https://doi.org/10.5194/egusphere-2026-2261
Preprint. Discussion started: 19 May 2026

Short communication: A linear regression model for amino acid dating of *Bithynia* opercula from deep-core material

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Abstract. Estimating numerical ages from the extent of amino acid racemisation observed in fossil biominerals has been the aim of many researchers in the field of amino acid geochronology. Here, the use of temperature profiles and independent age estimates to build a linear regression model for IcPD with uncertainty calculated using a Bayesian approach is explored. This work presents a pilot study to test the potential of this methodology and determine what next steps need to be taken to make this a viable approach to produce numerical ages from IcPD data. To progress this work, a comprehensive study of the sources of uncertainty in the model needs to be made.

1 Introduction

Amino acid geochronology (AAG) is a relative dating technique that relies on the predictable breakdown of protein in fossil biominerals (Hare and Mitterer 1966). The intra-crystalline protein decomposition (IcPD) approach to AAG (Penkman et al., 2008) has become a valuable technique for dating the European Quaternary (e.g. Penkman et al., 2011; 2013; 2024; Dickinson et al., 2019; Tesakov et al., 2020; Conti et al., 2024; Nelson et al., 2024; 2025a; 2025b). This approach isolates the protein within faceted voids of mollusc shell (Gries et al., 2009). These intra-crystalline proteins behave as a closed system. As such, the extent of protein decomposition within this fraction is due to burial temperature and time since burial, yielding less variable data when compared to the whole biomineral (Penkman et al., 2008). A key reaction pathway that takes place during protein decomposition is racemisation. In the majority of living organisms only the L-isomer of each amino acid is incorporated into the protein chain. When tissue turnover ceases, amino acids will start to spontenously racemise until a racemic equilibrium is reached. This is quantified as the D/L value, and is used to place sites containing fossil biominerals into chronological order (Hare and Mitterer, 1966).

By building regional aminostratigraphic frameworks from specimens correlated with robust independent chronology to act as tie-points, the extent of IcPD for chronostratigraphic stages can be determined. These frameworks can then be used to constrain the age of deposits where the chronology is uncertain (Penkman et al., 2013; Nelson et al., 2025b). In addition, IcPD can be used independently to test existing age models (Preece et al., Preece et al.; Tesakov et al., 2020; Nelson et al., 2024). Modelling the impact of temperature on protein decomposition and racemisation has been a common route of investigation for AAG studies (e.g. Bada et al., 1975; Crisp et al., 2013; Demarchi et al., 2013). Early works employed isothermal heating

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experiments at elevated temperatures to accelerate protein decomposition at timescales that could be studied in the laboratory (e.g. Bada and Schroeder, 1972; Mitterer, 1975; Goodfriend and Meyer, 1991; Miller et al., 1999; Kaufman, 2000; 2006). Various mathematical expressions have been used to describe the relationship between protein decomposition, time and temperature. These include the integrated rate equation, which can be used to describe the relationship between the rate of protein decomposition reactions (e.g. racemisation) with time and temperature when it conforms to reversible first-order kinetics (Clarke and Murray-Wallace, 2006). However, the rate of racemization within fossils do not strictly follow first-order kinetics, and the apparent conformity is not observed for the entire range of D/L values (e.g. Sejrup and Haugen, 1992; Clarke and Murray-Wallace, 2006). Other mathematical expressions, such as logarithmic equations, parabola curve fitting, simple linear and stepped linear models, power transformations, Bayesian approaches (Allen et al., 2013) and a modified integrated rate equation have also been explored to model the rate of racemization throughout the full range of D/L values for an individual amino acid (reviewed in Clarke and Murray-Wallace, 2006). Although some approaches have proved better than others to model this relationship, as these mathematical models do not describe the kinetic behaviour of the reactions (Crisp et al., 2013), there is no single standard approach to describe the extent of racemization with time. In addition, the work of Tomiak et al. (2013) demonstrated that the rate-determining step in some biominerals for protein decomposition varies between low (~25 °) and high temperatures (80-140 °). This means that even if a mathematical expression describes the kinetic behaviour of protein decomposition well at high temperatures, it is unlikely to describe the reaction kinetics at low temperatures. In addition, burial temperatures are unlikely to have been isothermic throughout the fossil's burial history, and therefore are challenging to model successfully.

The opportunity to model kinetic behaviour at burial temperatures could help to provide more accurate age models for IcPD data. Possible terrestrial archives to explore this behaviour are alluvial plains within tectonically subsiding basins (e.g. Pannonian Basin in Hungary). Quaternary fluvial sediments within such basins often contain *Bithynia* opercula, a common substrate for IcPD (e.g. Penkman et al., 2011; 2013; 2024; Tesakov et al., 2020; Nelson et al., 2024). A well-dated suite opercula found from such archives, where the temperature of sediments is known throughout the core, could be used to explore the relationship between the extent of racemisation with time and burial temperature. This would enable an age-depth model to be developed from IcPD data, using common statistical approaches such as linear regression, which may provide a more accurate description of the kinetic behaviour of IcPD at lower temperatures. In addition, this model may help to provide numerical ages from IcPD data when the burial temperature and depth below the surface are known for opercula recovered from long core material.

IcPD analysis of the Pannonian Basin cores provide a unique opportunity to do this. *Bithynia* opercula found throughout the cores were analysed using the IcPD approach by Nelson et al. (2024). Opercula were located between ~5-460 m, with the majority located in depths >100 m below ground level, where the influence of the climate on burial temperature is attenuated, and therefore the degree of variability in burial temperature is reduced. The age of these sediments were constrained by a previously developed age model that used magnetic stratigraphy, biostratigraphy and cycles of magnetic susceptibility and grain size to determine the age of sediments throughout each core and also correlate the cores to one another (Püspöki et al., 2013,; 2016; 2020; 2021a; 2021b; 2023), known hereafter as the Püspöki age model. The steep and variable geothermal gradient

(∼40-50 °C/km; Bodri, 1981; Horváth et al., 2014) of this region means that burial temperature does not increase uniformly with depth between borehole locations. This provided an opportunity to design a model for the relationship of IcPD with time and temperature under burial conditions. It will also further test the validity of the Püspöki age model. In addition, this model may help to provide numerical ages from IcPD data when the burial temperature and depth below the surface are known for opercula recovered from long core material.

Here, the relationship between the extent of IcPD, estimated age and burial temperature has been modelled using a linear regression model (LRM). This model is then used to estimate the age of a test dataset. Possible sources of uncertainty within the model are evaluated, and next steps to improve the model are proposed. The ultimate aim is to develop a new method using a statistically valid approach to estimate numerical ages from IcPD analysis, which is based on the modelled behaviour of racemisation during real-world burial conditions.

2 Materials and Methods

2.1 Quaternary sediments of the Pannonian Basin (Hungary)

2.1.1 Geological setting

Surrounded by the Carpathian mountain range, the Pannonian Basin (Figure 1) is a large, tectonically subsiding basin. Quaternary sediments within the basin extend between 150-700 m below the surface (Franyó, 1992), comprising fluvial deposits that lie within an alluvial plain that contains multiple glacial and interglacial cycles (Rónai, 1985). Glacial deposits are characterised by fine-grained sediments, indicative of low-transport capacity of rivers running into the basin during these periods. Conversely, interglacial sediments are characterised by coarser-grained material, due to increased transport capacity of rivers as conditions became warmer and wetter (Nádor et al., 2003).

Table 1. Sub-basin and boreholes within the Pannonian Basin (Hungary), depth of Quaternary sediments (m below ground surface) and geothermal gradient (°C/km) within each core (Nelson et al., 2024)

Basin	Boreholes	Quaternary sediment depth (m)	Geothermal gradient (°C/km)
Körös Basin	Vésztő	431	49.4
	Dévaványa	328	46.4
	Szarvas	442	54.9
Makó Trough	Mindszent	670	40.5
Jászság Basin	Jászladány	254	57.4
Békés Basin	Pusztaottlaka	431	47.8
	Kevermes	431	53.9

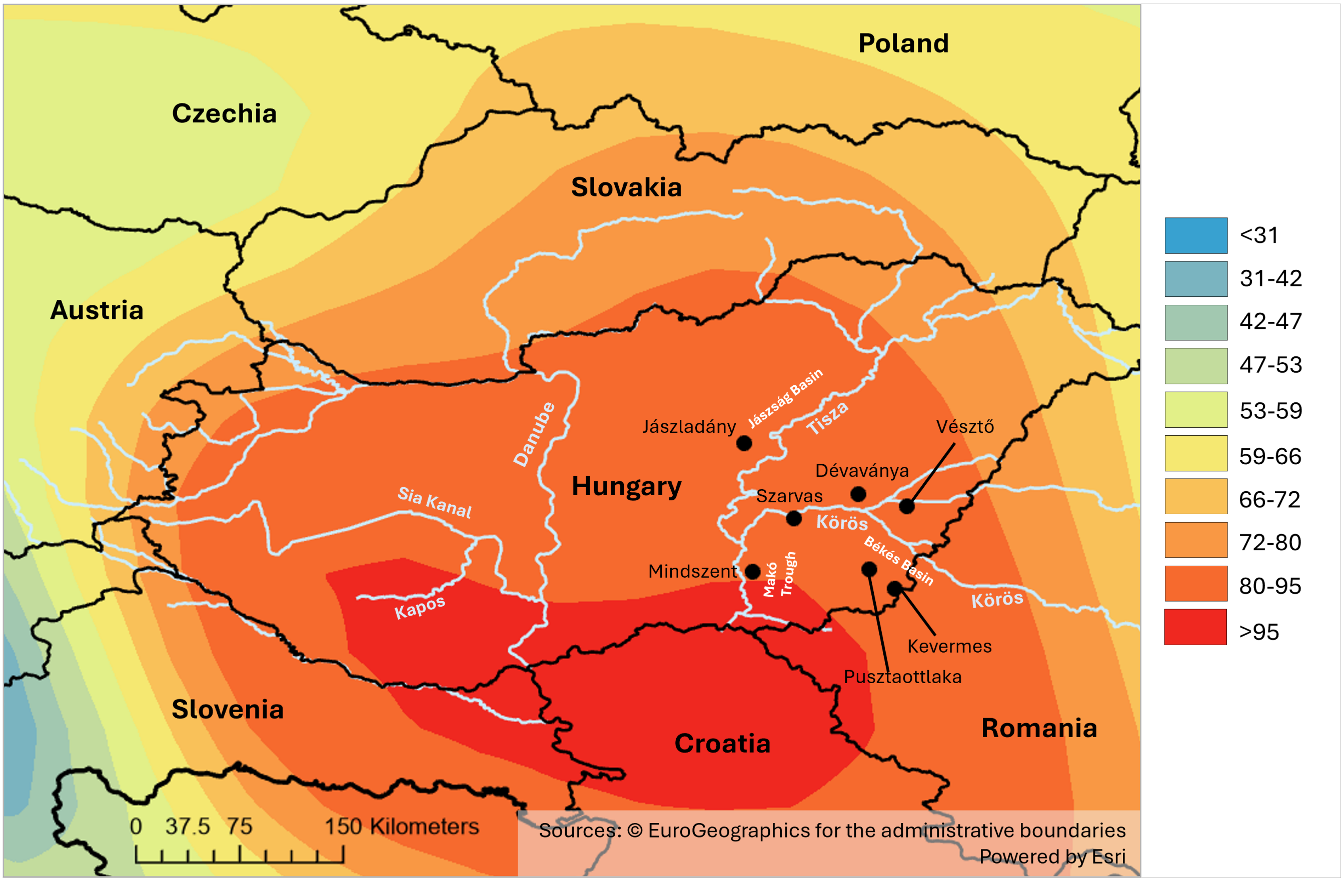

Figure 1. Estimated Surface heat flow mW/m^2 of the Pannonian Basin (Hungary; Davies et al., 2013,). All borehole localities and sub-basins are located in an area where the 30 °C isotherm is located between 300-350 m below ground level, and average is 90-100 mW/m. Sources: Esri

The Hungarian portion of the Pannonian Basin is known to possess a positive geothermal anomaly (Toth, 2017), with a mean heat density of 90-100 mW/m^2 (Fig. 1) and a geothermal gradient of ∼45 °C/km (Dövényi et al., 1983; Lenkey et al., 2002). Rock temperatures are known to reach 30 °C between 250-450 m across the study region (Toth, 2017. 15 out of the 59 opercula-containing sedimentary horizons within the cores were located between 250-450 m. Modern mean annual temperature at the surface is 10.5-11.5 °C (Hungarian Meteorological Service, 2024), demonstrating that the temperature gets significantly warmer throughout the sediment column. The geothermal gradient is not consistent across the study area 1.

2.1.2 Previous work defining chronology of the sediments

The Püspöki age model previously developed by Püspöki et al. (2013; 2016; 2020; 2021a; 2021b; 2023) for the Quaternary sediments within the Pannonian Basin cores was developed using a combination of magnetic and molluscan biostratigra-

phy, and cycles of magnetic susceptibility and mean grain size. The paleomagnetic data (Cooke et al., 1979) from the Vésztő and Dévaványa cores demonstrated multiple short-lived polarity events throughout the Quaternary sediments. Magnetic susceptibility (MS) measurements by (Nádor et al., 2003), supported by mineralogical data, indicated that early postglacial melt-waters resulted in episodes of significant sedimentation. This resulted in magnetic susceptibility peaks due to climate-controlled thawing of permafrost within the surrounding mountainous catchment areas (Püspöki et al., 2021a).
The Quaternary succession has been divided into MS cycles. Each cycle begins with an MS maxima followed by a disappearance of magnetic minerals from the sediment load, defined as "susceptibility termination surfaces" (STS). The MS maxima have been correlated with cold marine oxygen isotope stages (MIS) and STS with the subsequent warm MIS. MIS correlations have been constrained by the timing of the polarity events identified throughout the Dévaványa and Vésztő cores and the first and last appearance of the important mollusc stratigraphic marker *Viviparus boeckhi* (Halaváts 1888; first appearance: Olduvai subchron (∼1.9-1.8 Ma), last appearance ∼550 ka (Püspöki et al., 2016)). A similar pattern of MS cycles has been observed in cores collected throughout the Pannonian Basin, which has been used to correlate sediments between cores (Püspöki et al., 2021a).

2.1.3 The relationship between IcPD, depth, temperature and time

Opercula IcPD (Nelson et al., 2024) was used to independently test the correlations between cores made by the Püspöki age model. Assuming continual sedimentation had occurred (excepting known unconformities), a linear interpolation model was used to estimate the age of sediments containing opercula (Nelson et al., 2024).
Initial analysis of the Körös Basin cores supported the correlations between the boreholes previously made. However, systematically higher D/L values were observed for material attributed to < 450 ka within the Jászladány, Kevermes and Mindszent when compared to the Körös Basin cores. Investigation into the cause of these differences in IcPD suggested that they were due to the variable burial depths for equivalent age sediments and the steeper than average geothermal gradient of the region. Opercula buried deeper below the surface had been exposed to warmer temperatures for longer periods of time, resulting in a greater extent of protein decomposition than more shallowly buried specimens. The relationship between depth and the geothermal gradient was described by the geothermal effect (ΔT) for each core. This was strongly correlated with the interpolated D/L values for the cores. This therefore provides an opportunity to design a model for the relationship of IcPD with time and temperature under burial conditions. The model may also provide any additional test of the validity of the Püspöki age model.

2.2 Linear Regression Model (LRM)

To build the model, a dataset comprised of amino acid dating results from seven Pannonian Basin cores containing ∼600 m deep Quaternary sediments were used. To build the linear regression model (LRM) the following assumptions were made:

1. The Püspöki age model created by Püspöki et al. (2013; 2016; 2020; 2021a; 2021b; 2023) is correct.
2. The interpolated geothermal effect (ΔT) for each borehole has been used to describe the temperature history over time.

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Rationale: The geothermal effect (ΔT) is used to describe the relationship between burial depth and temperature. It is calculated by multiplying the depth of the sample by the slope of the geothermal gradient estimated for the vicinity of each borehole (Nelson et al., 2024).

3. Only total hydrolysable amino acid (THAA) fraction of alanine (Ala), glutamic acid/glutamine (Glx) and valine (Val) were considered in the analysis.

   Rationale: Nearly all opercula specimens analysed by Nelson et al. (2024) can be attributed to the Middle and Early Pleistocene. The three amino acids selected for this analysis have been demonstrated to provide consistently chromatographically resolved pairs of D and L isomers for bithyniid opercula. In addition, as moderate (Ala) to slow (Glx/Val) racemizers, these amino acids have been proven to provide temporal resolution for Middle and Early Pleistocene within Europe (Penkman et al., 2011; 2013; Tesakov et al., 2020; Nelson et al., 2024; 2025a, 2025b.).

4. An exponential decay in time model was assumed, including the temperature profile.

   Rationale: Previous studies have investigated the impact of increasing temperature on the rate of racemization in fossil material. They have demonstrated that the rate of racemization increases exponentially with temperature (Miller et al., 1999; Murray-Wallace, 2000). Therefore, an exponential decay was assumed for the increase in the extent of IcPD against temperature.

5. The LRM model does not start at 1 as initial rate of racemization (<40 ka) cannot be predicted by the model. An intercept has been added to the equation to account for this.

   Rationale: The age of the youngest opercula specimen analysed by Nelson et al. (2024) was ~49 ka, as such the extent of IcPD due to time and temperature in material younger this is not known, resulting in the need to include an intercept into the equation to account for this.

Considering these assumptions, a model describing the relationship between the increase in racemization, accumulated temperature and time was created. Namely, for $E_i = 1 - R_i(t)$, where $R_i(t)$ is the D/L value of the amino acid i at depth d.

$$E_i(d) = Ae^{\lambda_1^i (\int_0^d k(\gamma)d\gamma) g(d)}. \tag{1}$$

For a sample found at depth d, the LRM model will describe the extent of racemisation (exponential decay) by the rate parameter λ_1^i for each amino acid i. $k(\gamma)$ is the known temperature profile and $g(d) = t$ is the established estimated age-depth model mentioned above.

The temperature profile $k(d)$ is an estimated linear model $k(d) = a + bd$, and $g(d)$ is an interpolated age-depth model, that both vary from borehole to borehole. To avoid a more complex notation we leave the dependence on the borehole implicit. For each sample j of amino acid i, found at depth d_j, we take the log and assume a normal error to estimate a regression,

$$log(E_{i,j}) = \lambda_0^i - \lambda_1^i \left(\int_0^{d_j} k(\gamma) d\gamma \right) g(d_j) + \epsilon_{i,j}; \quad \epsilon_{i,j} \sim N(0, \sigma_i) \tag{2}$$

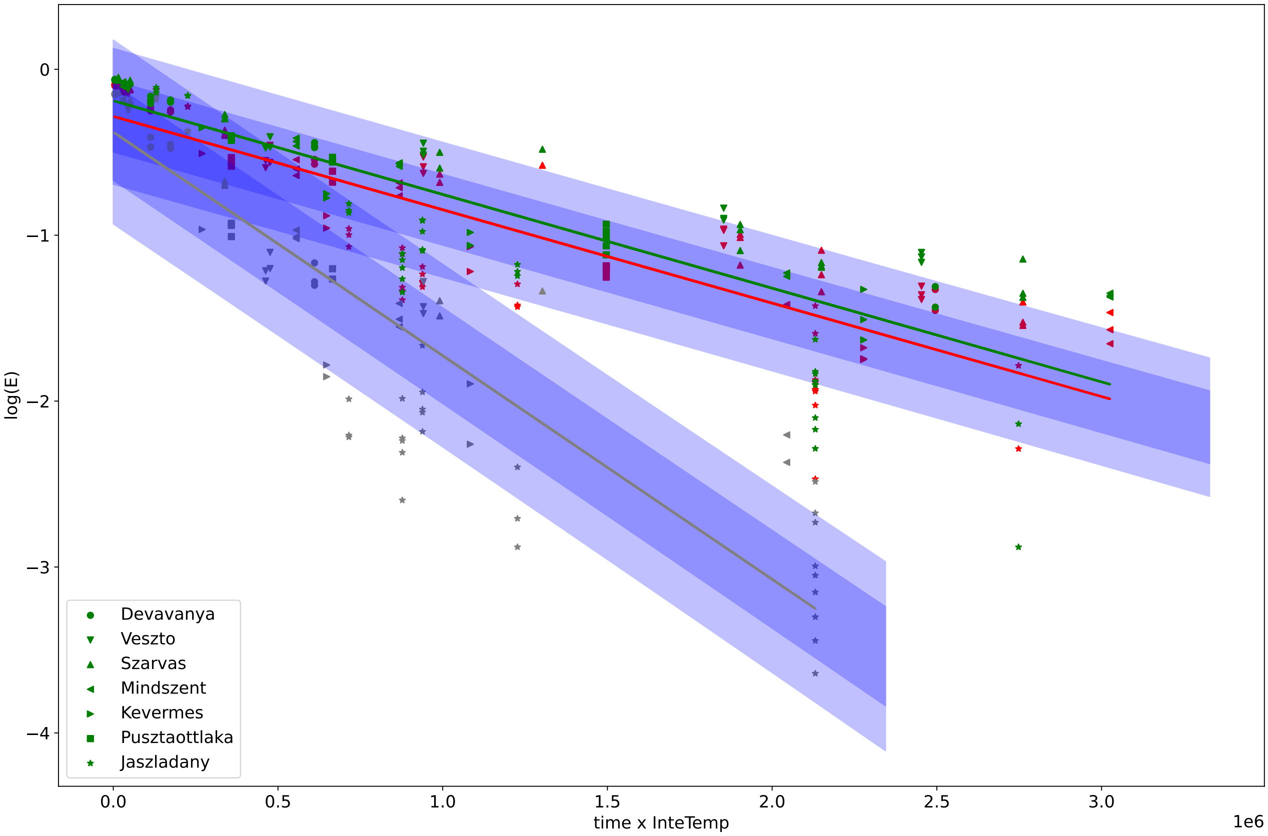

Figure 2. Linear regression model (LRM) of three amino acids: Glx = red, Ala = gray and Val = green, combining data from all sites (see legend). Probability intervals for the regression are also presented, $[0.1, 0.9]$ (light blue) and $[0.25, 0.75]$ (blue), for Ala, Val and Glx. These intervals for Val are very similar to Glx and are not shown.

where λ_0^i represents the start of the model at depth 0. A Bayesian approach was taken to estimate λ_0^i, λ_1^i and σ_i and to predict the age of the sample.

All amino acids reach a state of racemic equilibrium after sufficient time has past since the cessation of protein turnover within an operculum. The time in which this occurs depends on the rate of racemisation for each amino acid and integrated temperature. For the Pannonian Basin opercula, Ala began to approach racemic equilibrium in specimens attributed to c. 750 ka and c. 1 Ma for Glx and Val. Therefore, data in excess of these ages have been removed from the LRM model for the relevant amino acids.

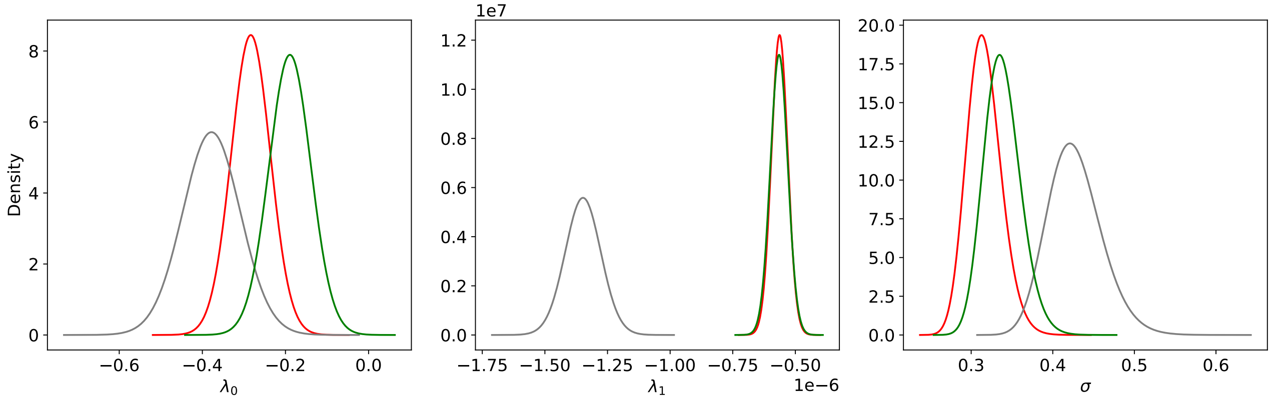

Figure 3. Posterior distributions for λ_0, λ_1 and σ (standard deviation in the regression mode, see Eq. 2), for each of the three amino acids in opercula used Glx = red, Ala = gray and Val = green. The posteriors for λ_0 and σ are similar, while, as expected, the posterior for the slope λ_1 is nearly identical for Glx and Val and quite different for Ala (see text).

3 Results

Once the LRM model was defined, a regression for each amino acid, including data from all of the boreholes, was produced (Fig. 2). As expected, Ala showed a steeper increase in the extent of racemization with time compared to Val and Glx, due to it being the fastest racemiser of these three amino acids (e.g. Penkman et al., 2008; 2013; Nelson et al., 2024). Val and Glx presented a nearly identical slope. The unknown start of the LRM model, λ_0 is very similar for Ala, Val and Glx, which is to be expected. This may be clearly seen in Fig. 3 where the posterior distribution of λ_0, λ_1 and the error precison are presented. Following the usual Bayesian procedure, a predictive distribution of the age of a sample at depth d, given its observed $log(E_i)$ and its temperature profile $z = \int_0^d k(\gamma) d\gamma$, may be easily produced (Aitchison and Dunsmore, 1975). Since we are using three amino acids, we produce a predictive distribution corresponding to each Ala, Val and Glx. We have proposed multiplying and re-scaling as our method to calibrate the D/L data R_1, R_2, R_3 ($E_i = 1 - R_i$) into a single posterior distribution for the predicted calendar age of the sample.

As an example, four samples from three of the boreholes were used to test the model, where the D/L values were used to calculate a calibrated age prediction, (Fig. 4). These age estimates are point estimates from the Püspöki age model model, which inhibits the inclusion of the uncertainty within the model developed by Püspöki and colleagues.

Three out of the four samples tested produced a predictive age distribution that covered the age previously estimated (Püspöki et al., 2016; 2021a; 2023; Fig. 4). The exception was Mindszent 275.3-276.10 m, where the LRM model estimates a predictive age distribution that is younger than the age estimated by Püspöki et al. (2021a). All calibrated age distributions are relatively broad, covering several hundred ka. In the case of Dévaványa (E23-1 HD2941Blo1), the calibrated age distribution was uninformative as the lower half of the distribution was truncated at zero and the upper half covered a broad age range of ∼1 million years. These predictions are a first attempt to use a linear regression model that uses the geothermal gradient of

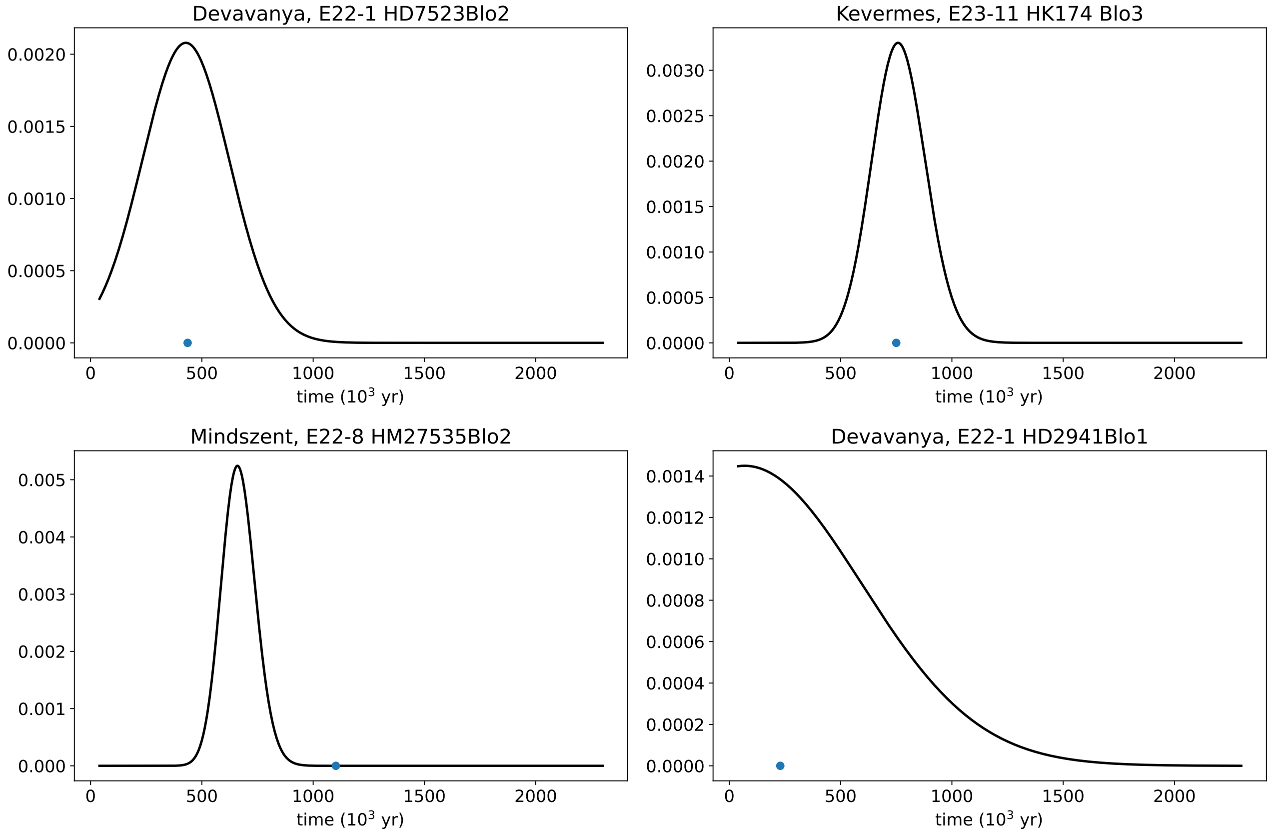

Figure 4. The predictive age distribution made by the model for four samples and the original interpolated age from the age model created by Püspöki et al. 2013, 2016, 2020, 2021a, 2021b, 2023 is represented by the blue circle on each plot.

sediments and independent age estimates to create an age calibration model for IcPD. The current estimates from the model are broad and do not yet provide informative age estimates. In the next section we discuss sources of uncertainty that may be hindering the effectiveness of the model and propose next steps to improve the precision and accuracy of the model.

4 Discussion

Here, we have used a linear regression approach to model the extent of racemisation of three amino acids within fossil opercula buried in Quaternary sediments from the Pannonian Basin. Burial depth and temperature is not consistent across the Pannonian Basin for equivalently aged opercula fossils (Nelson et al., 2024) . As both an estimated age and burial temperature (based on the geothermal gradient) is available for all opercula samples analysed for IcPD analysis, a model that considers both the impact of time and temperature on IcPD was produced.

Amino acids Ala, Glx and Val were considered in the analysis. Using a standard exponential decay model for the D/L ratios, compensated by the temperature profile (Eq. 1), a regression model was proposed (Eq. 2). A Bayesian approach was used and accordingly, a posterior distribution for the predicted age of a sample may be produced (Fig. 4).

Although the inherent uncertainty in both the borehole temperature profile $k(d)$ and the age-depth model $g(d)$ were not taken into consideration in the model, the resulting quantified uncertainty for the age results is large. This was to be expected, due to the variability in the extent of racemisation used in the construction of the LRM model. However, in some cases, results with reasonable precision may be produced (e.g. sample E22-8 HM27535Blo2 in Fig. 4).

A source of uncertainty is the error associated with the point estimates from the Püspöki age model. Quantification of the uncertainty of these age estimates will involve evaluation of all parts of the process, including the palaeomagnetic measurements (e.g. Püspöki et al., 2016), and correlations with marine oxygen isotope record (e.g. Püspöki et al., 2021a). This also makes the comparison of the age estimates by the new LRM for the test samples challenging to compare. Point estimates were also used in the estimation of the geothermal effect (Nelson et al., 2024). A quantification of the uncertainty of these age and temperature estimates is needed to build an improved age-depth model.

Additional uncertainty comes from the initial burial phase temperature profile. During the initial phase of protein decomposition, the opercula will have been buried much closer to the surface, where the climate would have predominantly influenced the temperature of the burial environment. It is likely that the unknown influence of the climate on the burial temperature for the initial phase of racemisation is contributing to the broader age predictions of the younger test samples (4). Dévaványa (E22-1 HD2941Blo1) was located 29.4 m below ground level, whereas all other test samples were buried <75 m below ground level. Nelson et al. (2024) observed that systematic differences in extent of racemisation with age could be observed in material buried in excess of 80-100 m. Opercula buried below these depths were interpreted to be buried below the influence of the surface climate on burial temperature. The extent of IcPD in these opercula will, therefore, by more greatly influenced by sub-surface factors than those buried more closely to the surface.

An intercept was included in our regression model in an attempt to address the uncertainty of IcPD in younger opercula samples buried closer to the surface (λ_0^i in Eq. 2), however, the uncertainty in estimating this intercept does add to the overall age predictives. Investigation of the depth at which the influence of surface conditions on burial temperature is lost may help to determine a more suitable intercept for this model.

Only the THAA D/L values of Ala, Glx and Val were used in the LRM due to these three amino acids providing the best temporal resolution for the Quaternary in the Pannonian Basin and the enantiomeric pairs of each being consistently resolved by RP-HPLC analysis (Penkman et al., 2008). IcPD analysis produces a multi-variant dataset with other variables that are indicative of age of the operculum. Further development of this model should seek to explore the use of other IcPD variables that have been demonstrated to be an indicator of sample age, including the FAA D/L values, ratio of the concentration of serine over alanine ([Ser]/[Ala] and proportion of free amino acids (e.g. Penkman et al., 2008; Nelson et al., 2024).

There is a still a great degree of uncertainty unaccounted for within the LRM. In order to improve the age-depth model, future work will need to investigate these sources of uncertainty, so their impact on the model can be understood.

5 Conclusions

In this study, we have explored a potential new approach to model the extent of opercula IcPD with time to produce a calibrated age-depth model. A linear regression model was developed using the extent of THAA Ala, Glx and Val racemisation, estimated age and burial temperature described by Nelson et al. (2024) for Quaternary sediments within seven boreholes from the Pannonian Basin (Hungary). Four test samples from three of the boreholes were used to test the accuracy of the model. All calibrated age distributions were relatively broad, covering several hundred ka. This provided lower resolution than is currently possible with the tradition approach to interpretation of IcPD data. More informative and narrower distributions were produced in the older/more deeply buried opercula test samples suggesting that this approach was more effective in deeper material where the influence of the surface climate on the rate of IcPD has been attenuated. An overall sensitivity analysis needs to be undertaken, to establish the greater contribution to age uncertainty and corresponding strategies for further sampling, temperature profile updating and an improved age-depth model.

Code availability. A Python code is available upon request from JAC.

Data availability. The data used here is available in the SI of Nelson et al. (2024) and also on the NOAA database (https://www.ncei.noaa.gov/pub/data/paleo/aar/)

Author contributions. Both authors contributed equally to building the model, overall research and drafting and finalising the manuscript. JAC made the code and plots with the results. EN provided the background for the model, the published data, and lead on the first draft of the manuscript.

Competing interests. No competing interests are present.

Acknowledgements. This research has received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement No. 865222). JAC is partially supported by a ONRG grant (N62909-24-1-2016). We would like to thank the University of Cambridge's Accelerate Programme for Scientific Discovery and C2D3 AI and Statistical Innovations for their support in facilitating this collaboration and for their assistance in developing this model.

https://doi.org/10.5194/egusphere-2026-2261
Preprint. Discussion started: 19 May 2026

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Preprint. Discussion started: 19 May 2026

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