliridae) uncovered at the Villafranchian (MN 16b?) site of Węże 2 in southern Poland. Although the site has been known since the early 1960s (Sulimski, 1962), much of the fossil material collected still awaits a systematic description. This study is part of a larger project intended to provide a comprehensive report on the rodent fauna of Węże 2. The data provided will contribute to current knowledge on the palaeobiogeography, palaeoecology and evolution of particular taxa.

The Gliridae (dormice) are an ancient family of omnivorous Old World rodents. They first appeared in the Eocene and underwent a major radiation during the Miocene. Nonetheless, at the end of the Miocene several phyletic lineages became extinct, which resulted in the modern genera being rather distantly related (Nadachowski, 1989; Daoud, 1993; Rose, 2006; Kurtén, 2007). The oldest glirid fossils from Poland are probably the *Glirudinus* sp. remains from the MN 5–6 (Lower Miocene) of Bełchatów (Kowalski, 1990).

Modern dormice are mostly associated with various kinds of arboreal and shrubby habitats, and generally are capable climbers, nesting in tree hollows or among branches. Caves are also sometimes inhabited and used as hibernacula, and areas with caves may be preferred by some species (Nadachowski, 1989;

Kurtén, 2007; Kryštufek, 2010). It has been suggested that fossil dormice displayed greater ecological diversity than the surviving taxa (Nadachowski, 1989). Among recent genera, *Eliomys* differs from the typical Gliridae as it is known to thrive in open rocky environments and semi-desert areas of Northern Africa (Daoud, 1993; Amori et al., 2008).

There are nine extant genera of glirids comprising 29 species and grouped into three subfamilies (Holden, 2005). The *Glis* genus is today represented by the fat dormouse, *G. glis*. This species, as well as *Glirulus japonicus* (the Japanese dormouse) belong to the Glirinae subfamily, which is thought to have originated in the Oligocene (Holden, 2005; Kurtén, 2007; Holden and Levine, 2009). The evolutionary lineage *G. minor*–*G. sackdillingensis*– *G. glis* is commonly inferred from the fossil record (Nadachowski, 1989; Daoud, 1993; Siori et al., 2014; Striczky and Pazonyi, 2014). Here I report the presence of *G. minor* and *G. sackdillingensis* at the Villafranchian (MN16?) site of Węże 2 in southern Poland. Both species are considered to be associated with arboreal environments (de Bruijn, 1998; Popov, 2004; Hellmund and Ziegler, 2012; Siori et al., 2014; Striczky and Pazonyi, 2014; Colombero et al., 2017).

GEOLOGICAL SETTING

Węże 2 is a Villafranchian site situated on the NW slope of Zelce Hill (51°06'00"N 18°47'30"E; 228 m a.s.l.) in the Wieluń Upland, near the village of Węże, in the vicinity of the town of Działoszyn, in Pajęczno County, southern Poland (Fig. 1). The site comprises a vertical karst crevice etched in Upper Jurassic (Oxfordian) limestone and infilled with fossiliferous sediment of terra rossa type. The crevice itself is a part of a larger karst cave
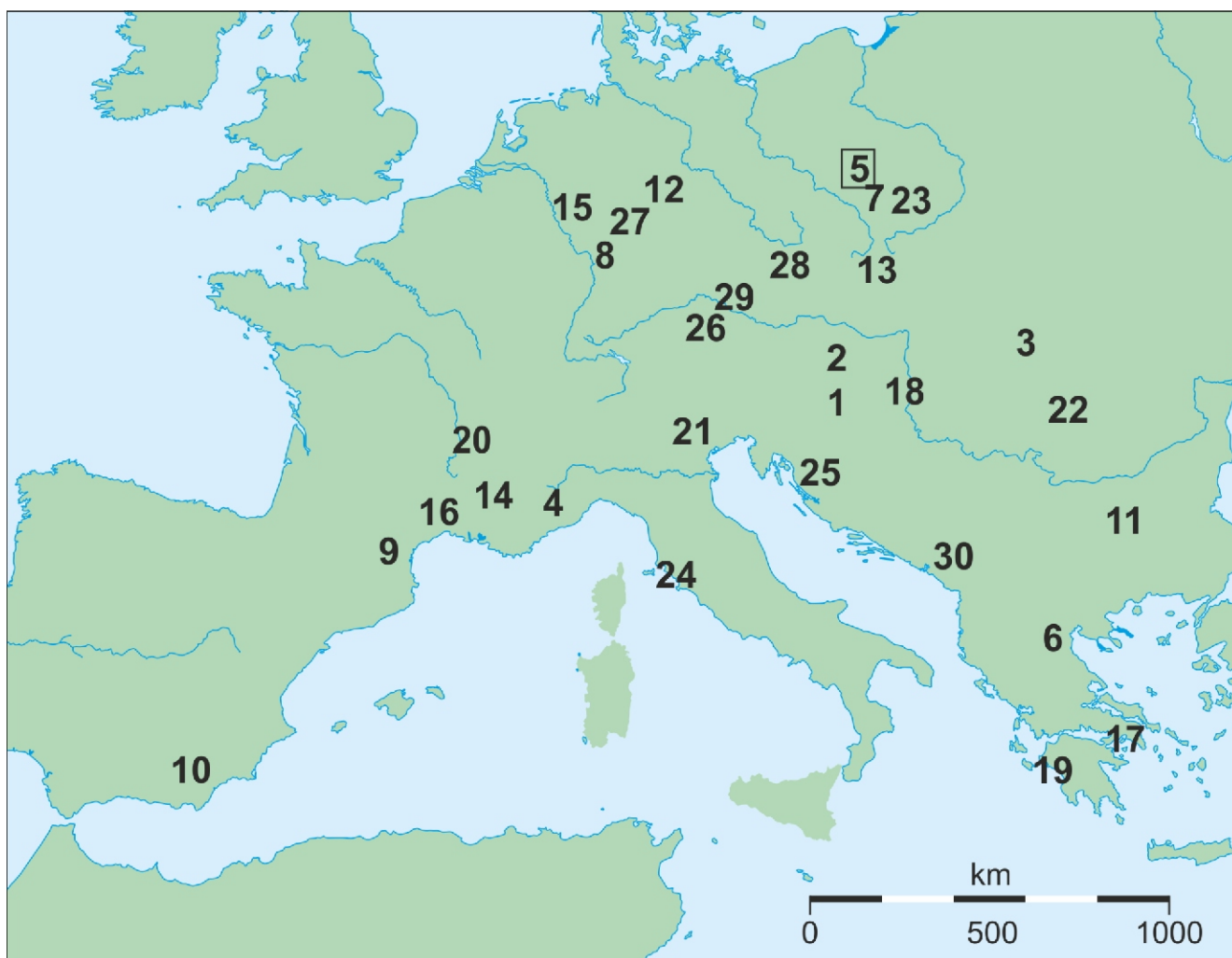
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Fig. 1. Location of Węże 2 and other sites mentioned in Table 2, the Węże 2 area highlighted

1 – Oberdorf, Kohfidisch; 2 – Richardhof; 3 – Rudabánya, Osztramos, Kövesvárad, Tarkő, Uppony Rock Shelter 1; 4 – Moncucco Torinese; 5 – Mała Cave, Raciszyn 1, Węże 1, Węże 2; 6 – Komanos 1, Notio 1; 7 – Pańska Góra, Podlesice, Rębielice Królewskie, Kamyk, Kielniki, Żabia Cave; 8 – Wölfersheim; 9 – Mont Hélène; 10 – Moreda; 11 – Muselievo; 12 – Sondershausen; 13 – Vitošov; 14 – Grand Serre; 15 – Hambach; 16 – Mas Rambault; 17 – Tourkovounia 1; 18 – Csarnóta, Somssich Hill 2, Beremend 14, Villány-Kalkberg-Nord; 19 – Kaiafas; 20 – Les Valerots; 21 – Monte la Mesa; 22 – Betfia; 23 – Kadzielnia, Kozi Grzbiet; 24 – Monte Argentario; 25 – Razvodje, Podumci; 26 – Schernfeld; 27 – Untermassfeld; 28 – Chlum; 29 – Sackdillinger Cave; 30 – Trlica

system of the hill (Sulimski, 1962; Stefaniak, 1995; Stefaniak et al., 2020) and is located ~150–200 m north from the better known Węże 1 site, which has been dated as MN 15 (e.g., Sulimski, 1964; Fostowicz-Frelik, 2007).

The Węże 2 site (abbreviated as W2) was discovered and initially explored between 1958 and 1961 by Sulimski, who detected an abundant fossil vertebrate fauna dominated by small mammal remains, whereas the large mammal fossils were rare and highly fragmented (Sulimski, 1962; Stefaniak et al., 2020). The terra rossa deposits (~3.5 t in total) were collected during fieldwork organized by the Department of Paleozoology (now: Institute of Paleobiology) PAS in Warsaw and the Department of Paleozoology of Wrocław University (Sulimski, 1962).

So far, the fossil remains have been described only in part, more detailed studies concerning cervids (Stefaniak, 1995; Stefaniak et al., 2020), rhinoceroses and elephantids (Stefaniak et al., 2020), and lagomorphs (Fostowicz-Frelik, 2007). The presence of diverse rodent and lipotyphlan faunas was mentioned (Sulimski, 1962; Nadachowski, 1989; Rzebik-Kowalska, 1989), but these were not studied in detail.

The accompanying, generally scarce reptilian remains included *Lacerta* sp., *Anguis* cf. *fragilis*, *Ophisaurus pannonicus*, *Testudo* sp. and *Emys wermuthi*, while amphibians were represented by rare and fragmented long bones of *Rana* sp. (Sulimski, 1962). The Węże 2 fossil assemblage is currently dated to the Late Pliocene (Lower Villafranchian) MN 16b zone (2.9–2.6 Ma) based on its faunal composition compared to the nearby site of Rębielice Królewskie 1 (Sulimski, 1962, 1964; Stefaniak, 1995; Stefaniak et al., 2020).

MATERIAL AND METHODS

The *Glis* material consists of isolated teeth and one mandible fragment with m1–m2 *in situ* (Fig. 2). All dental loci are represented in the sample, although the most numerous are m1/M1 and m2/M2, whereas m3/M3 and p4/P4 are underrepresented in the sample (see Table 1). The bias results most probably from the size factor, the premolars and the ultimate molars being the smallest teeth in the dental row, and thus
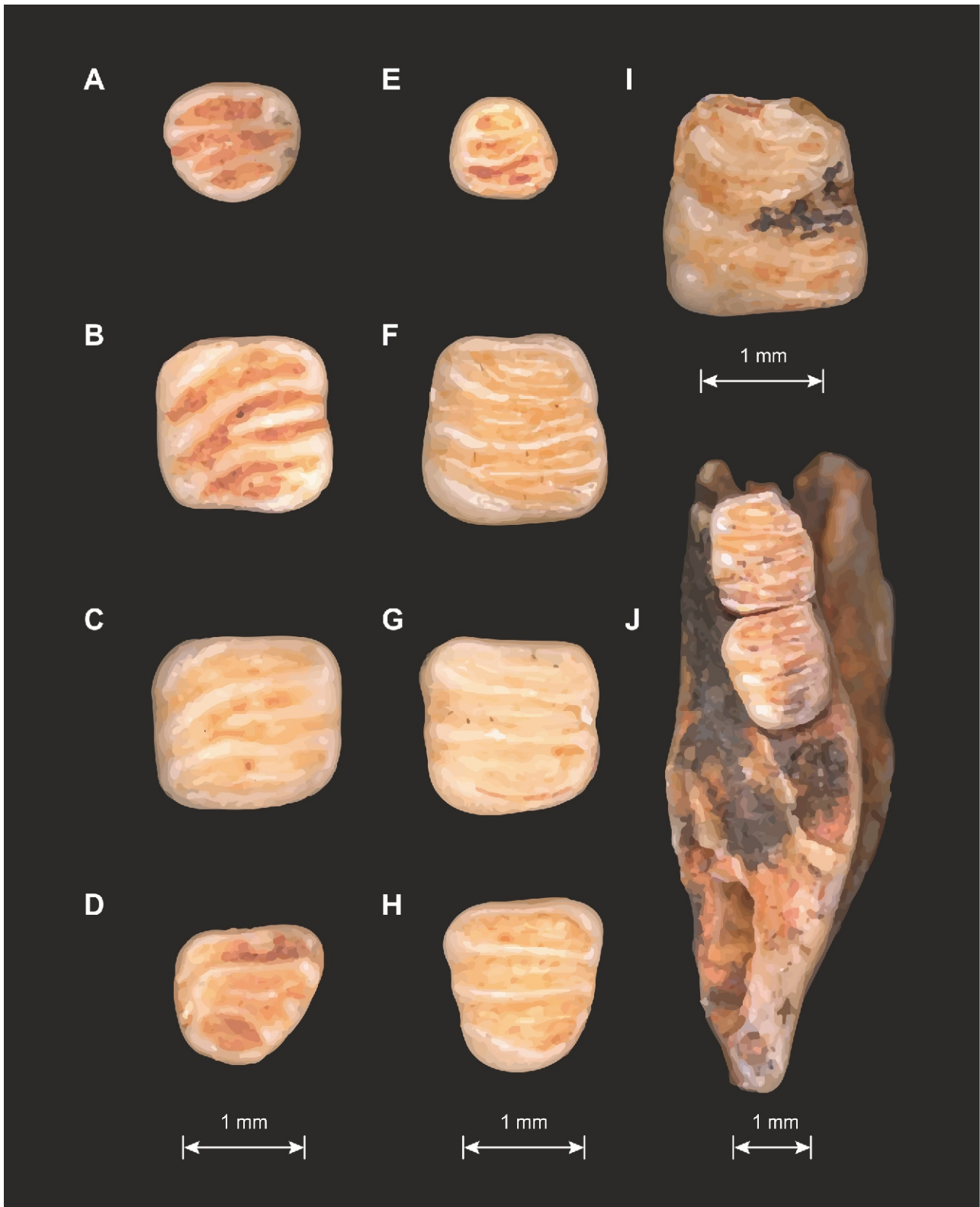
Fig. 2. *Glis* **ex gr.** *minor-sackdillingensis* **from Węże 2**

A, **C**, **D**, **E**, **G**, **H** – *G.* ex gr. *minor-sackdillingensis*; **B**, **F**, **J** – *G. minor*; **I** – *G. sackdillingensis*; A – P4, B – M1, C – M2, D – M3, E – p4, F – m1, G – m2, H – m3, I – m1, J – left mandible with m1 and m2; all in occlusal view

Isolated teeth of Gliridae from Węże 2 – material and measurements

Species/ tooth locus	N	Length: min.	Length: mean	Length: max.	Width: min.	Width: mean	Width: max.
Glis ex gr. *minor-sackdillingensis*							
p4	6	0.87	0.99 ±0.0793	1.06	0.89	0.97 ±0.0563	1.02
m2	48	1.4	1.51 ±0.0606	1.63	1.4	1.52 ±0.0610	1.64
m3	11	1.3	1.42 ±0.0741	1.56	1.3	1.33 ±0.0773	1.45
P4	8	0.97	1.01 ±0.0294	1.04	1.05	1.11 ±0.0353	1.14
M2	29	1.35	1.45 ±0.0494	1.56	1.48	1.59 ±0.0538	1.7
M3	4	1.17	1.2 ±0.025	1.23	1.31	1.34 ±0.0424	1.4
Glis minor							
m1	61	1.34	1.52 ±0.068	1.63	1.32	1.48 ±0.0731	1.65
M1	62	1.38	1.5 ±0.0557	1.66	1.32	1.49 ±0.0611	1.62
Glis sackdillingensis							
m1	6	1.65	1.7 ±0.0715	1.84	1.53	1.58 ±0.0450	1.66

easier to overlook during collecting and preparation. The morphology of the teeth is typical of *Glis* teeth described from coeval localities in Poland (Kowalski, 1960b, 1963; Daoud, 1993).

The remains were recovered from the bone breccia site of Węże 2 by hand picking. Some larger portions of more calcified sediment were dissolved using acetic acid and then the residue was sifted. The specimens were examined, measured and photographed with the *Keyence VHX 900-F Digital Microscope System*.

The glirid dental terminology follows Striczky and Pazonyi (2014) and is illustrated in Figure 3. The enamel microstructure of the cheek teeth was made visible using the method described in Fostowicz-Frelik et al. (2012). It was then studied under SEM (*Philips XL20* at the Institute of Paleobiology PAS). The material is housed in the collection of the Institute of Paleobiology PAS (abbreviated ZPAL).

SYSTEMATIC PALAEONTOLOGY

Order Rodentia Bowdich, 1821
Family Gliridae Muirhead, 1819
Subfamily Glirinae Thomas, 1897
Genus *Glis* Brisson, 1762
Glis sackdillingensis (Heller, 1930)
Glis minor Kowalski, 1956

MATERIAL

Glis sackdillingensis, isolated teeth: 6 m1 (ZPAL M.VIII/b/ G2/1–6).

Glis minor, isolated teeth: 61 m1 (ZPAL M.VIII/b/G1/ 16–76), 62 M1 (ZPAL M.VIII/b/G1/77–138); a fragment of the left mandible with m1–m2 *in situ* (ZPAL M.VIII/b/G1/1).

Glis ex gr. *sackdillingensis-minor*, isolated teeth: 6 p4 (ZPAL M.VIII/b/G1/2–7), 8 P4 (ZPAL M.VIII/b/G1/8–15), 48 m2 (ZPAL M.VIII/b/G1/139–186), 29 M2 (ZPAL M.VIII/b/G1/ 187–215), 11 m3 (ZPAL M.VIII/b/G1/216–226) and 4 M3 (ZPAL M.VIII/b/G1/227–230).
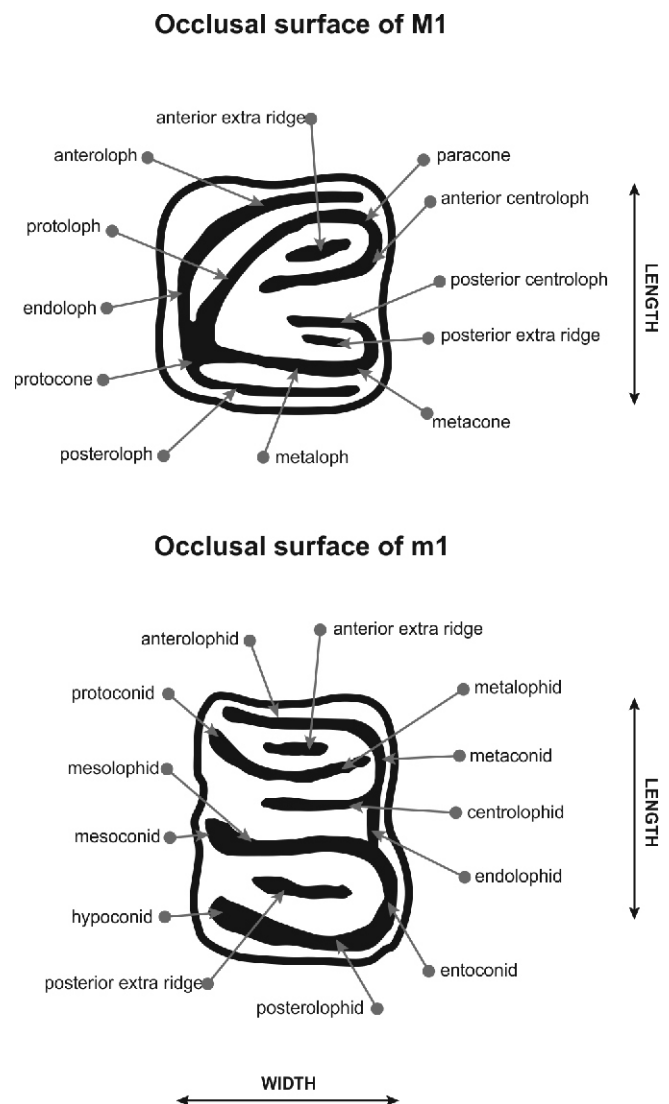
Occlusal surface of M1

Occlusal surface of m1

Fig. 3. Schematic drawings of the M1 and m1 occlusal surface of *Glis* ex gr. *minor-sackdillingensis* (after Striczky and Pazonyi, 2014, modified)

DESCRIPTION

Glis sackdillingensis
m1 (Fig. 2F)

A vaguely rectangular, anteriorly narrowed tooth. The anterolophid, the metalophid, the centrolophid, the mesolophid and the posterolophid are present. The metalophid, the mesolophid and the posterolophid are clearly curved. Extra ridges may be present (Fig. 3). In W2 the length of the tooth ranges from 1.65 to 1.84 mm and the width from 1.53 to 1.66 mm (Table 1 and Fig. 4D).

Glis minor
M1 (Fig. 2B)

A squarish tooth with rounded corners. The anteroloph, the protoloph, the anterior centroloph, the metaloph and the posteroloph are present. The anteroloph is clearly rounded. Extra ridges may be present (Fig. 3). In W2 the length of the tooth ranges from 1.38 to 1.66 mm, and the width from 1.32 to 1.62 mm (Table 1 and Fig. 4C).

m1 (Fig. 2F)

Morphologically indistinguishable from *G. sackdillingensis* (Fig. 3). The anterolophid, the metalophid, the centrolophid, the mesolophid and the posterolophid are present. The length of the teeth from W2 ranges from 1.34 to 1.63 mm and the width from 1.32 to 1.65 mm (Table 1 and Fig. 4D).

Glis ex gr. *minor-sackdillingensis*
P4 (Fig. 2A)

The outline of the occlusal surface is roughly oval. The anteroloph, the protoloph, the metaloph, and the posteroloph are present. The length of the Węże 2 specimens ranges from 0.97 to 1.04 mm, and the width from 1.05 to 1.14 mm (Table 1 and Fig. 4A). These specimens, as are all the other non-diagnostic teeth, are attributed to *G.* ex gr. *minor-sackdillingensis* as an exact specific assignment is not possible with adequate certainty and both species are present at the site (see Striczky and Pazonyi, 2014).

M2 (Fig. 2C)

A broad, squarish tooth with its corners slightly rounded. The anteroloph, the protoloph, the anterior centroloph, the metaloph and the posteroloph are present. The length of the Węże 2 specimens ranges from 1.35 to 1.56 mm, and the width from 1.48 to 1.7 mm (Table 1 and Fig. 4E).

M3 (Fig. 2D)

It is approximately triangular in shape, posteriorly narrowed. The anteroloph, the protoloph, the anterior centroloph, the metaloph and the posteroloph are present, as well as a residual posterior centroloph, located posterior to the anterior centroloph. The length of the M3 specimens collected from Węże 2 ranges from 1.17 to 1.23 mm and the width from 1.31 to 1.4 mm (Table 1 and Fig. 4G).

p4 (Fig. 2E)

The shape of the occlusal surface resembles a circular triangle. It is also the smallest of the teeth (Fig. 4B). The anterolophid, the metalophid, the mesolophid and the posterolophid are present. The length of the Węże 2 specimens ranges from 0.87 to 1.06 mm and the width from 0.89 to 1.02 mm (Table 1 and Fig. 4B).

m2 (Fig. 2G)

A vaguely rectangular tooth, posteriorly narrowed. The anterolophid, the metalophid, the centrolophid, the mesolophid and the posterolophid are present. The length of the teeth collected at Węże 2 ranges from 1.4 to 1.63 mm and the width from 1.4 to 1.64 mm (Table 1 and Fig. 4F).

m3 (Fig. 2H)

It is similar to m2 but still more narrowed posteriorly. The anterolophid, the metalophid, the centrolophid, the mesolophid and the posterolophid are present. The length of the Węże 2 specimens ranges from 1.3 to 1.56 mm and the width from 1.3 to 1.45 mm (Table 1 and Fig. 4H).

Preliminary observations of the Węże 2 material show the ridges at the occlusal surfaces of the cheek teeth in *Glis* ex gr. *minor-sackdillingensis* as being low and delicate. The enamel layer covering the circumference of the teeth and the ridges is relatively thin, ranging from 38 to 93 µm. It is usually thickest along the ridges and at the lingual and buccal margins of the teeth. Also, its thickness changes from the root to the crown (in vertical sections, as demonstrated by Koenigswald, 2004). The most even enamel layer is observed in p4 (Fig. 6).

REMARKS

In the inferred *G. minor–G. sackdillingensis–G. glis* lineage a general increase in molar dimensions is supposed to be observed in the fossil record (Kowalski, 1956; Daoud, 1993; Striczky and Pazonyi, 2014). The cheek teeth of *G. minor* are morphologically indistinguishable from those of *G. sackdillingensis* (Striczky and Pazonyi, 2014). Instead, the two species either have been arbitrarily distinguished by the size of their molars, or by their supposedly complementary strati-
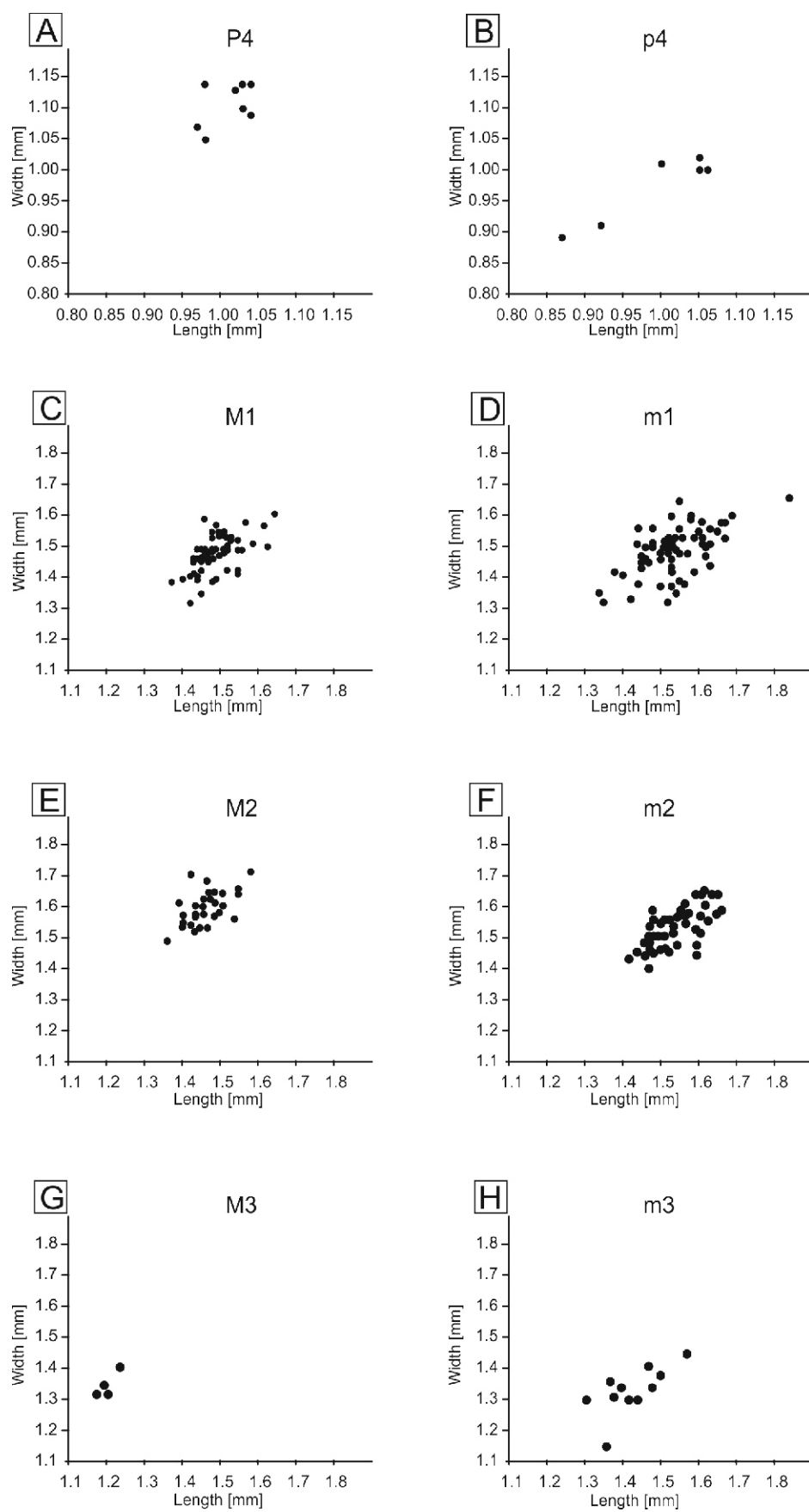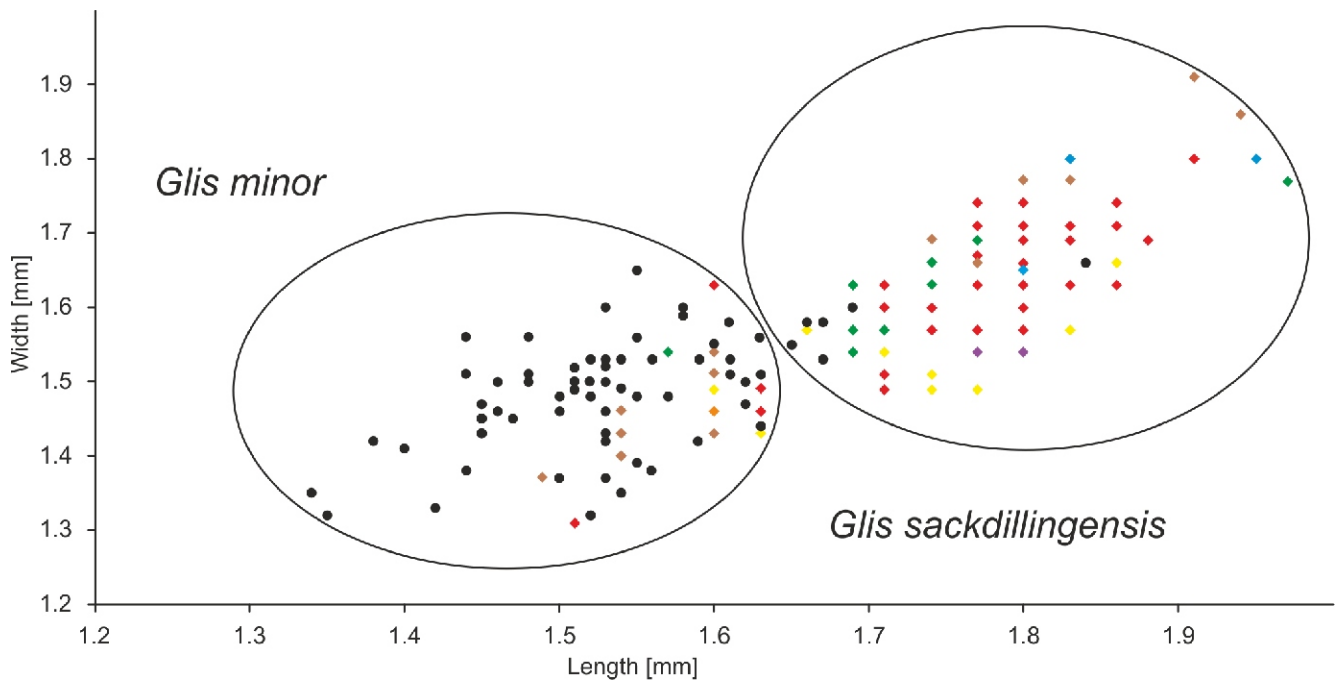
Fig. 4. Bivariate plots showing the measurements of *Glis* teeth from Węże 2

Fig. 5. Bivariate plots showing the measurements of *G. minor* and *G. sackdillingensis* m1 specimens from Węże 2 (black circles) and several central European sites studied by Striczky and Pazonyi 2014 (diamond shapes)

Brown – Somssich Hill 2; yellow – Osztramos 1; orange – Osztramos 1/E; red – Tarkő; green – Kövesvárad; violet – Uppony Rock Shelter 1; blue – Sackdillinger Cave

graphic ranges, with geologically older material being routinely assigned to *G. minor* (Table 2). Using statistical tools, Striczky and Pazonyi (2014) have established that in *G. minor* the length of m1 is <1.65 mm (Fig. 5) while the width of M1 is <1.7 mm.

DISCUSSION

The genus *Glis*, which represents the Glirinae lineage of the Gliridae family, is considered to have originated in the Middle Oligocene of Anatolia and to be descended from *Gliravus* (Daams and de Bruijn, 1995). Several extinct and one extant species (*G. glis*) are known (Daams and de Bruijn, 1995; Holden, 2005; Holden and Levine, 2009; Kryštufek, 2010). The stratigraphic range of the *G. minor-sackdillingensis* complex spans from the late Early Miocene to the late Early Pleistocene and both forms are known predominantly from Central Europe, with clusters of sites located in Austria, Hungary and Poland (Table 2 and Fig. 1). *G. minor* was first described by Kowalski (1956) as *G. sackdillingensis minor*, based on the material from Podlesice, as the dimensions of the Podlesice form "are distinctly smaller than all the corresponding dimensions of specimens from Germany, which strongly suggests its establishment as a separate subspecies". This smaller form was then raised to the rank of a species (*G. minor*) by Kretzoi (1959), a decision which was supported by Kowalski (1963).

Two specimens of p4 seem significantly smaller than the rest (Fig. 4B) but specimens narrower than 0.95 mm were already known from Węże 1 (Kowalski, 1963) and Sondershausen, and the measurements of the *Glis* teeth from Węże 1, Węże 2 and Rębielice Królewskie often fall quite close to the lower end of the typical *G. ex gr. sackdillingensis-minor* ranges (Hellmund and Ziegler, 2012). Furthermore, Kowalski,

in his description of some fossil rodent fauna from Rębielice Królewskie, reported a finding of a small (0.9 mm long, 0.9 mm wide) detached p4 that he classified as cf. *Glis* sp. and considered to possibly represent "a thus far unknown, very minute form of the genus *Glis* Brisson" (Kowalski, 1960b).

G. minor is considered to be the immediate ancestor of *G. sackdillingensis* which in turn is thought to have evolved into the modern *G. glis* (Nadachowski, 1989; Daoud, 1993; Siori *et al.*, 2014; Striczky and Pazonyi, 2014). The direct ancestor of *G. minor* has not been recognized. Although a synonymy between *G. sackdillingensis* and *G. minor* has been proposed (de Bruijn and van der Meulen, 1975), this suggestion has not generally been followed and "complementary stratigraphic ranges" have been cited as an argument in favour of keeping the specific status of the alleged smaller form (Popov, 2004). However, when the criteria elaborated by Striczky and Pazonyi (2014) are applied to the previously described *G. minor* / *G. sackdillingensis* material, there seems to be little such complementarity (see Table 2). At the same time, the statistical analyses of Striczky and Pazonyi (2014) seem to support the existence of two separate species, distinguishable only by morphometric criteria.

So far, the incisor enamel of the Glires (rodents and lagomorphs) has been studied more extensively than that of the molars. In the case of the Gliridae, Koenigswald (1993) provided a detailed study of their incisor enamel structure only. A more comprehensive study by Koenigswald (2004) provided a survey of the molar enamel structure in both fossil and extant rodents, concerning three types of schmelzmuster (spatial organization of enamel types) and their distribution across the phylogenetic tree. The Gliridae are virtually not mentioned there, apart from *Muscardinus* and *Leithia*, a large, insular form from the Pleistocene of the Mediterranean.

Occurrences of *Glis* ex gr. *minor-sackdillingensis*

No.	Locality	Age	Species detected	References
1.	Oberdorf (Austria)	MN 4	*G. minor*	de Bruijn (1998)
2.	Richardhof-Golfplatz (Austria)	MN 9	*G. minor*, **G. sackdillingensis*	Daxner-Höck and Höck (2009)
3.	Rudabánya (Hungary)	MN 9	*G. minor*, **G. sackdillingensis*	Daxner-Höck (2005)
4.	Richardhof-Wald (Austria)	MN 10	*G. minor* (* = *G. sackdillingensis*)	Daxner-Höck and Höck (2009)
5.	Kohfidisch (Austria)	MN 11	*G. minor*	Daxner-Höck and Höck (2009)
6.	Moncucco Torinese (Italy)	MN 13 (5.41–5.33 Ma)	*G. minor*, **G. sackdillingensis*	Colombero et al. (2014, 2017)
7.	Mała Cave (Poland)	MN 14	*G. minor*, **G. sackdillingensis*	Sulimski et al. (1979); Nadachowski et al. (1989)
8.	Komanos 1 (Greece)	Late Turolian	(?) *G. minor*	Hordijk and de Bruijn (2009)
9.	Notio 1 (Greece)	Late Turolian	*G. minor*	Hordijk and de Bruijn (2009)
10.	Pańska Góra (Poland)	Early Pliocene	*G. minor*, **G. sackdillingensis*	Bednarczyk (1993); Daoud (1993)
11.	Wölfersheim (Germany)	Early Pliocene	*G. minor*	Dahlmann (2001)
12.	Podlesice (Poland)	MN 14	*G. minor*, **G. sackdillingensis*	Kowalski (1956, 1963); Sulimski et al. (1979); Daoud (1993)
13.	Mont Hélène (France)	Ruscinian	*G. sackdillingensis* (* = *G. minor*)	Aguilar et al. (1986)
14.	Moreda (Spain)	Ruscinian	*G. sackdillingensis*	Martin-Suarez (1998)
15.	Muselievo (Bulgaria)	MN 15	*G. minor*	Popov (2004)
16.	Raciszyn 1 (Poland)	MN 15	(?) *G. minor*	Nadachowski (1989); Nadachowski et al. (1989)
17.	Sondershausen (Germany)	MN 15	*G. minor*, **G. sackdillingensis*	Hellmund and Ziegler (2012)
18.	Węże 1 (Poland)	MN 15	*G. minor*, **G. sackdillingensis*	Sulimski (1964); Daoud (1993); Stefaniak et al. (2020);
19.	Vitošov (Czechia)	MN 15/16	*G. minor* (* = *G. sackdillingensis*)	Čermák et. al. (2016)
20.	Grand Serre (France)	Late Pliocene	*G. sackdillingensis*	Aguilar et al. (1993)
21.	Hambach (Germany)	Late Pliocene	*G. minor* (* = *G. sackdillingensis*)	Mörs et al. (1998)
22.	Mas Rambault (France)	Late Pliocene	*G. sackdillingensis*	Aguilar et al. (2002)
23.	Rębielice Królewskie (Poland)	MN 16	*G. minor*, **G. sackdillingensis*	Kowalski (1963); Daoud (1993); Stefaniak et al. (2020)
24.	Tourkovounia 1 (Greece)	MN 16	(?) *G. sackdillingensis*	Koufos (2001)
25.	Węże 2 (Poland)	MN 16?	*G. minor*, *G. sackdillingensis*	Sulimski (1962); Stefaniak et al. (2020);
26.	Csarnóta (Hungary)	Late Pliocene/Early Pleistocene	(?) *G. minor*	Kretzoi (1959); Jánossy (1986)
27.	Kamyk (Poland)	Late Pliocene/Early Pleistocene	**G. minor*, *G. sackdillingensis*	Kowalski (1960a, 1963); Daoud (1993)

28.	Osztramos 1 (Hungary)	Late Pliocene/Early Pleistocene	G. minor, *G. sackdillingensis*	Jánossy (1986); Striczky and Pazonyi (2014)
29.	Osztramos 1/E (Hungary)	Late Pliocene/Early Pleistocene	G. minor, *G. sackdillingensis*	Striczky and Pazonyi (2014)
30.	Osztramos 7 (Hungary)	Late Pliocene/Early Pleistocene	(?) *G. minor*	Jánossy (1986)
31.	Osztramos 9 (Hungary)	Late Pliocene/Early Pleistocene	G. minor	Striczky and Pazonyi (2014)
32.	Kaiafas (Greece)	MNQ 19	(?) *G. sackdillingensis*	Koufos (2001)
33.	Les Valerots (France)	Early Biharian	*G. minor*	Chaline (1972)
34.	Monte la Mesa (Italy)	Early Biharian	*G. sackdillingensis*	Marchetti et al. (2000)
35.	Betfia (Romania)	Biharian	(?) *G.* cf. *minor*, (?) *G. sackdillingensis*	Terzea (1996)
36.	Beremend 14 (Hungary)	Early Pleistocene	*G. minor*, **G. sackdillingensis*	Pazonyi et al. (2016)
37.	Kadzielnia (Poland)	Early Pleistocene	**G. minor,* G. sackdillingensis	Daoud (1993); Urban et al. (2019)
38.	Kielniki 3A (Poland)	Early Pleistocene (Early Biharian)	(?) *G. sackdillingensis*	Nadachowski (1989); Nadachowski et al. (1989)
39.	Kielniki 1 (Poland)	Early Pleistocene (Late Biharian)	G. sackdillingensis (*= *G. minor*)	Nadachowski (1989); Nadachowski et al. (1989); Daoud (1993)
40.	Monte Argentario (Italy)	Early Pleistocene	(?) *G. sackdillingensis*	Siori et al. (2014)
41.	Osztramos 3 (Hungary)	Early Pleistocene	(?) *G. sackdillingensis*	Jánossy (1986)
42.	Osztramos 14 (Hungary)	Early Pleistocene	(?) *G. sackdillingensis*	Jánossy (1986)
43.	Razvodje (Croatia)	Early Pleistocene	(?) *G. sackdillingensis*	Paunovic and Rabeder (1996)
44.	Schernfeld (Germany)	Early Pleistocene	**G. minor*, G. sackdillingensis	Dehm (1962)
45.	Untermassfeld (Germany)	Early Pleistocene	*G. sackdillingensis*	Maul (2001)
46.	Villány-Kalkberg-Nord (Hungary)	Early Pleistocene	(?) *G. sackdillingensis*	Jánossy (1986)
47.	Żabia Cave (Poland)	Early Pleistocene	(?) *G. sackdillingensis*	Stefaniak et al. (2009); Nadachowski et al. (2011)
48.	Somssich Hill 2 (Hungary)	Late Early Pleistocene	*G. minor*, *G. sackdillingensis*	Striczky and Pazonyi (2014)
49.	Chlum 4 (Czechia)	Early/Middle Pleistocene	(?) *G. sackdillingensis*	Horáček et al. (2016)
50.	Kozi Grzbiet (Poland)	Early/Middle Pleistocene	*G. minor**, *G. sackdillingensis*	Nadachowski (1989); Nadachowski et al. (1989); Daoud (1993)
51.	Podumci (Croatia)	Early Middle Pleistocene	*G. sackdillingensis*	Malez and Rabeder (1984)
52.	Sackdillinger Cave (Germany)	Early Middle Pleistocene	*G. sackdillingensis*	Heller (1930); Striczky and Pazonyi (2014)
53.	Trlica (Montenegro)	Early Middle Pleistocene	(?) *G. sackdillingensis*	Agadzhanian et al. (2017)
54.	Kövesvárad (Hungary)	Middle Pleistocene	*G. minor*, *G. sackdillingensis*	Striczky and Pazonyi (2014)
55.	Tarkő (Hungary)	Middle Pleistocene	*G. minor*, *G. sackdillingensis*	Jánossy (1986); Striczky and Pazonyi (2014)
56.	Uppony Rock Shelter 1 (Hungary)	Middle Pleistocene	*G. minor*, *G. sackdillingensis*	Jánossy (1986) Striczky and Pazonyi (2014)

* – revised according to the criteria given by Striczky and Pazonyi (2014); (?) – measurements of diagnostic teeth not provided
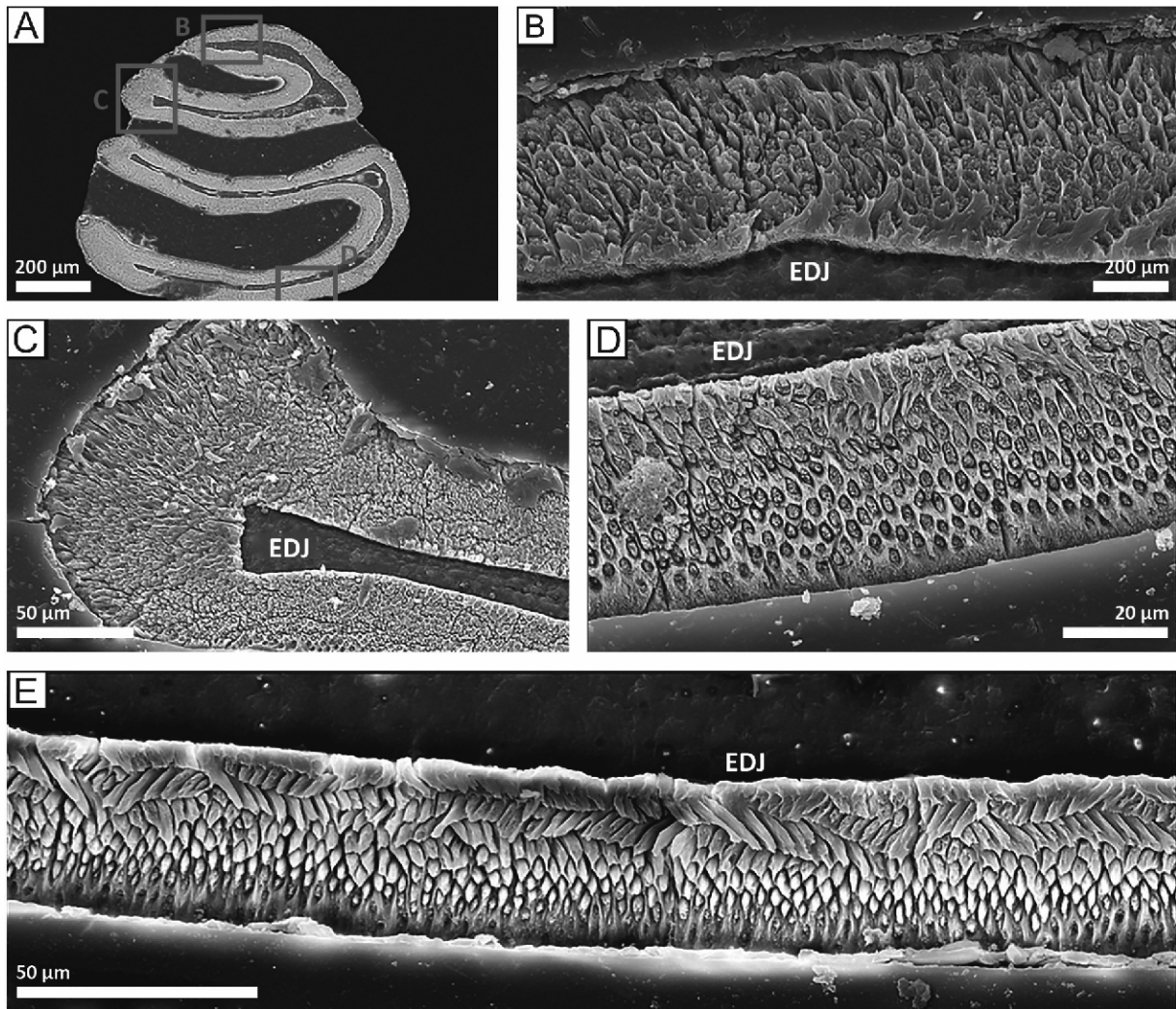
Fig. 6. Enamel structure of some *Glis* teeth from Węże 2 in cross section

A–D – p4: A – general view, B – anterolophid, C – protoconid, D – posterolophid; **E** – enamel structure of the posterolophid
of m1 showing a BRLE (basal ring of lamellar enamel) near the base of the crown; EDJ – enamel-dentine junction

The observations performed for the purpose of this study show that the enamel structure is simple and similar along the whole tooth perimeter. It is formed predominantly of radial enamel. A thin layer of lamellar enamel, occurring close to the enamel-dentine junction (EDJ), may be present (Fig. 6). The lamellar enamel forms a structure known as the basal ring of lamellar enamel (BRLE). Such a type of schmelzmuster, where radial and lamellar enamel co-occur, was recognized as the C-type (Koenigswald, 2004). Generally, it is typical of the Myomorpha, the species-rich clade of rodents encompassing the Muroidea (the mouse-like rodents) and Gliridae (Koenigswald, 2004; see also Nowakowski et al., 2018).

CONCLUSIONS

At the Villafranchian site of Węże 2 the genus *Glis* is represented by over 200 isolated teeth and a partially preserved mandible. The material belongs to *G. minor* and *G. sackdillingensis*, two species that differ only in the dimensions of their cheek teeth. Based on the morphometric criteria elaborated by Striczky and Pazonyi (2014), the mandible, all 62 isolated M1 specimens, as well as 61 m1 specimens, are assigned to *Glis minor*, while 6 m1 specimens are assigned to *Glis*

sackdillingensis. The remaining material is assigned to *G*. ex gr. *sackdillingensis-minor*, due to the lack of clear morphometric or morphological criteria permitting their attribution to one of the species with sufficient certainty. The presence of the dormouse genus *Glis* suggests that the fossil assemblage of Węże 2 represents at least a partly arboreal environment.

The traditional two-species paradigm for *G*. ex gr. *minor-sackdillingensis* is maintained in this study as the statistical analysis performed by Striczky and Pazonyi (2014) on the *Glis* material collected at several central European sites seems to support it. However, applying the criteria elaborated through that analysis to the previously described *G. minor/G. sackdillingensis* material also shows these two species as having almost parallel stratigraphic ranges and not infrequently coexisting at the same site, which was previously not thought to be the case. A more comprehensive statistical analysis may be needed to confirm or disprove the existence of two separate species, as opposed to one species, *G. sackdillingensis*, which displays some intraspecific variability of morphometric traits and a general evolutionary tendency to increase in size.

It is also possible that further studies of enamel structures are going to provide some additional means of distinguishing these species as differences in diet and lifestyle may have led to differences in enamel structure. Preliminary observations of the

enamel of the dormice from Węże 2 show that the structure typical of the Myomorpha is discernible, formed predominantly by radial enamel, with a thin layer of lamellar enamel occurring close to the enamel-dentine junction.

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