



Biostratigraphic significance of the root vole (*Alexandromys oeconomus*) for dating late Middle and early Late Pleistocene (MIS 8-MIS 3) Neanderthal sites in southern Poland

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Abstract

Determining the age of late Middle and Late Pleistocene (MIS 8-MIS 3) Neanderthal sites can be difficult as radiometry has limitations. Biostratigraphic methods can be used to overcome these difficulties. A species useful in these analyses is *Alexandromys oeconomus* (Pallas, 1776), which has a wide modern geographical distribution in the Northern Hemisphere. During the Pleistocene, its range significantly increased, occurring in large numbers both in interglacials and glacials. We distinguished Middle Pleistocene from Late Pleistocene and modern populations of this species based on temporal variation in the morphological structure of the first lower molar (m1) occlusion surface, and the relative proportions of the typical “*oeconomus*” and atypical “*gud*,” “*nivalis*,” and “*malei*” morphotypes. Our results showed that the mean values of metric parameters of the occlusion surface m1 of *A. oeconomus* varied over time. We found that this variation distinguished between populations of species from the late Middle Pleistocene (MIS 8-MIS 6) and early Late Pleistocene (MIS 5) from those from the Late Pleistocene (MIS 4-MIS 2), and some measurements and coefficients were correlated with climate-environmental changes. Using variation in *A. oeconomus* m1 morphology can be used as a tool in biostratigraphy requires further research including, among others, studies on how morphology varies between regions.

Keywords Biochronology · Small mammals · Biometrics · Middle Palaeolithic · Central Europe

Introduction

At Neanderthal sites from the late Middle and Late Pleistocene (MIS 8-MIS 3), to determine the stratigraphic position of sediments and their correlation with climatic-environmental changes, we can use radiometric methods, which have many limitations, and biostratigraphic methods. In these studies, the remains of *Arvicolinae* voles are key sources of information due to their common occurrence, well-known phylogenetic lines, and well-expressed diagnostic features on the first lower molars (m1), whose occlusal surface has a highly variable shape (e.g. Chaline 1972; Rabeder 1981;

Nadachowski 1982; Borodin 2009). Its variability manifests as, among other things, root and enamel islet atrophy; an increase in hypsodonticity, complexity, and size of the occlusal surfaces; and changes in enamel thickness at the edges of the triangles (e.g. Jánossy 1969; Kretzoi 1969; von Koenigswald 1973; Chaline 1972; Rabeder 1981; Herrmann 2002; Schmidt-Kittler 2002; Borodin 2009; Markova et al. 2010). This variation may be the result of evolutionary processes, or represent interspecies, intraspecies, temporal, and/or environmental variability. These phenomena lead to differences in metric parameters and their indices that can be used as indicators in biostratigraphy spanning both long and short time frames (e.g. Heinrich 1982; Maul and Markova 2007; Escudé et al. 2008; Berto et al. 2021; Fadeeva et al. 2021). Therefore, this is group one of the most useful for studying the biostratigraphy palaeoenvironment and palaeoclimate at archaeological and palaeontological sites (e.g. Chaline 1972; Heinrich 1982; Nadachowski 1982; López-García et al. 2010; Socha 2014a; Klimowicz et al. 2016; Berto et al. 2018; Luzi et al. 2018; Montuire et al. 2019; Lemanik et al. 2020).

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A key biostratigraphic parameter used to study Quaternary sediments is the enamel differentiation quotient (“Schmelz-band-Differenzierungs-Quotient”—SDQ) described for the *Mimomys-Arvicola* lineage. It can be used to evaluate changes both between and within the genera *Mimomys* and *Arvicola* (e.g. von Koenigswald 1973; Heinrich 1982; von Koenigswald and van Kolfschoten 1996; Abbassi and Desclaux 1996; Abbassi et al. 1998; Desclaux et al. 2000; Kalthoff et al. 2007; Escudé et al. 2008; Ruddy 2011; Agadzhanian 2012). It is assumed that in these voles, the decline in mean SDQ values over time is an evolutionary process. In the genus *Mimomys*, the Middle Pleistocene *Arvicola*, and modern *Arvicola sapidus* Miller, 1908, the enamel making up the trailing edges of the triangles is thicker than that found on the leading edges (*Mimomys-like* or negative-differentiation). In Late Pleistocene and modern representatives of *Arvicola amphibius* (Linnaeus, 1758), the opposite trend is observed, whereby the trailing edges of the triangles are thinner than found on the leading edges (*Microtus-like* or positive-differentiation) (e.g. von Koenigswald 1973; Heinrich 1978; Martin 1987; Röttger 1987). In contrast, studies in *Lasiopodomys gregalis* (Pallas, 1779) show that its mean SDQ values increase over time (Klimowicz et al. 2016). Moreover, mean SDQ values in both species vary with higher-order (glacial/interglacial) and lower-order (stadial/interstadial) periods which indicates they depend on climate and habitat conditions (Socha 2010, 2014a; Klimowicz et al. 2016; Fadeeva et al. 2021) and perhaps also animal migrations.

Problems in interpreting changes in SDQ values are due to geographic, climatic, and altitudinal variation (Kratochvíl 1980, 1981; Röttger 1986, 1987; Escudé et al. 2008). SDQ values depend on the food base, the transition from soft to hard food as a result of climatic-habitat changes (Herrmann 2002; Schmidt-Kittler 2002). In many vole genera, e.g. *Microtus*, *Arvicola*, and *Dicrostonyx*, in time, the role of the enamel band forming the trailing edge of the triangle in fragmenting food has decreased (Herrmann 2002). As enamel thickness depends on the above-mentioned factors, the use of the SDQ index in short-term biostratigraphy is controversial (Escudé et al. 2008). Therefore, identifying the relationships between the factors influencing morphometry of the m1 occlusal surface will help resolve the usefulness of this indicator in short-term biostratigraphy.

Species with a wide geographic distribution and high climate and habitat plasticity play an important role in biostratigraphic studies. One such species is the root vole *Alexandromys oeconomus* (Pallas, 1776), which has the widest modern geographical distribution of all *Alexandromys* Ognev, 1914. The root vole occurs in three climate zones, polar, boreal, and temperate, where it inhabits damp, densely vegetated areas along the edges of lakes, streams, and marshes; it can be found in tundra, taiga, forest-steppe, and

even semi-desert. Wet meadows, bogs, fens, riverbanks, and flooded shores are all important habitats (e.g. Mitchell-Jones et al. 1999; Hernández Frenández 2001; Shenbrot and Krasnov 2005; IUCN 2021). Middle and Late Pleistocene sediments from Europe show that the root vole was abundant and widely distributed in both glacial and interglacial periods, and that its historical range was much larger than its modern one (e.g. Chaline 1972; Nadachowski 1982; Kowalski 2001; Socha 2014a). Recent representatives of *A. oeconomus* have a well-recognised, variable morphology of the m1 occlusal surface. This manifests as an increase in atypicality in isolated populations and in the eastern extremes of its range (Jorga 1971, 1974; Angermann 1974, 1984; Voyta et al. 2013, 2019). In Pleistocene populations of this species, m1 morphology is also known to vary over time (Hinton 1907; Chaline 1972; Rabeder 1981; Nadachowski 1982, 1991; Socha 2014a; Lemanik 2018), which makes it useful as a biostratigraphic indicator (Nadachowski 1982; Nadachowski et al. 2009; Socha 2010, 2014a; Lemanik 2018). These studies evaluated the proportion of typical “*oeconomus*” to atypical “*gud*,” “*nivalis*,” and “*malei*” morphotypes. An increase in the proportion of atypical morphotypes and especially “*malei*” is considered a feature that distinguishes between Middle Pleistocene, and Late Pleistocene and recent populations (Nadachowski 1982; Nadachowski et al. 2009; Socha 2010, 2014a; Lemanik 2018). The aim of this study was to determine how morphometric features of the m1 occlusion surface of *A. oeconomus* vary with changes in climate, and to test whether this knowledge can be applied to short-term biostratigraphic studies at archaeological sites.

Material and methods

Material

The material comprised of 3 447 (fossil = 3 348, recent = 99) first lower molars of *A. oeconomus*. Fossil material came from five archaeological sites in the Kraków-Częstochowa Upland (Biśnik cave, Deszczowa cave, Komarowa cave, Stajnia cave) and Podhale (Obłazowa cave), and one palaeontological site in Podhale (Obłazowa II) (Fig. 1). Sediments at these sites were deposited from the Middle Pleistocene to the Holocene (STab. 1) (Nadachowski et al. 2009; Valde-Nowak et al. 2003; Cyrek et al. 2000; Gašiorowski et al. 2014; Krajcarz et al. 2014; Socha 2014a; Valde-Nowak and Nadachowski 2014; Źarski et al. 2017). The sites are described in the Supplementary information. The recent material came from Dolny Śląsk, Białowieża, and Rajgród (Podlasie) (Fig. 1).

We excluded from the study both damaged teeth and those belonging to juveniles, which were characterised by thin and undifferentiated enamel, lack of breaks in enamel continuity,

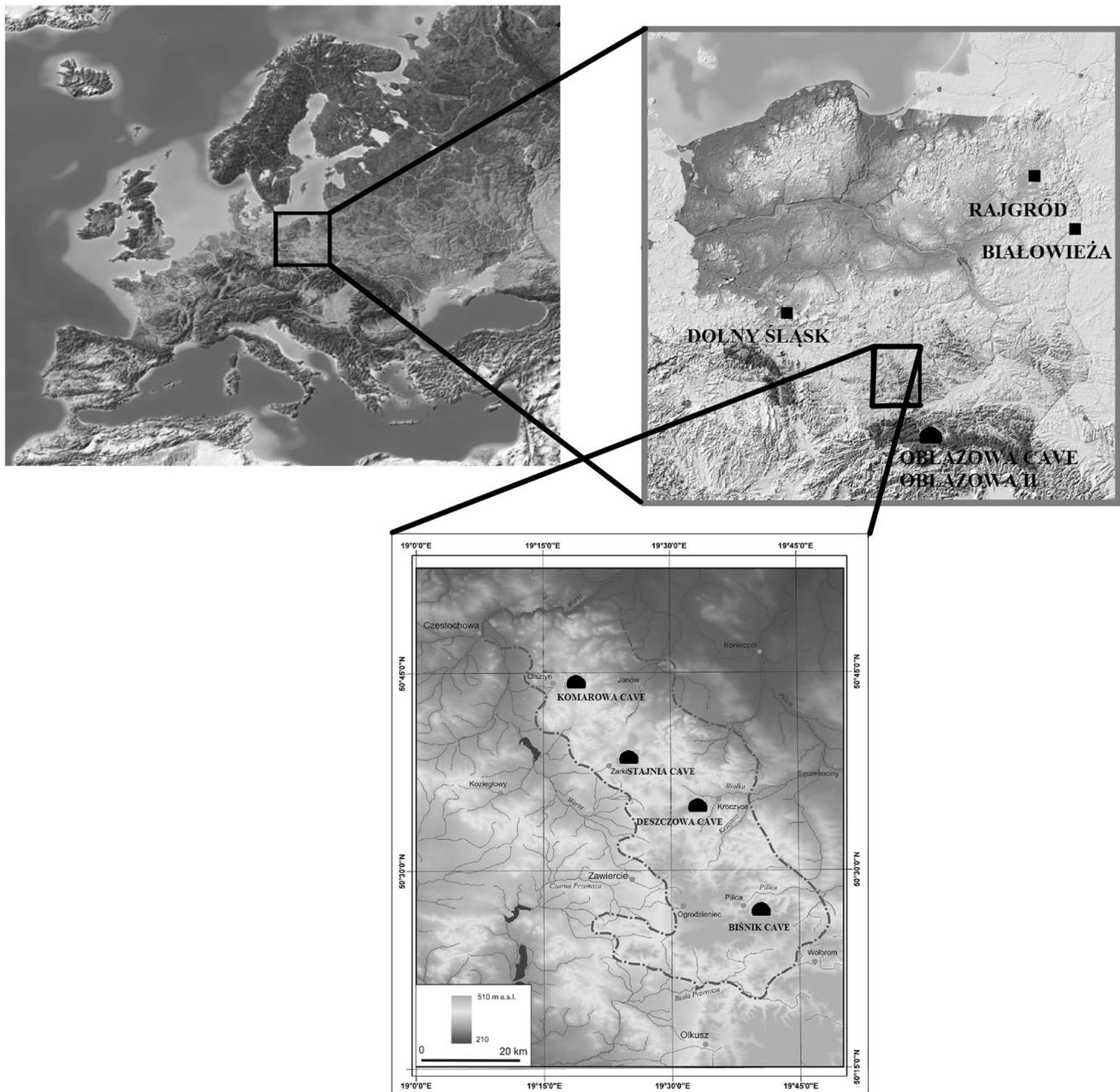


Fig. 1 Location of the study sites

and incompletely formed triangles with wide connections between them (Oppenheimer 1965; Nadachowski 1982; Borodin 2009; Markova et al. 2013).

The studied material is stored at the Department of Palaeozoology of the University of Wrocław (Biśnik and Stajnia caves, and Dolny Śląsk), the Institute of Systematics and Evolution of Animals Polish Academy of Sciences in Kraków (Deszczowa, Komarowa, and Obłazowa caves, and Obłazowa II), and the Institute of Mammal Biology Polish Academy of Sciences in Białowieża (Białowieża, Rajgród).

Methods

Morphology

We used the nomenclature of Hibbard (1950) to describe the elements forming the m1 occlusal surface in voles (Fig. 2). We determined the morphotypes of m1 of the root vole based on the schemes proposed by Chaline (1972), Angermann (1974, 1984), Nadachowski (1982, 1991), Markova (2013), and the compilation of these schemes proposed by

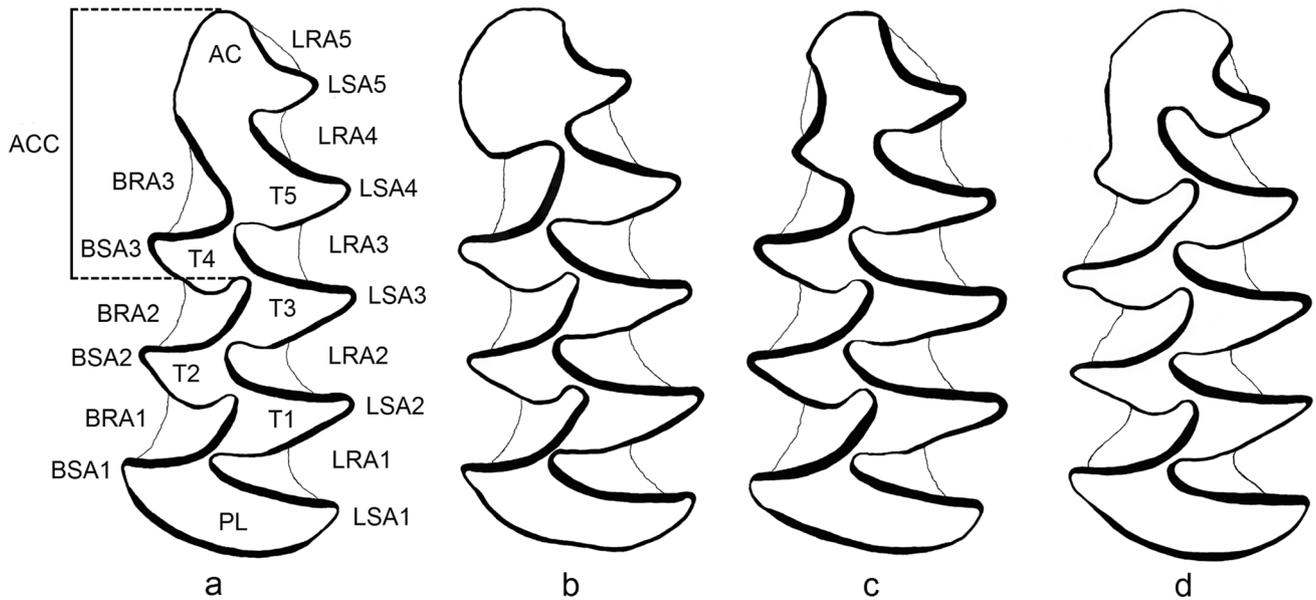


Fig. 2 Morphological structure of occlusal surface of *A. oeconomicus* m1, T, triangle; ACC, anteroconid complex; AC, anterior cap; PL, posterior lobe; LSA, lingual salient angles; BSA, buccal salient

angles; LRA, lingual re-entrant angle; BRA, buccal re-entrant angle. **a** Morphotype “*oeconomicus*,” **b** morphotype “*nivalis*,” **c** morphotype “*gud*,” **d** morphotype “*malei*”

Lemanik (2018). The basic diagnostic features were as follows: the number of closed dentin fields on the occlusal surface, the width of the connection between the LSA4 field and the rest of the anteroconid, and the tendency to develop additional elements in the anteroconid complex (Chaline 1972; Angermann 1974, 1984; Nadachowski 1982, 1991; Markova 2013; Lemanik 2018). In this species, the m1 occlusal surface occurs in four basic morphotypes: “*oeconomicus*” (typical); and “*nivalis*,” “*gud*,” and “*malei*” (atypical) (Fig. 2).

The “*oeconomicus*” morphotype is characterised by five well-developed dentin fields taking the form of a triangle (T1-LSA2; T2-BSA2; T3-LSA3; T4-BSA3; T5-LSA4) according to the criteria of Markova (2013) (Fig. 2a). In the anteroconid complex, there is an LSA5 dentin field that can take the form of a T7 triangle (LSA5) with varying degrees of formation and complexity depending on the degree of development of the LRA5 re-entrant angle. The dentin fields T1-LSA2; T2-BSA2; T3-LSA3; and T4-BSA3 always form closed triangles. There is a wide connection between the dentin field LSA4-T5 and the rest of the anteroconid complex (triangle T5 is open) (Fig. 2a). In the anteroconid complex, the dentin field BSA4 does not form a triangle because the re-entrant angle BRA4 is absent or is present in an unmeasurable form.

The “*nivalis*” morphotype is characterised by the presence of five well-developed dentin fields (T1-LSA2; T2-BSA2; T3-LSA3; T4-BSA3; T5-LSA4) (Fig. 2b). In the anteroconid complex, there is an LSA5 dentin field, which can take the form of a T7 triangle with varying degrees

of formation and complexity depending on the degree of development of the LRA5 re-entrant angle. The dentin fields T1-LSA2; T2-BSA2; T3-LSA3; and T4-BSA3 always form closed triangles. The field LSA4-T5 forms a closed triangle (without a connection between T5 and the rest of the anteroconid) (Fig. 2b). BSA4 is as a distinct thickening and does not form a triangle because the re-entrant angle BRA4 is absent or present in an unmeasurable form.

The “*gud*” morphotype is characterised by seven well-developed dentin fields, four on the lingual side and three on the buccal: T1-LSA2; T2-BSA2; T3-LSA3; T4-BSA3; T5-LSA4; T6-BSA4; T7-LSA5 (Fig. 2c). The dentin fields T1-LSA2; T2-BSA2; T3-LSA3; and T4-BSA3 always form closed triangles (Fig. 2c). Within the anteroconid, fields T6-BSA4 and T7-LSA5 are present as triangles (Fig. 2c). The re-entrant angle BRA4 is well developed (Fig. 2c). There is a connection between LSA4 (T5) and the rest of the anteroconid complex, but it is narrower than in “*oeconomicus*” (Fig. 2).

The “*malei*” morphotype is characterised by seven well-developed dentin fields, four on the lingual side and three on the buccal: T1-LSA2; T2-BSA2; T3-LSA3; T4-BSA3; T5-LSA4; T6-BSA4; and T7-LSA5 (Fig. 2d). The dentin fields T1-LSA2; T2-BSA2; T3-LSA3; and T4-BSA3 always form closed triangles. Within the anteroconid complex, developed dentin fields T6-BSA4 and T7-LSA5 are present (Fig. 2d). The re-entrant angle BRA4 is well developed (Fig. 2d). The LSA4-T5 field forms a triangle (without a connection between T5 and the rest of the anteroconid)

(Fig. 2d). This morphotype has most complex occlusal surface.

Measurements

Measurements were carried out according to the schemes of van der Meulen (1973) (L — maximum length of m1 occlusal surface, A — length of anteroconid complex, B — anterior constriction of the anterior part of the anteroconid) and Nadachowski (1991) (measurement of displacement between re-entrant angles BRA3 and LRA4 (P)) (Fig. 3). We then calculated the A/L ratios (van der Meulen 1973) and the B/P shift. Enamel thickness was measured at the anterior and posterior edges of the dentin fields, excluding for fields BSA4 and LSA5 (Fig. 3). We then calculated the enamel differentiation quotient SDQ (Heinrich 1982). It was calculated for each field by dividing the trailing edge enamel thickness by that of the leading edge. It was then also calculated for the entire m1 by summing the SDQ of

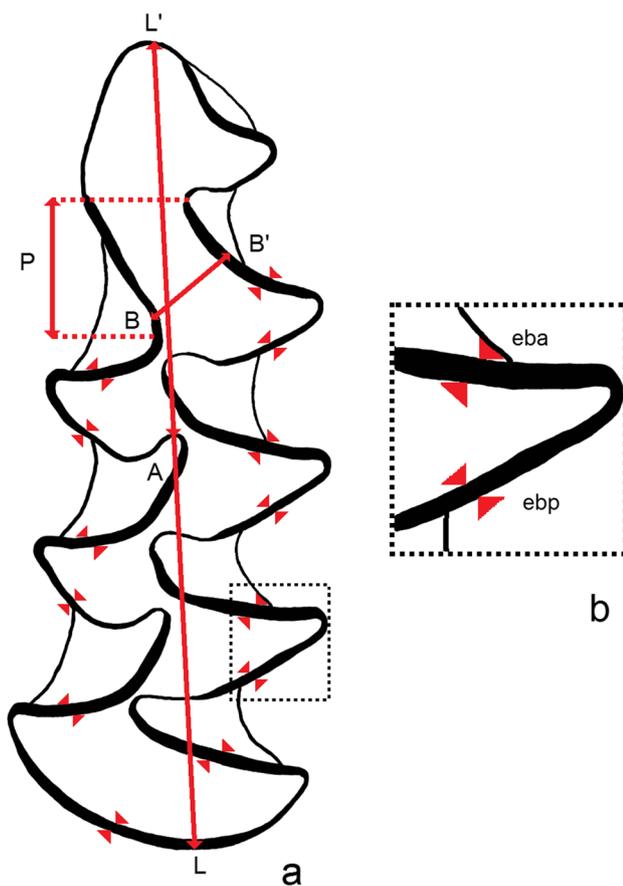


Fig. 3 Measurement methods. **a** L'–L, maximum length of m1 occlusal surface (L); L'–A, length of anteroconid complex (A); B–B', anterior constriction of anterior part of anteroconid (B); P, the displacement between re-entrant angles BRA3 and LRA4 (P). **b** ebp, the trailing edge enamel thickness; eba, leading edge enamel thickness

the individual dentin fields and dividing by their number. Finally, it was calculated for the lingual (SDQ_{la}) and buccal (SDQ_{ba}) dentin fields of the tooth.

All measurements were made to the nearest 0.01 mm, using an Olympus SZX-10 stereo microscope with an Olympus DP71 camera and Cell-D software.

Statistical analyses of the results were performed using the CSS software “Statistica” version 12 PL. The following descriptive statistics were used to characterise the measurements and coefficients: N—sample size, Min.—minimum value, Max.—maximum value, M—mean, Me—median, Var—variance, CV—coefficient of variation, and SD—standard deviation. Normality of the distributions was tested using Lilliefors and Shapiro–Wilk tests. For multiple comparisons between several groups, the Kruskal–Wallis test was used. The R-Spearman correlation coefficient was also calculated. The study used a significance level of $p < 0.05$.

Results

Results of morphological analysis

All four morphotypes of *A. oeconomicus* m1 were recorded among the collected material. The studied populations differed in their frequencies of occurrence of the different morphotypes (Figs. 4 and 5). Both in Pleistocene and recent populations, the morphotype “*oeconomicus*,” typical for this species, was dominant (Figs. 4 and 5). The Middle Pleistocene had higher proportions of the more complex morphotypes (“*nivalis*,” “*gud*,” “*malei*”) compared to the Late Pleistocene and recent populations (Figs. 4 and 5). In the Middle Pleistocene, a constant presence of atypical morphotypes was found, whereas in the Late Pleistocene, these morphotypes were less numerous or disappeared completely (Fig. 5). Among the Middle Pleistocene populations, the population from MIS 6 had the highest proportion of atypical morphotypes (39.16%). This population also had the highest share of “*malei*” (15.38%), the morphotype with most complex occlusal (Fig. 5). In the Late Pleistocene, only populations from MIS 5c and MIS 2 hosted all morphotypes of m1 *A. oeconomicus*. However, atypical morphotypes were few and altogether their presence did not exceed 17% in MIS 5c and 6% in MIS 2 (Fig. 5). In recent populations, only two morphotypes were found, “*oeconomicus*” and “*nivalis*,” the latter having the least complex occlusal surface among the atypical morphotypes (Figs. 4 and 5).

Results of metric analyses

The results of the statistical analysis of the studied parameters are presented in Supplementary information STabs. 2–14. They indicate how the mean values of the studied

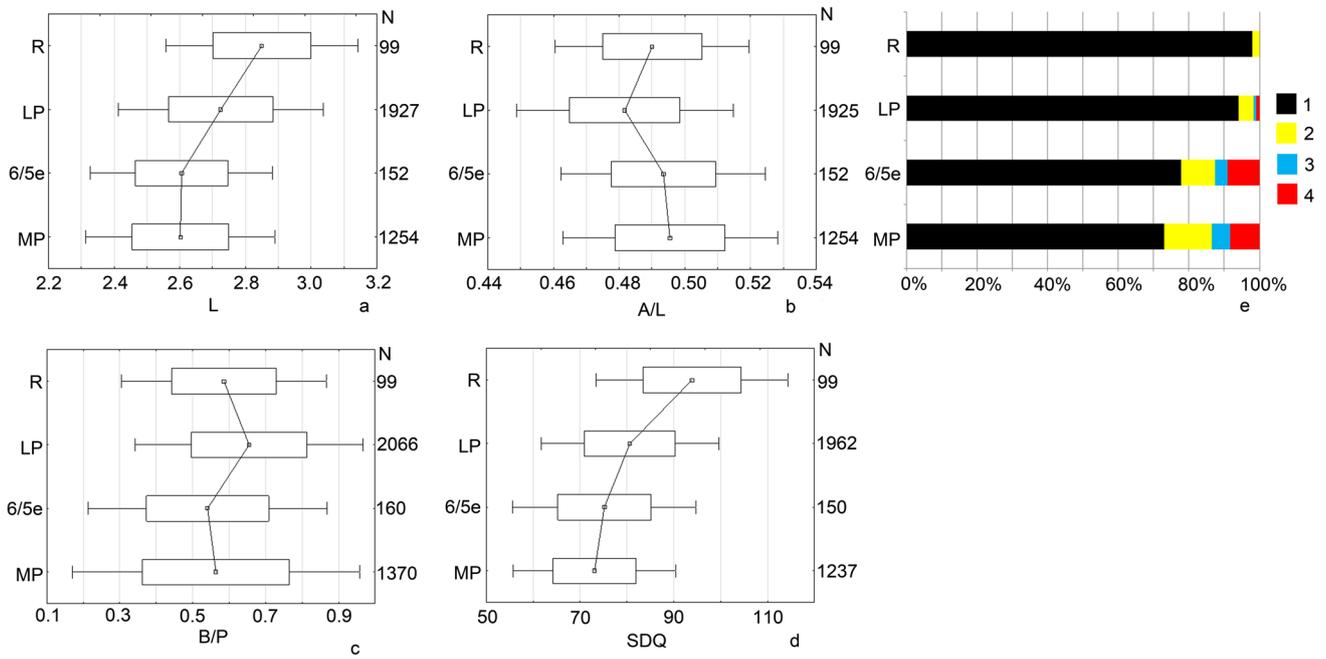


Fig. 4 Measurements and coefficients of variation (mean and double standard deviation) (a–d), and morphological variation (frequency of different morphotypes) (e) in *A. oeconomus* populations. MP, Middle Pleistocene; 6/5e, marine isotopic stage 6/5e — boundary between

Middle and Late Pleistocene; LP, Late Pleistocene; R, recent; N, number of specimens, (1) morphotype "oeconomus," (2) morphotype "nivalis," (3) morphotype "gud," (4) morphotype "malei"

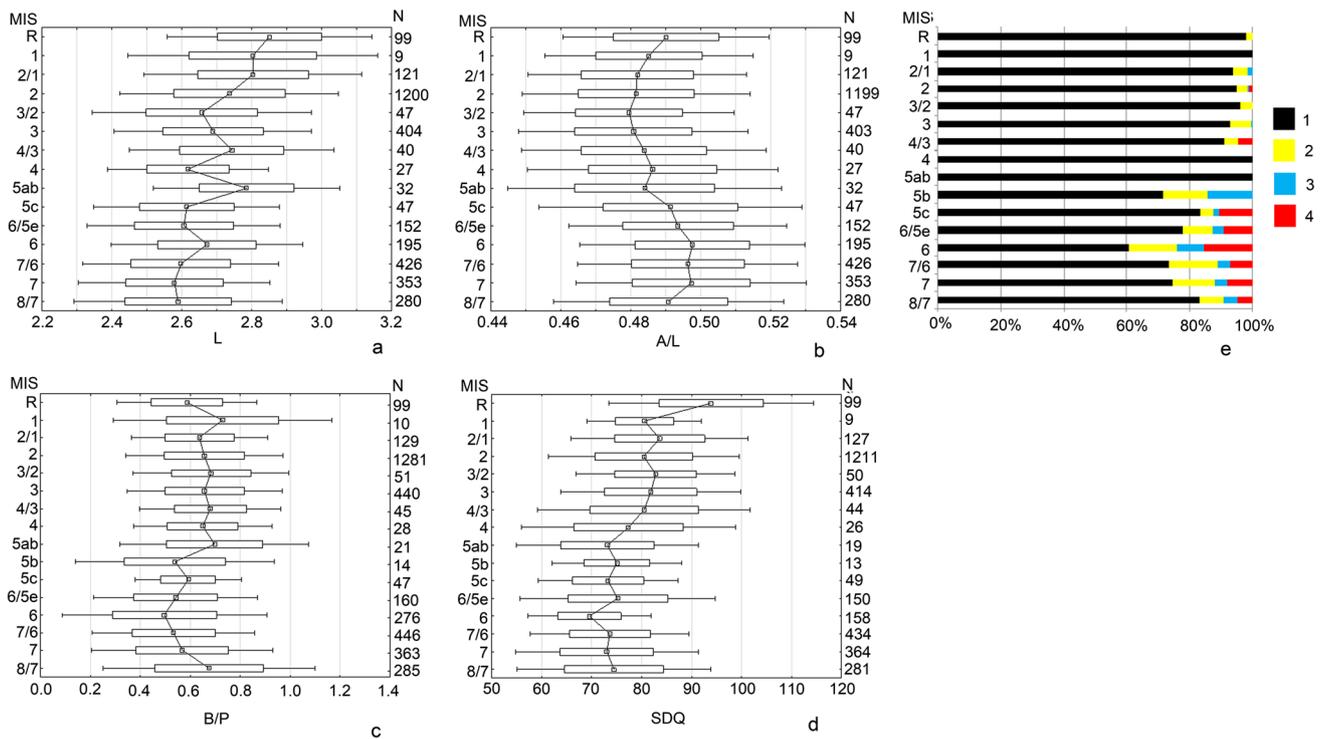


Fig. 5 Measurements and coefficients of variation (mean and double standard deviation) (a–d), and morphological variation (frequency of different morphotypes) (e) in *A. oeconomus* populations. MIS, marine

isotopic stage; N, the number of specimens, (1) morphotype "oeconomus," (2) morphotype "nivalis," (3) morphotype "gud," (4) morphotype "malei"

measurements and coefficients varied with time (STabs. 2 and 3, Figs. 4 and 5, S Figs. 1 and 2).

Linear measurements and ratios of m1 occlusal surface

Middle Pleistocene populations had significantly lower maximum m1 occlusal surface length (L), anteroconid length (A), anterior anteroconid constriction (B), displacement between re-entrant BRA3 and LRA4 (P), and shift coefficient B/P than Late Pleistocene and modern populations of *Alexandromys oeconomicus*. On the other hand, A/L ratios were higher in Middle Pleistocene populations (STabs. 2–11, Figs. 4 and 5, S Figs. 1 and 2).

Measurements such as the anteroconid length and displacement between re-entrant BRA3 and LRA4, and the shift coefficient (B/P) had a low correlation ($R=0.2-0.3$, $p<0.05$) with growth mean values from the Middle Pleistocene to the recent (STabs. 2–4, Figs. 4 and 5, S Figs. 1 and 2), whereas the increase in m1 length and anterior anteroconid constriction was moderately correlated ($R=0.4$, $p<0.05$) during this time (STabs. 2–4, Figs. 4 and 5, S Figs. 1 and 2). On the other hand, A/L ratio values showed a decreasing trend over time ($R=-0.3$, $p<0.05$) (STabs. 2–4, Figs. 4 and 5).

The measurements and linear indices showed differential trends of change between populations correlated with different marine isotopic stages (MIS) (STabs. 3 and 4, Fig. 5, S Fig. 2). In Middle Pleistocene populations, the increase in the mean values of L, A, P, and A/L ratio over time was weakly correlated ($R=0.1-0.2$, $p<0.05$) (STabs. 3 and 4, Fig. 5, S Fig. 2). In the Middle Pleistocene, the A/L ratio increased over time, in contrast to the general decreasing trend found in this parameter (STab. 4). On the other hand, B and the B/P were characterised by decreasing trend of these parameters ($R=-0.3$ to -0.2 , $p<0.05$) during the Middle Pleistocene (STabs. 3 and 4, Fig. 5, S Fig. 2). In the Middle Pleistocene, B and B/P decreased over time, in contrast to the general increasing trends found for these parameters (STab. 4). The changes in the measurements and linear coefficients confirm the statistically significant differences between the populations from this period (STabs. 6–11).

The transition between the Middle and Late Pleistocene (MIS 6 and 5e) was characterised by changes in most of the analysed linear parameters (STabs. 3 and 4, Fig. 5, S Fig. 2). During this time, mean values of L and A as well as the A/L ratio decreased ($R=-0.1$ to -0.2 , $p<0.05$), as indicated by the statistically significant differences between the populations from MIS 6 and 6/5e (STabs. 2–11, Figs. 4 and 5, S Figs. 1 and 2). The decrease in L and A at the Middle and Late Pleistocene boundary contrasts with their general increasing trend from the Middle Pleistocene to the recent times and also with that found in the Middle and Late Pleistocene (STab. 4). On the other hand, the B and the B/P ratio

were characterised by a weak ($R=0.1$, $p<0.05$) and moderate ($R=0.2$, $p<0.05$) increase over time, respectively (STabs. 3 and 4, Figs. 4 and 5, S Figs. 1 and 2).

In the Late Pleistocene populations, most of the linear parameters were characterised by less dynamic changes over time (STab. 4). Of the six linear parameters studied, four (L, A, B, and P) were characterised by a weakly and low correlated increase in their mean values over time (STabs. 3 and 4, Fig. 5, S Fig. 2). In contrast, the A/L as well as B/P ratios showed no overall change over the Late Pleistocene (STabs. 3 and 4, Fig. 5).

In contrast to the Middle Pleistocene, in the Late Pleistocene, the linear parameters of most populations varied little between MIS (STabs. 3 and 4, Fig. 5, S Fig. 2). Most of the variation was in L and A and occurred between Early and Middle Vistulian and Late Vistulian populations (STabs. 3 and 4, Fig. 5, S Fig. 2). Differential trends of L and A were most pronounced in populations from MIS 5c to MIS 4. In contrast, in Late Vistulian populations, they were characterised by a weak increase over time (STabs. 3 and 4, Fig. 5, S Fig. 2). In Early and Middle Vistulian populations, the other linear parameters did not show significant trends over time (STabs. 3 and 4, Fig. 5, S Fig. 2). In Middle Vistulian and Late Vistulian populations, B, P, and B/P showed differential trends over time (STabs. 3 and 4, Fig. 5, S Fig. 2).

In the Late Vistulian and recent populations, only P significantly increased over time ($R=0.3$, $p<0.05$) (STabs. 3 and 4, S Fig. 2).

SDQ index

Middle Pleistocene populations had lower mean SDQ values than Late Pleistocene and recent populations. Mean SDQ values for the whole m1, as well as for the lingual and buccal sides, increased from the Middle Pleistocene to recent times ($R=0.2-0.4$, $p<0.05$) (STabs. 2–4, Figs. 4 and 5, S Figs. 1 and 2).

In the Middle and Late Pleistocene, SDQ values had varying trends over time (STabs. 3 and 4). In the Middle Pleistocene, the values of this index decreased over time ($R=-0.1$, $p<0.05$), whereas in the Late Pleistocene, they increased (STab. 4). By contrast, SDQla and SDQba showed no general trend in the Middle and Late Pleistocene (STabs. 3 and 4).

SDQ varied between populations from different MIS, indicating this index had contrasting trends in different MIS (STabs. 3 and 4, Fig. 5). These observations are confirmed by the statistically significant differences in the mean values of SDQ different MIS (STab. 12). These contrasting trends were observed more frequently in populations corresponding to the end of the Middle Pleistocene (MIS 7 and 6) and the boundary between the Middle and Late Pleistocene (STabs.

3 and 4) and were characterised both by increases (between MIS 7 and 7/6) and decreases (between MIS 7/6 and 6).

In contrast, in Late Pleistocene populations, despite a general upward trend, SDQ values did not have significantly different trends between MIS (STabs. 3 and 4). Similarly, at that time, SDQla and SDQba values did not have significantly different trends between populations from different MIS (STab. 4, STabs. 13 and 14, SFig. 2). Only at the end of the Late Pleistocene (MIS 3/2-MIS 2/1) where there are significant changes in the mean values of these parameters (STabs. 3 and 4, SFig. 2). Also between the Late Pleistocene and recent populations, SDQla and SDQba values increased over time (STabs. 3 and 4, SFig. 2).

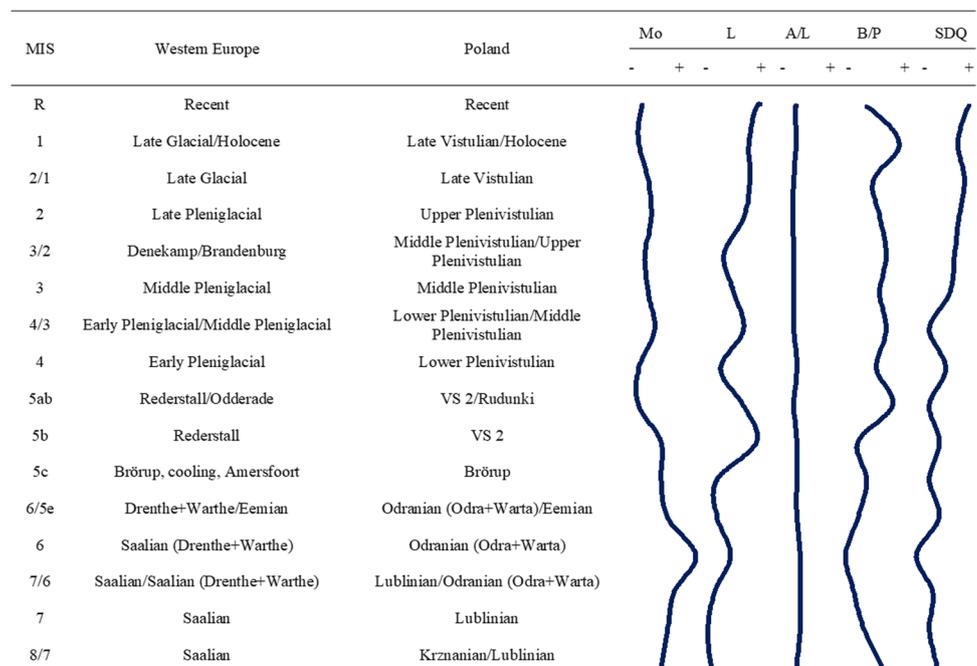
Discussion

General variation in morphology and metric parameters

Our results indicate that the measurements and indices of the occluded surface m1 of *Alexandromys oeconomicus* and its morphological structure varied over time. On the one hand, morphological composition and mean values of metric parameters subject to long-term trends between the Middle Pleistocene and the present day; on the other hand, they were also subject to short-term trends between different MIS (STab. 4, Figs. 4–6, SFig. 1–3).

Long-term trends were clearly visible between populations from the late Middle and Late Pleistocene. These periods had different morphological compositions and mean values of metric parameters (Fig. 4, SFig. 1). The presence of morphotypes with a higher degree of complexity, especially “malei,” was typical for Middle Pleistocene populations. In the Late Pleistocene atypical, morphotypes “nivalis,” “gud,” and “malei” were rare or disappeared completely (Figs. 4 and 5). In modern populations, studies have found the m1 of *A. oeconomicus* to have a varied morphology, where atypical morphotypes occur in isolated populations at the extremes of the species range and in eastern populations (Jorga 1971, 1974; Angermann 1974, 1984; Voyta et al. 2019). Its morphology has also been found to be highly variable in fossil populations (e.g. Hinton 1907; Chaline 1972; Rabeder 1981; Nadachowski 1982, 1991; Socha 2014a; Lemanik 2018) making it a useful biostratigraphic indicator (Nadachowski 1982; Nadachowski et al. 2009; Socha 2010, 2014a; Lemanik 2018). Such studies assess the proportion of typical to atypical morphotypes and the increase in the proportion of atypical morphotypes over time; this especially concerns the “malei” morphotype, whose high abundance is considered a feature that distinguishes Middle Pleistocene from Late Pleistocene and recent populations (Nadachowski 1982; Nadachowski et al. 2009; Socha 2010, 2014a; Lemanik 2018). Our results on the morphological variation of *A. oeconomicus* m1 confirm these observations and indicate it can be used as a marker in biostratigraphic studies (Figs. 4 and 5).

Fig. 6 Variation in the studied parameters describing *A. oeconomicus* m1 over time from the Middle Pleistocene to the recent. Mo, morphological variation; –, decrease in morphological variation or mean parameter values; +, increase in morphological variation or mean parameter values; MIS, marine isotopic stage



Late Middle Pleistocene variation in relation to climate

Climate conditions reconstructed from sediments corresponding to MIS 7, 7/6, 6/5e (Biśnik cave), and MIS 6 (Deszczowa cave) indicate that the climate varied between these periods (Socha 2010, 2014a, 2014b; Klimowicz et al., 2016). In this region, MIS 7 represents an interglacial (Lublinian interglacial), with a climate with average temperatures of the warmest month reaching +14 °C (Lindner 1992). Climate conditions reconstructed from sediments from the Biśnik cave corresponding to MIS 7 indicate a boreal (thermoboreal) climate prevailed at that time in the vicinity of the cave. The mean annual monthly temperature was +3.2 °C, the mean July temperature was +15 °C, and the total annual precipitation was 983 mm (Socha 2010, 2014a). Climate conditions reconstructed from sediments from MIS 7/6 showed that the mean annual monthly temperature was +5 °C, mean July temperature was +15.8 °C, mean temperature of the coldest month was −5.4 °C, and total annual precipitation was 1038 mm (Socha 2010, 2014a). MIS 6 includes the Odrarian glaciation (Odra + Warta) and was characterised by a cold climate. In Poland, during the Odra stage, the ice sheet reached the Lublin and the Małopolska Uplands as well as the Sudetes and even reached Czechia. The regression of the Oder Ice Sheet was oscillatory (e.g. Marks and Pavlovskaya 2006; Ber et al. 2007; Lindner and Marks 2008, 2012; Lang et al. 2018; Marks et al. 2018). The climate conditions reconstructed from sediments corresponding to MIS 6 indicated a cooling of the climate. Mean annual monthly temperatures were around 0 °C and ranged from −2.9 to +0.8 °C. The average July temperature ranged from +10.2 to +12 °C and that of January from −14.6 to −9.6 °C. The reconstructed mean temperatures of the warmest and coldest months had large amplitudes, indicating an increase in climate continentalism (Socha 2014b; Klimowicz et al. 2016). The period represented by MIS 6/5e was characterised by warming climate conditions. The climate conditions reconstructed from sediments Biśnik cave sediments corresponding with MIS 6/5e showed that they were formed while the mean annual temperature was in the range +4.2–+4.5 °C, the mean temperature of the warmest month +15.4–+15.5 °C, and of the coldest month −6.5 to −0.6 °C, and annual precipitation was 1004–1008 mm (Socha 2010, 2014a).

Late Pleistocene variations in relation to climate

The beginning of the Late Pleistocene Eemian interglacial (MIS 5e) in Poland was characterised by warmer climate with average July temperatures ranging from +14 to +24 °C, and those of January from −5 to 0 °C, and forest being the dominant environment (Mamakowa 1989; Cheddadi et al.

1998; Mojski 2005; Lindner and Marks 2008; Marks et al. 2016). After the Eemian interglacial, climate cooled and ice sheets developed (e.g. Lindner 1992; Svendsen et al. 2004; Mojski 2005; Lindner et al. 2006; Lindner and Marks 2008; Marks et al. 2016, 2019). The Brörup Interstadial (MIS 5c) in Poland was characterised by an average temperature of the warmest month falling between +12 and +13 °C and of the coldest month below −5 °C (Mirośław-Grabowska et al. 2015; Marks et al. 2019). Climate conditions reconstructed from Biśnik cave sediments showed that during this period, the average annual monthly temperature was +4.3 °C, the average temperature of the warmest month +16.2 °C and of the coldest −7.3 °C, and annual precipitation of 917 mm (Socha 2010, 2014a). The Rederstall cooling (MIS 5b) in Poland had an average temperature of the warmest month not exceeding +10 °C and of the coldest month in the range −10 to −8 °C (Kozarski and Nowaczyk 1999; Granoszewski 2003; Lorenc 2007; Kuprjanowicz 2008; Marks et al. 2016). In Europe, the ice sheet covered the Scandinavian Peninsula without its southern extremities (Svendsen et al. 2004). In Poland, during the Odderade warming (MIS 5a), mean July temperatures were in the range +10–+15 °C and mean January temperatures around −5 °C (Bocheński 1974; Tobolski 1991; Aalbersberg and Litt 1998; Granoszewski 2003; Lorenc 2007; Kuprjanowicz 2008; Marks et al. 2016); this high temperature amplitude indicates a continentalising climate (Aalbersberg and Litt 1998; Marks et al. 2016, 2019). The Early Pleniglacial (MIS 4) was characterised by ice sheet encroachment on to the present Vistula Delta and neighbouring areas from the south and west (Lindner 1992; Svendsen et al. 2004; Mojski 2005). In Poland, the mean temperatures of the warmest month ranged from +5 to +14 °C (Lorenc 2007). However, analyses of pollen profiles and composition of avifauna have indicated that the temperature oscillated around +10 °C (Bocheński 1974; Kozarski 1980; Granoszewski 2003). The climate conditions reconstructed from layer 12 of Biśnik cave indicate a cooling of the climate. The mean annual temperature was +1.4 °C, the mean temperature of the warmest month +13.8 °C, and of the coldest month −10.6 °C, with annual precipitation of 914 mm and an increase in climate continentalisation (Socha 2010, 2014a). However, the stratigraphic position of layer 12 from Biśnik cave is controversial. According to Socha (2014a), it corresponds to MIS 4, while according to Krajcarz et al. (2014), to MIS 5. In Europe during the Middle Pleniglacial (MIS 3), at its maximum extent, the ice sheet was limited to the Scandinavian Peninsula (Helmens and Engels 2010; Meerbeek et al. 2011). Climate conditions of MIS 3 were characterised by a highly dynamic (van Andel and Davis 2003; Mojski 2005). In Poland, mean temperatures of the warmest month ranged from +10 to +17 °C (Rotnicki and Tobolski 1969; Kozarski 1980; Granoszewski 2003). Climate conditions reconstructed from Biśnik cave sediments

showed that during this period, the mean annual monthly temperature ranged from +1.5 to +2.4 °C, the mean temperature of the warmest month +13.6 to +14.2 °C, and of the coldest month −10.5 to −9.0 °C, and annual precipitation was 921–1049 mm (Socha 2010, 2014a). The Late Pleniglacial (MIS 2) was also characterised by highly dynamic climate. During this period, the last transgression of the ice sheet into Poland took place with its maximum extent during the LGM (Marks 2002; Svendsen et al. 2004; Marks et al. 2019). In Poland during the LGM, the mean annual monthly temperature ranged from −8 to −5 °C, the mean temperature of the warmest month did not exceed +3 °C, and the mean temperature of January was −20 °C (Maruszczak 1980; Goździk 1994; Mojski 2005; Marks et al. 2016). After the LGM as a result of progressive warming, the ice sheet gradually disappeared, and mean annual temperatures ranged from +10 to +17 °C (Tobolski 1998; Ralska-Jasiewiczowa et al. 1998; Lorenc 2007). Climate conditions reconstructed for Biśnik cave sediments showed that during this period, the mean annual monthly temperature was in the range +0.7–+4.3 °C, the mean temperature of the warmest month +12.1–+15 °C and the coldest −10.1 to −5.9 °C, and annual precipitation was 964–1237 mm (Socha 2010, 2014a). In contrast, climate conditions reconstructed from MIS 3 and MIS 2 from Deszczowa cave indicate a cool climate. The reconstructed mean annual temperatures ranged from −6.3 to +4.4 °C, the mean temperature of the warmest month +7.8 to +14.3 °C, and of the coldest month −19.8 to −4.6 °C (Socha 2014b; Klimowicz et al. 2016).

Temporal variation in relation to morphology and morphometry

Comparing the temporal variation in m1 morphology in the studied populations of *A. oeconomus* with the reconstructed climate data revealed that complexity mainly increased in the Middle Pleistocene populations. The high proportion or presence of the highest complexity morphotype (“malei”) in both the Middle and Late Pleistocene is characteristic for periods of cool climate condition. That the morphological structure of populations depends on climate was also reflected in the short-term changes in the mean values of the studied metric parameters. However, long- and short-term trends in the mean values of metric parameters of m1 *A. oeconomus* may have different causes. Long-term variation may result from evolutionary trends in the subfamily Arvicolinae, whereas variation over shorter time intervals will depend on changes in climate and the morphological structure of m1 in *A. oeconomus* populations.

In the studied populations of *A. oeconomus*, tooth length (L) and anteroconid length (A) consistently increased over time. But in periods of climate cooling, the mean values of these measurements were higher, while in periods of

warming, they were lower (Fig. 6, SFig. 3). This observation is consistent with Bergman’s rule, to which modern populations of *A. oeconomus* adhere to, whereby their body size increases in cold climates (Meiri and Dayan 2003; Baláž and Fraňová 2013). According to Martin (1993), with an increase in body size comes an increase in the length of the contralateral skull, which, according to Nadachowski (1991), directly increases tooth size. The results we obtained for *A. oeconomus* are similar to changes in the mean values of L observed in *Lasiopodomys gregalis* (Socha 2010; Klimowicz et al. 2016).

The observed decrease in mean A/L values from the Middle Pleistocene to the recent (Figs. 4–6) contrasts with the evolutionary trend proposed for this species by Rekovets and Nadachowski (1995). It also differs from the evolutionary trend of increasing A/L values found in many vole species (Rekovets and Nadachowski 1995; Maul and Markova 2007; Maul et al. 2007; Klimowicz et al. 2016; Rekovets and Kovalchuk 2017; Luzi et al. 2021 among others). However, the trend we observed was not always constant over time and is subject to short-term fluctuations. These fluctuations are associated with climate, habitat, and morphological structure (STab. 4, Fig. 6). An increase in the A/L ratio is associated with an increase in ACC complexity. A longer anteroconid may reduce pressure on the tooth during chewing, thus slowing tooth wear (Maul 2001). The observed deviations from the proposed evolutionary trend in *A. oeconomus* (Rekovets and Nadachowski 1995) may result from regional differences in morphological structure and environmental, and may ultimately correspond to a regional trend. Changes in morphological structure also result in changes in the mean values of B, P, and the B/P ratio. The typical “*oeconomus*” morphotype is characterised by larger B values compared to higher complexity morphotypes. P and the B/P ratio also depend on the complexity of the occlusal surface. Thus, Middle Pleistocene populations have lower mean values of these parameters than Late Pleistocene ones (STab. 4, Fig. 4, SFig. 1).

The SDQ, SDQla, and SDQba indices increased over time from the late Middle Pleistocene to the present day, but, like other measurements and indices, displayed short-term deviations from the trend, which we pronounced in the Middle Pleistocene (STab. 4, Figs. 5 and 6, S Figs. 2 and 3). The observed trend of increasing mean SDQ values over time is opposite to the trend found in *A. amphibius* (e.g. Heinrich 1982; Röttger 1987; van Kolfshoten 1992; von Koenigswald and van Kolfshoten 1996; Desclaux et al. 2000; Kalthoff et al. 2007; Escudé et al. 2008; Ruddy 2011) and consistent with the results obtained in *L. gregalis* (Klimowicz et al. 2016). *A. amphibius* (Socha 2010) and *L. gregalis* (Klimowicz et al. 2016) specimens from Biśnik and Deszczowa caves display similar short-term trends of changes in SDQ values as those we found in *A. oeconomus*.

All three species undergo a clear change in this index in populations from the boundary between the late Middle and Late Pleistocene, and/or those from the beginning of the Late Pleistocene (MIS 6/5e and MIS 5e). Thus, changes in mean SDQ index values are a useful tool in biostratigraphy for distinguishing late Middle Pleistocene and early Late Pleistocene populations from Late Pleistocene and recent populations. These previous studies on the trend in SDQ values over time indicate that the observed changes may be a consequence of several processes. Firstly, they were influenced by evolutionary trends during the transition from *Mimomys-like* to *Microtus-like* (e.g. von Koenigswald 1973; Heinrich 1978; Martin 1987; Röttger 1987), whereby the trailing edges of the triangles lost their importance for food fragmentation and instead began to primarily play a stabilising role (Herrmann 2002). Secondly, they were affected by changes in the complexity of the occlusal surface. As complexity increases, the enamel bands become thinner (Herrmann 2002; Schmidt-Kittler 2002), which decreases the SDQ value. The complexity of the occlusal surface depends on the food base, with species feeding on harder food having a more complex occlusal surface and thinner enamel bands (Herrmann 2002). Our results confirm the relationship between mean SDQ values and the m1 morphological structure of *A. oeconomicus* populations. In the populations with higher proportions of complex morphotypes, mean SDQ values were lower (Figs. 5 and 6). Thirdly, changes in the SDQ index in *A. oeconomicus* are also affected by the climate polyzone and habitat polyzone, or both simultaneously. The phenomenon of polyzonality influences both, the use of a diverse food base and the colonising of areas differing in climatic parameters. The dependence of mean SDQ on climate conditions has also been found in *L. gregalis* (Klimowicz et al. 2016) and *A. amphibius* (Fadeeva et al. 2021). Thus, in the root vole, changes in mean SDQ values over time are also influenced by migratory phenomena resulting dynamically changing climate and environmental conditions. Despite the difficulty in interpreting the obtained results, the SDQ index can be used as a climobiostratigraphic marker at sites with a long-term sediment sequence.

Conclusions

The results of this study on the morphometric variation of the occlusal surface of m1 *Alexandromys oeconomicus* indicated that both the morphological structure and the mean values of measurements and indices in the studied populations varied over time. A decrease in the proportion of morphotypes with higher occlusal surface complexity in favour of the typical “*oeconomicus*” morphotype was observed from the Middle Pleistocene to the present day. The occurrence

of the most complex morphotype “*malei*” was characteristic for Middle Pleistocene populations.

Most of the measurements and ratios showed a long-term increasing trend from the Middle Pleistocene to the present day except for the A/L ratio, which showed a decreasing trend.

Both the morphological structure and mean values of measurements and ratios also varied in the short-term, between different stratigraphic units. These trends mainly arose due to changes in prevailing climate conditions at the time the *A. oeconomicus* remains were deposited, both in the Middle and Late Pleistocene. The variation in the mean values of metric parameters was also influenced by the morphological composition of the studied populations.

The study’s recognising of the morphological composition of the studied populations and mean values of the studied parameters, especially SDQ index, will contribute to determining climobiostratigraphy at late Middle and Late Pleistocene archaeological sites. Moreover, knowledge on the morphological and morphometric traits of *A. oeconomicus* m1 populations will also be useful in palaeoecology and reconstructing migration directions.

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Declarations

Conflict of interest The authors declare no competing interests.

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